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# Spatio-temporal Analysis of the Influence of a Heterogeneous Environment on the Behaviour of Red Deer (Cervus elaphus)

**Master Thesis - GEO 511**

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# Summary

The red deer (*Cervus elaphus*) is a prominent ungulate in the border region of the cantons Ticino and Grisons as well as the Lombardy which is a part of Italy. The heterogeneous characteristics of this area with a high climatic variability and different degrees of anthropogenic influence make it difficult to predict red deer behaviour. This thesis aims at the investigation of red deer movement and activity patterns in relation to contextual variables over a period of three years.

In a first step, the migration patterns of 36 animals were analysed using an adjusted version of the Net Squared Displacement, the Mean Squared Displacement (MSD) as well as a combination of the Minimum Convex Polyongs (MCP) and Kernel Density Estimations (KDE). The migration classifications were then used for the interpretation of subsequent results. Next, a home range size analysis was conducted, using the MCP and KDE results from the previous computations in combination with a dynamic Brownian Bridge Movement Model (dBBMM) approach. The resulting home range size estimates of the three methods were then compared to each other using a one way analysis of variance (ANOVA). Temporal activity patterns were then investigated with the use of activity data which was classified into the activity types resting, slow locomotion / feeding and fast locomotion. In addition, the diurnality and crepuscularity indices were used to investigate daily activity patterns over the course of the study period. Resource use patterns were then investigated in relation to forest, grasslands, urban areas, agricultural land and vineyards which are the main soil cover types within the study area. In addition, the use of game reserves was analysed as well since they constitute an important tool in red deer management. In a last step, the activity types were analysed in relation to the used resources to gain information about which activity type is usually performed within a specific resource type.

The results showed that red deer cannot be classified into a simple resident and migratory type scheme since a lot of individuals do not perform full migration. In addition, it could be illustrated that not only euclidean distances should be included into the analysis of migration patterns in alpine environments but also differences in elevation. Moreover, the inclusion of temperature is not enough to predict the start of migrations since several factors determine whether an individual starts migration or not. Home range sizes were generally overestimated by the MCP method. Winter and summer home ranges which were calculated with the KDE and the dBBMM were similar in size while the home ranges of resident animals tend to be smaller than those of non-resident animals. The analysis of temporal activity patterns revealed a bimodal activity distribution over the course of a day for all study periods. In addition, nocturnal activity was preferred during most of the year with a short exception at May and June. The anthropogenic influence on the activity is illustrated as well. Investigation into the resource use of red deer showed a clear preference of forests during daytimes with negative preference at night and a general higher use of forests during the winter months. Contrary to this, grasslands were more often accessed at night. In addition, it was found that red deer access urban areas at winter and during the hunting periods to profit from enhanced ecological conditions (e.g. less snow cover) and to seek protection from hunting activities. Surprisingly, negative preference was shown for agricultural areas. However, it is assumed that this is the result of an unfavourable selection of the study seasons for this particular analysis. Moreover, the results indicate that a good dispersion of red deer in space is reached thanks to game reserves since they prevent that all red deer individuals seek shelter in urban areas during the hunting seasons. In the end, the analysis of resource use in the context of activity types revealed that resting behaviour is most often carried out within forests while the share of grassland use increases for slow locomotion and feeding at the expense of forest use.

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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.

Jaqueline Boog

Date

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# 1. Introduction

## 1.1. Motivation

The red deer (*Cervus elaphus*) has always been a part of the native fauna of Switzerland. Archaeological excavations show that red deer belonged to the most important hunting game already in the Bronze Age. Since then the history of red deer was marked by a constant up and down of the population size due to overhunting. As the biggest ungulate in Switzerland, red deer was a very popular resource for meat consumption and tool manufacturing. Having its habitat at lower altitudes and flat to moderately steep regions exposed this large ungulate even more to hunting pressure of humans. The intensive agricultural and forestry land use of Switzerland with only a little amount of cover providing forests increased this pressure noticeably. The development of firearms, acts of war and unfavourable weather conditions finally led to the near extinction of red deer in Switzerland in the middle of the 19th century (Haller 2002, Jenny et al. 2011). However, the first federal hunting law, which was established in 1875 set a milestone for red deer to successfully repopulate Switzerland. These animals migrated from the Principality of Liechtstein and Voralberg as well as the South and North Tyrol into the Canton of Grisons and hunting of red deer was officially approved again in 1905. More recently, a new hunting law was implemented in 1986 in the whole canton of Grisons, including the Swiss National Park (SNP), with which a sustainable regulation of the red deer population got supported. This hunting law calls for an annual hunting plan based on wildlife monitoring (Jenny et al. 2011). In addition, from 1990 onwards partial and complete hunting bans in non-hunting areas (*Eidg. Jagdbanngebiete*) and cantonal game reserves (*kantonale Wildschutzgebiete*) further supported the red deer population and guaranteed a good dispersion of the animals (Haller 2002, Bundesamt für Umwelt 2017). As can be seen in Figure 1, the red deer population in Switzerland increased constantly since the new regulations were set in place. This also applies to the cantons of Ticino and Grisons (Jenny & Filli 2014).

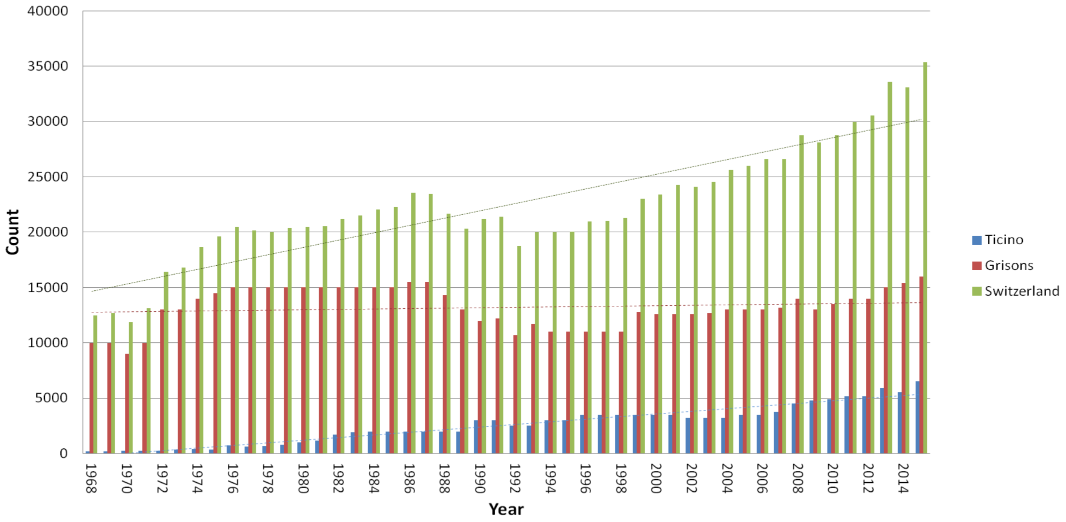

Figure 1: Development of the red deer population in Switzerland from 1968 to 2014 compared to the cantons of Ticino and Grisons based on observation estimates (Bundesamt für Umwelt 2015).

The re-establishment of red deer in the canton of Grisons was such a success story that the population was even able to exceed the maximum sustainable yield. This means that even though a healthy population of red deer is desirable, their number reached a point where economic and ecologic damages became apparent (Jenny & Filli 2014). Indeed, depending on the environment, if a certain density of ungulates is reached, they may impact their environment in a negative way. Damages which can be caused by red deer then start to occur increasingly in forestry as well as agriculturally used areas. In forests the growth of plants and trees can be hampered by feeding on germinating seedlings or tree fruit whereby the availability of new seeds is reduced. Moreover, browsing and bark-stripping leaves trees vulnerable to wind-shear and diseases such as fungal attacks. The damage related to agriculture concerns crops and pastures where red deer feed. In addition, costs which are aimed at reducing the damage through prophylactic measures have to be taken into account as well (Mitchell et al. 1977, Putman 1996, Godvik et al. 2009). Such conflicts are still prevalent in one particular region of the canton of Grisons where red deer density remains high: the Mesolcina. The Mesolcina is located in the very South of the canton of Grisons at the border region of the cantons of Ticino and Grisons as well as the Lombardy (Italy) and constitutes the study area of this thesis. A detailed description of this area will be given in Section 3.1. However, thanks to the hunting regulations of 1986 and ongoing research about red deer and other ungulates these conflicts could be reduced in most areas (Haller 2002, Jenny et al. 2011). Yet, there are not only conflicts related to economic and ecological damage. Nowadays, wild-living animals are not only put under pressure by hunting regulations but also by recreational activities of humans. Thus, a conflict between human recreation and tourism on the one hand and wildlife management on the other hand emerged (Löttker et al. 2009). This shows that the preservation of a healthy population size through sustainable management systems, requires to actively investigate red deer ecology in relation to human activity and ecological resources. The results from such research can also be used to discuss new management methods and problems in an objective way, without sparking too many emotional reactions in the public discourse. This will be necessary in order to regulate the red deer population in the Mesolcina so that the conflicts may be reduced to a minimum.

Understanding the temporal space use of animals is especially important when it comes to red deer management (Reinecke et al. 2014). To investigate spatio-temporal behaviour of large animals, several approaches have been used over the years. The most traditional way to study animal behaviour is through direct observation. But even though it is possible with this method to unambiguously determine what an animal is doing, it is rather unsuited for red deer ecology. This is because there are several limitations to direct observation. Firstly, there is a great risk that the animals are disturbed in their natural behaviour as soon as a human being approaches. Secondly, it is difficult to observe animals when the vegetation density and thus cover is high or in rough terrain. Observations during the night are quite adverse as well. Further, direct observations are labour and time consuming. All these points make direct observations unfavourable for the study of red deer behaviour, especially since this animal can travel great distances within a short period of time (Gervasi et al. 2006, Löttker et al. 2009). This is why scientists often relied on very high frequency (VHF) radio telemetry systems. This technology allowed researchers for the first time to follow individual animals for a long period of time (Nilsen et al. 2008, Cagnacci et al. 2010). However, the emergence of global positioning system (GPS) technology constituted a game changer in animal ecology research. It enabled the monitoring of several animals at the same time from a remote point. One of the main advantages of GPS technology is that high precision location data can be retrieved 24 hours a day. Moreover, position data from the animal can be received in very short succession (Cooke et al. 2004, Cagnacci et al. 2010, Hebblewhite & Haydon 2010). The thus acquired data can serve to add valuable information to traditional observational data, especially when it comes to mobility and activity patterns at a large spatial and temporal scale. On the other hand, there are also drawbacks of the GPS technology. Especially when the aim is to investigate small animals, it is difficult to attach GPS sensors to the organisms. The smaller the animal is, the lighter the GPS device has to be. Otherwise the weight of the sensor might influence the animal in a negative way, tiring it and altering its natural behaviour. However, small devices have the consequence that the battery is small as well, reducing the recording time of the GPS sensor so that records are either too short to be of use or two coarsely sampled (Cooke et al. 2004). In addition, GPS collars are costly and may lead to the purchase of only few collars and hence to small sample sizes. Another factor which influences the sample size is collar failure. Moreover, the number and position of visible satellites is crucial for the accuracy of the GPS data. Especially a dense tree canopy cover and terrain obstruction may lead to failed location records. Additionally, there is bound to be a trade-off between the study duration and the number of sampled locations per day since the battery life of the GPS device is limited (Pépin et al. 2004, Horne et al. 2007, Hebblewhite & Haydon 2010). And while the position of an animal can quite easily be determined with GPS and VHF technology, it remains difficult to assess the particular behaviour of the monitored animal. In this sense, the additional use of accelerometer data may come in handy (Naylor & Kie 2004, Löttker et al. 2009).

Due to the listed (dis-)advantages of the mentioned observation methods, researchers have to think of the most ideal method depending on animal size, environmental factors and costs before the actual data acquisition. The combination of different methods is possible as well. For example to examine how GPS data relate to the behaviour of an animal, direct observations may serve to develop algorithms to automatically link the collected data to a specific behaviour depending on several parameters such as locomotion speed or head movement (Löttker et al. 2009). Moreover, contextual information about the local environment might be used to enhance the interpretation quality of the behavioural data. Such information could consist of meteorological data, ground cover and land use categories. Comparisons with other studies and older data are valuable as well when it comes to the interpretation of the gathered data.

No matter which method is chosen, it has to be borne in mind that direct observation, VHF methods as well as GPS based methods may influence the behaviour of the examined animal or that a bias could be introduced during the animal catching process (Cagnacci et al. 2010). For example when using live traps it may happen, that only explorative animals step into the trap. Thus, the data would be biased by individuals with a very specific characteristic which does not constitute a good representation of the whole population[1]

### 1.2. Research Question

The main focus of this work lies on the analysis of the temporal variation of the space utilization as well as the migration and activity patterns of red deer in the region of the Mesolcina. As mentioned above, such studies have been conducted numerous times. However, the Mesolcina depicts a unique habitat for red deer. In the preceding works the habitat of the studied animals was mostly homogeneous, which is not the case in the Mesolcina with its high climatic variability, varying degrees of human influence as well as intensely used agricultural fields. As a consequence red deer might show a different behaviour than what is already known. Thus, the following research questions will be investigated in this thesis.

---

[1] Personal communication with Flurin Filli (Swiss National Park) and Hannes Jenny (AJFGR), 13.06.2017

1. **Migration pattern classification**
   What are the seasonal migration characteristics of the investigated animals?
   a) What kind of migration patterns can be found and what are the characteristics of these migration patterns?
   b) Are the migration patterns influenced by climate?
2. **Home range size analysis**
   What are the typical seasonal home range sizes of the investigated animals?
   a) What are the home range sizes of the study animals?
   b) Are there significant differences between the estimated home range sizes of different methods?
3. **Temporal activity pattern**
   What are the temporal activity patterns of the study animals?
   a) What is the monthly activity pattern?
   b) What is the daily activity pattern?
4. **Resource use**
   What kind of resources to the study animals access at what time?
   a) What is the relative resource use?
   b) What is the resource use when taking the abundance of the resources within the study area into account?
5. **Resource use in context of activity**
   Where (in which resource) are which activities performed most often?

To find answers for Research Question 1 and 3 additional datasets such as climatic data and ground cover information are required. Since the Mesolcina is a highly diverse region with a lot of different land cover and land use types resource use will be analysed using GPS positions in connection with forests, grassland, agriculturally used fields, urban areas and vineyards. This thesis stands in close connection to the TIGRA project, which is currently being conducted in the two cantons Ticino and Grisons as well as the border region of the Lombardy (Amt für Jagd und Fischerei Graubünden 2014). Moreover it can be seen as a complementary work to the Projekt Raetikon (Arnold et al. 2004) and the Master Thesis of James Patrick (2017) since the projects were similar and carried out in nearby locations. In all cases, the studies have the aim to facilitate red deer management. Since the TIGRA project is still ongoing, it must also be noted that the results which this thesis delivers may serve as a guideline or orientation point for further steps within the whole project.

### 1.3. Thesis Structure

In Chapter 2 a theoretical framework will be set up to provide background knowledge about the red deer ecology as well as tools for space utilization and migration pattern analysis which are commonly used in geographic information science. In addition, ecological tools are depicted as well. Chapter 3 deals with the study area and the given data sets, illustrating necessary pre-processing steps as well as limitations to the data. Data of environmental context information are discussed and illustrated as well. Chapter 4 then deals with the methodology which is used in order to answer the research questions. The results and the corresponding discussion with separate subsections for every research question are depicted in Chapter 5. The conclusion is being drawn by a short summary of the insights and major findings in Chapter 6 along with an explanation of the limitations of the used methods as well as improvement possibilities for future work.

# 2. Theoretical Framework and Background

To understand the behaviour of an animal, its physiology and reproductive cycle have to be understood and studied in relation to its environment. One of the probably most important and in-depth works relating to this subject was done by Clutton-Brock et al. (1982) on the Scottish island of Rum. Their research dates back to 1953 and is illustrated in the book "Red Deer: Behaviour and Ecology of Two Sexes". It provides in-depth knowledge of the breeding biology, rutting and feeding behaviour, population dynamics as well as activity patterns of red deer. Yet, it has to be borne in mind that these studies were conducted on the isolated Island of Rum which offers different conditions than in the study area of this work, namely the Alps. There are several papers, however, which describe behavioural patterns of red deer in central Europe such as the work of Bützler (2001), Georgii & Schröder (1983) and Reinecke et al. (2014) who focus on various aspects of the behaviour of red deer and their context. Some of these studies relied upon modern GPS and activity data to conduct home range[2] and activity analyses in order to examine red deer behaviour. This definition is still largely accepted in today's literature and activity analyses in order to examine red deer behaviour. In the following sections I will draw upon previous research to give an overview of red deer ecology the methods which are used in this work for the analysis of the space utilization and migration patterns of red deer.

## 2.1. Red Deer Ecology

### 2.1.1. Physiology and Reproduction

The red deer (Figure 2) belongs to the largest terrestrial animals in central Europe and occupies different landscapes such as forests, meadows and bush lands with varying human influence and anthropogenic or natural hunting pressures (Reinecke et al. 2014). The vast geographic range occupied by red deer shows how adaptive these animals are and how well they can cope with different environmental conditions.

While hinds weigh on average around 70 kg, stags are considerably bigger, weighing approximately 110 kg on average in the canton of Grisons in Switzerland (Bützler 2001). However, weighs up to 350 kg were observed in Europe as well. The maximal body length of middle European stags lies around 210 cm and 182 cm for hinds, with 124 cm and 110 cm respectively for body height (Wagenknecht 1996). Variations in size and weight throughout Europe are due to the adaption to different resource availability and climate conditions. The body mass generally increases from Western to Northern and from Eastern to Southern Europe, following the decrease of average annual temperature. This finding coincides well with the Bergamann's Rule which says that warm-blooded animals adjust their size to cold temperatures by increasing their body size and are thus taller than animals in warmer regions. With the increased body size, animals in colder regions tend to lose less body heat due to the reduced proportion of body surface and volume (Bützler 2001).

In any case, it takes a relatively long time for stags to mature. 6 - 8 years pass until they reach full body weight. This is also the time from which on stags are able to successfully hold harems of hinds (Clutton-Brock et al. 1982). However, it takes up to 10 - 14 years until the antlers are fully developed

In contrast to hinds, stags do not have such a high parental investment into individual offspring. The reproductive success of stags strongly depends on the breeding access to hinds as well as their ability

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[2] Burt (1943, 351) defines home range to be "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range. The home range need not cover the same area during the life of the individual".

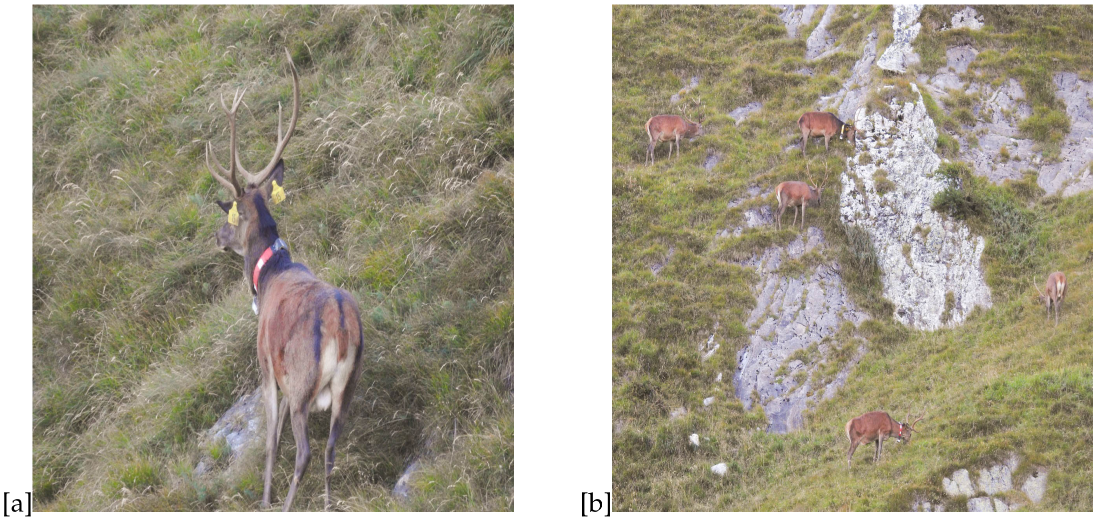


Figure 2: (Stag with a GPS collar (a) and a group of red deer of which two carry GPS Collars (b). Photographed by Nicola de Tann (gamekeeper and chief of hunting district VI Moesano).

to hold and protect harems (Clutton-Brock et al. 1982). The formation of groups of females happens during August and early September when the rutting season starts (Georgii & Schröder 1983). Stags compete intensely for such harems, making fights frequent and dangerous events. 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 his age. The breeding success of males and thus the ability to hold harems peaks at around the age of eight. However, holding and protecting a harem from other males requires a lot of energy. Thus, the parental investment of stags is limited to the rutting season. When having obtained a harem successfully, the stags start to move less, staying close to their harem and only moving when their harems travel to new feeding grounds. During this time, the activity pattern of stags changes dramatically. Especially harem-holders spend much less time with grazing during the day. The actual proportion of grazing falls from 44% a day in summer to approximately 5% during the rut. Thus, the stags lose up to 20% of their body weight during September and October due to the high investment of energy into rutting behaviour. This effect vanishes when the rutting season is over and the stags stop to care for the harems. At this point, the grazing activity goes back to a level which can be observed at any other time of the year. This change from rutting behaviour to non-rutting behaviour occurs quite abruptly, probably due to the mentioned physical deterioration and changing hormone levels. At the age of 11 the weight and general conditions of stags, as well as their ability to hold harems successfully, start to decrease (Clutton-Brock et al. 1982). Approximately 34 weeks after the rut, and thus during the months of April, May and June, the calves are born (Wagenknecht 1996, Bützler 2001).

While showing quite different behaviour during the rutting season, the red deer sexes show similar behaviour during the rest of the year. Both sexes gather in loose groups that can vary in size and membership at any time. However, hinds and stags stay segregated except during the rutting season. While hinds usually stay in the home ranges of their mother and thus form groups with their matrilineal family members, stags remove themselves from their mother's home range. They aggregate in herds where no particular kinship can be observed (Clutton-Brock et al. 1982). Since red deer aggregate in groups, there must be an important advantage of this behaviour. Especially since group living increases resource competition and feeding deer get interrupted by other individuals of the group. There are three advantages which group living might offer:

1. Enhanced ability to detect and avoid predators as well as fending them off. This is not limited to big predators such as wolves but also applies to insects such as mosquitoes or flies.
2. The search for food resources and the defence of it against conspecies might be facilitated.
3. Enhanced chances in gaining, retaining and monopolizing access to suitable mates (Clutton-Brock et al. 1982).

Of these three possibilities the most probable reason for grouping is the enhanced protection from predation. But this should also be possible in herds where the sexes are mixed. So why do the sexes segregate? Clutton-Brock et al. (1982) argue that the reason lies within the different nutritional needs of stags and hinds. They argue that the nutritional requirements vary between stags and hinds due to their difference in body size and reproduction costs. For example the protein requirements of hinds increases during the first days of their gestation and lactating hinds in captivity were observed to eat more than twice than usual. Stags on the other hand, have a high energy and protein demand for the growth of their muscles and antlers during summer months and then again during the rutting season. These differences influence the choice of altitude levels and plant communities (Clutton-Brock et al. 1982). In addition, Kamler et al. (2007) state that different activity patterns between sexes might also lead to sexual segregation and Georgii & Schröder (1983) observed that the adaptive strategies for the same environmental conditions differed between stags and hinds.

### 2.1.2. Daily Cycle

The daily activity pattern of red deer is mainly regulated by their rumination cycles and grazing bouts. These grazing bouts can last from 10 to over 200 minutes. The main driver of the duration of the grazing bouts is diet quality (Clutton-Brock et al. 1982, Godvik et al. 2009). As can be seen in Figure 3 these rumination and grazing activities stand in a cycle which starts with hygiene and grooming activities, after which social interactions follow. After this, the deer typically move to the grazing grounds. Subsequent to feeding, the herd moves back to their resting site where social interaction is continued before resting and rumination. All of these activities are constantly accompanied by predator avoidance. Thus, active periods alternate with resting periods several times within 24 hours (Bützler 2001).

Gillingham et al. (1997) state that one of the main drivers of the duration of grazing bouts of ungulates is forage quality. While the duration of grazing bouts also varies between the seasons, no significant difference could be observed between the sexes. So, during summer four to six grazing bouts occur during the day and one to three during the night. During wintertime the duration of the bouts increases, leading to only two to three grazing bouts at day and three or four bouts at night (Clutton-Brock et al. 1982). Usually, the grazing bouts are carried out in open habitats. Resting/rumination bouts occur more often in covered habitats where trees and shrubs provide cover against predators and other possible sources of disturbance (Mysterud et al. 1999). However, the bouts are not spread evenly across the day or night (Clutton-Brock et al. 1982). On the other hand, Ensing et al. (2014) observed a bimodal daily activity pattern in red deer. They found peaks of activity at dawn and dusk, indicating a crepuscular activity pattern in elk (*Cervus e. canadensis*). However, a more nocturnal preference was found in red deer living in the Netherlands. As the main cause for this difference, Ensing et al. (2014) see the human disturbance which was higher in the study area of the Netherlands and especially during the day. This shows that red deer are prone to human disturbance and adjust their behaviour accordingly. As did Ensing et al. (2014), Georgii (1981) found peaks of activity during twilight hours. In most of the cases (19 / 21), the duration between morning and evening peak was higher than the duration from the evening to the morning peak, with morning peaks usually being higher and having a longer duration than evening peaks. Quite the contrary, Kamler et al. (2007) found no such bimodal pattern in the Bialowieza National Park in Poland. Both hinds and stags showed peaks in activity but these peaks were scattered throughout the day and night with more peaks during daytime. During the winter months, both sexes showed a higher activity level during the day with increasing levels as the daylight hours progressed, which indicates that daily temperature variations also have an influence on activity patterns. However,Kamler et al. (2007) argue too that the bimodal activity pattern which was found in other studies probably developed as a response to human activity as was the case in the study of Ensing et al. (2014). Anyway, (Clutton-Brock et al. 1982) state that grazing dominates the daily activity pattern with a share of up to 50% of the whole daily activity. During night-time grazing accounts for 15 - 30% of the activity.

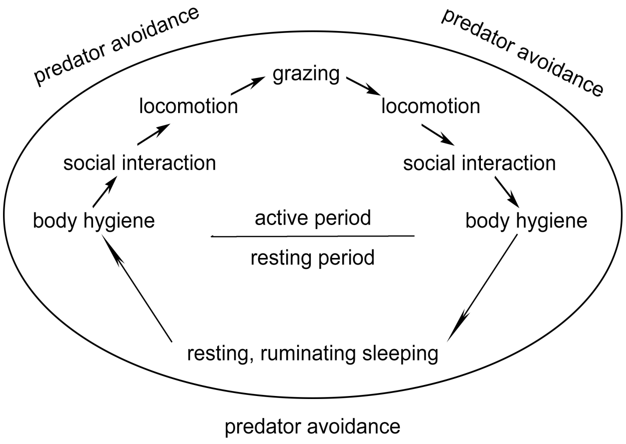


Figure 3: Representation of the daily activity cylce of red deer as explained by Bützler (2001) and illustrated by Patrick (2017, 8).

In general, grazing and resting does not occur at the same place. As previously mentioned, red deer rotate between grazing and resting sites during their daily activity cycle. The distance which is covered during these daily migrations usually is small, with an average of 1.8 km in winter and 3 km in summer (Clutton-Brock et al. 1982, Wagenknecht 1996).

### 2.1.3. Annual Cycle

As migratory animals which can travel over large distances, most of the red deer individuals in the Alps exhibit seasonal migrations, wandering from high altitudes in summer to lower altitudes in winter, which results in spatially separate home ranges; a summer and a winter home range. The average distance between those two areas is 2.5 km, whereas distances of up to 25 km could be observed as well (Georgii & Schröder 1983). Filli & Suter (2006) observed a seasonal migration distance of 5 - 19 km with a mean of 11 km. Migrations from summer to winter home ranges and back are necessary due to changing conditions in the environment such as varying seasonal temperatures, food availability as well as snow cover, and usually happen within one day. In some cases, the home ranges are coupled to traditional rutting areas (Georgii & Schröder 1983). Moreover, in regions with high elevation differences, red deer were observed to change between high elevations in summer to low elevation in winter following low snow cover levels (Jarnemo 2008). The winter home ranges are generally smaller than the summer home ranges, since red deer stay close to their feeding grounds after the first snow fall to minimize energy loss (Georgii & Schröder 1983). Yet, Reinecke et al. (2014) found the difference between summer and winter home range tend to be more pronounced for stags. In addition, hinds were observed to have larger home ranges than stags during winter months and vice versa during summer (Reinecke et al. 2014). Moreover, the animals usually spend winter months at lower altitudes, where the snow cover is smaller and temperatures milder (Jarnemo 2008). With increasing snow accumulation the extents of the winter home ranges decrease. Hence, snow seems to be one of the major causes of the decreased mobility of red deer. Yet, especially during times of the "Föhn", a warm and dry downwind, when the weather conditions are better for the red deer and the snow cover starts to melt, they go on short excursions, leaving their usual home range. In contrast, the growth of fresh vegetation during spring inverts the importance of the snow cover (Georgii & Schröder 1983). Now, especially hinds start to follow the retreating snow line (Albon & Langvatn 1992). One hypothesis as for why females move to higher altitudes during spring and summer is the forage maturation hypothesis. It states that newly grown plants are of higher quality due to an increased amount of proteins and are thus more valuable for herbivores. As a consequence, following the green-up gradient may constitute an advantage to migrating animals (Mysterud et al. 2011). Thus, while the migration pattern of females reflects the availability of food and feeding strategies, stags are more oriented to mating strategies

In general however, the seasonal home ranges do not vary much from year to year even though individual differences can be observed. The extent and the spatial position stay more or less the same. Only the home range patterns of young stags go through modifications during the lifespan of the individual animal. But with increasing age, their home ranges become more stable as well, yet still differ from those of females

Overall, Georgii (1981) detected systematical changes in the duration of activity bursts over a year. In addition, Georgii & Schröder (1983) observed different activity patterns during summer and winter. While the animals showed a more diurnal activity pattern during summer, during winter months a more nocturnal behaviour is exhibited. In addition, during and after the rutting season in September and October, especially stags show a higher level of activity (Georgii 1981, Beier & McCullough 1990). This can be explained with the increased energy demand during the rutting season for stags, which requires them to gain enough fat reserves to be able to survive the following cold winter months. Hinds on the other hand, perform longer bursts of activity during summer than in winter (Georgii 1981). Moreover, during winter months the activity level during the day is very low (reduction of 50%), which coincides with the smaller winter home ranges, whereas the activity at night remains relatively high. These findings correspond with the discoveries of Arnold et al. (2004) that the heart rate of red deer decreases to a minimum in January and February, with increased heart rate and locomotor activity from April to June. However, even though activity is lowest in winter, Beier & McCullough (1990) found that female white-tailed deer (*Odocoileus vir- ginianus*) were more active than males, resulting in the highest difference of activity between the two sexes from January to June. The reduction of activity and home range size during the winter months is explained to be an adaptation to conserve energy during unfavourable climatic conditions (Georgii, 1981). Besides these findings, Georgii (1981) observed a strong increase of activity of hinds in April, suggesting the increased need of energy during gestation to be the cause. Georgii (1981) also implies red deer to have a fixed quota of activity due to a complementary change of the daily and nightly activity levels.

Ensing et al. (2014) found that elks (Cervus elaphus) in Canada were most active in the summer while red deer from the Netherlands were most active in the winter. As was probably the case in the daily activity patterns, Ensing et al. (2014) argue that this difference has its roots in the evasion of human disturbance, which was higher in the Dutch study area, especially during summer times. However, even though distinctions between stags and hinds can be observed, habitat use and activity patterns can vary considerably with age and sex, demonstrating the individual nature of red deer (Beier & McCullough 1990).

### 2.1.4. Foraging

As could be seen in section 2.1.2 foraging and grazing belong to the main activities of red deer and stand in contrast to resting and ruminating bouts. However, due to red deer living in a wide range of habitat types it is difficult to define food requirements that apply to all red deer individuals. Varying nutritional values within same plant species, depending on their location and fertilization, impede the task of finding universal rules for food requirements of red deer (Wagenknecht 1996). Moreover, the nutritional requirements of red deer are dependent on several other factors such as age and condition of the animal (Mitchell et al. 1977). Generally, grasses seem to represent the staple food all year round as long as there is no snow cover preventing the animals from having access to grass. In such cases, the share of tree parts (for example bark, leaves and pines) and bushes consumed increases and can even constitute the main food during harsh weather conditions and in some regions even all year round (Wagenknecht 1996). And even though red deer are known to be quite stationary (choosing the same home ranges every year), they have several forage sites within their home range which they visit over the day. However, these grazing sites are divided into locations that are only visited by night and locations that are only visited by day. In the night-time forage locations the food quality is generally higher than in the day-time forage locations. Moreover, cover does not seem to be one of the crucial characteristics of night-time grazing sites. The day-time locations, on the other hand, usually consist of small forest glades, shrublands and forest aisles (Bützler 2001).

Overall, it could be observed that there is a seasonal trend for red deer when it comes to feeding behaviour (Mitchell et al. 1977, Gebert & Verheyden-Tixier 2001). However, differences between sexes could be found. For example, in spring captive lactating hinds consume more than double the amount of food from what they usually eat, which can be explained by increased nutritional requirements during gestation and raising of the calves. On the other hand, stags grow muscles and antlers during summer and the rutting season during which they have an increased energy and protein demand (Clutton-Brock et al. 1982). Hence, at the beginning of March, grazing activity starts to increase and reaches its maximum in May and July when food is most abundant and the calves are being born. This period of increased food intake lasts until August in order to build up fat reserves for the coming rutting season. Especially stags lose most if not all of these reserves and their weight can decrease to 75% of their original weight. The food intake of hinds also gets reduced but the difference is not as distinct as for stags. The second maximum of food intake occurs during autumn when the animals are preparing themselves for the winter months by building up their fat reserves again. From December to February the minimum of grazing activity is then observed. This state cannot only be explained by the absence of forage possibilities but also by a worse digestibility of winter foods. Moreover, day-length seems to play an important role as well since the animals also showed this seasonality when an adequate amount of forage possibilities was provided (Wagenknecht 1996, Mitchell et al. 1977).

### 2.1.5. Human Influence on Red Deer Behaviour

In the study area of this work, home ranges of red deer individuals are often intertwined with human settlements and areas used for recreational activities. In addition, roads cut through connected home ranges. Having so many points of contact between red deer and humans it is only natural that interactions between the two species will arise. Some of the results are damage to agricultural fields as well as damages in forestry. Moreover, the increasing intrusion of humans into natural environments forces wild animals to adjust their time and space requirements according to human behaviour (Bützler 2001, Gebert & Verheyden-Tixier 2001, Löttker et al. 2009). Often, behavioural differences between animals in natural environments and urban areas or suburban settings are not well known, making the management of these animals a difficult task (Etter et al. 2002). Especially hunting and recreational activity by humans are perceived as a threat by red deer and thus have a serious impact on the daily life cycle of the animal. Deviations from the daily activity cycle can cause problems with the microbiology of the red deer rumina and may render the digestive process inefficient. This again leads to a decrease of the energy and protein supply. If the daily activity pattern of a red deer individual constantly gets interrupted, red deer will end up in a bad condition, producing weak offspring and degraded antler growth. Especially daily recreational activities such as skiing, riding and hiking may force red deer to stay and seek shelter within forests during the day, forcing the animals to feed from trees and bushes. This again leads to an increase of damage caused by game animals (Mitchell et al. 1977, Wagenknecht 1996, Jayakody et al. 2008). In addition, it was found that red deer and white-tailed deer avoid hunters by the use of private lands. A factor that contributes to this behaviour is the abundance of high quality forage such as hayfields crops, gardens and fertilized lawns (Burcham et al. 1999, Etter et al. 2002). Furthermore, Kamler et al. (2007) did not find crepuscular peaks of activity in the Biolowieza National Park as was found in other studies (Clutton-Brock et al. 1982, Georgii 1981, Georgii & Schröder 1983). They explain this particular behaviour of missing crepuscular activity peaks with the absence of human activity and the presence of natural predators. This theory is supported by Kitchen et al. (2000) as well as Frank & Woodroffe (2001) who found that hunting pressure from humans results in the transformation from diurnal carnivore species to nocturnal or crepuscular animals. Additionally, Grund et al. (2002) found that white-tailed deer which live in the urban environments of Minneapolis (USA) reduce the size of their home ranges and that the seasonal shifts are smaller compared to white-tailed deer living in forested landscapes. These findings are backed up by Etter et al. (2002) who found similar conditions in suburban Chicago, Illinois and Minnesota. On the other hand, the size variation between the seasonal home ranges was similar. The smaller home range size is explained by the fact that the deer stayed within secluded areas where high human activity could be avoided. In addition, the density of red deer within urban areas might also play a role in the home range size. Furthermore, particularly in the northern region of the study area of this work it is not uncommon that there is snow fall down to the valley floor which again forces deer to stay close to populated areas (Graubünden 2014, Mysterud et al. 2011). Yet, the individuals who shift their winter home range to urban areas might have an advantage during harsh winter months due to decelerated wind movement between buildings and thus a reduced wind-chill effect (Grund et al. 2002, Etter et al. 2002). An additional benefit constitutes the thermal radiation stemming from heated buildings as well as ploughed roads and walkways. Grund et al. (2002) were able to observe deer using such ploughed passages to reduce their energy demand which would have been higher if they traversed through deep snow. These factors lead to a high survival rate within (sub-)urban animals causing an overabundance of white-tailed deer within certain areas (Grund et al. 2002, Etter et al. 2002).

## 2.2. Space Utilization and Migration Pattern Analysis Tools

As was illustrated in Section 2.2.3, red deer often exhibit seasonal migrations whereas they have distinctive summer and winter home ranges which are used again over the years. Thus, a useful approach to analyse space use and migration patterns is to look at the home ranges of the animal of interest. Over the years, numerous methods were used to describe home ranges. Two of the most commonly used methods are the Minimum Convex Polygon (MCP) and the Kernel Density Estimation (KDE) (Reinecke et al. 2014, Kolodzinski et al. 2010). During recent years, alternative approaches for the home range and migration pattern analysis were developped and implemented (Horne et al. 2007, Bunnefeld et al. 2011, Mysterud et al. 2011, Kranstauber et al. 2012). Horne et al. (2007) developped the Brownian bridge movement model (BBMM) to estimate animal home ranges. The BBMM was then further developped by Kranstauber et al. (2012) into the dynamic Brownian brige movement model (dBBMM). In addition, net squared displacement (NSD) was used to determine travel distances and migration patterns (Bunnefeld et al. 2011). In addition, the meaning of the ecological context to derive meaningful results in behavioural GPS data studies gained significance (Cagnacci et al. 2010). In the following chapters the mentioned methods as well as the integration of context data into GPS location studies are going to be illustrated and discussed in detail.

### 2.2.1. Minimum Convex Polygon (MCP)

The simplest and still widely used method to conduct home range analyses in animal studies is to create an MCP (Reinecke et al. 2014, Laver & Kelly 2008, Beier & McCullough 1990). MCPs are also called convex polygons since the outermost points are connected to form a polygon (Haller 1996). Thus an MCP consists of the smallest polygon which encompasses all measured sites. At the same time, internal angles which exceed 180 degrees are not allowed (Burgman & Fox 2003). In addition, "occasional sallies outside the area [...traversed by an individual]" which Burt (1943) describes in his definition of home range, can partially get omitted by defining a percentage of points which should be included in the creation of the convex hull. It is common to chose 90 - 95% of all points, meaning that 5 - 10% of the outermost points are excluded from the computation (Moorcroft & Lewis 2006) as was done in the MCP computation of Figure 4.

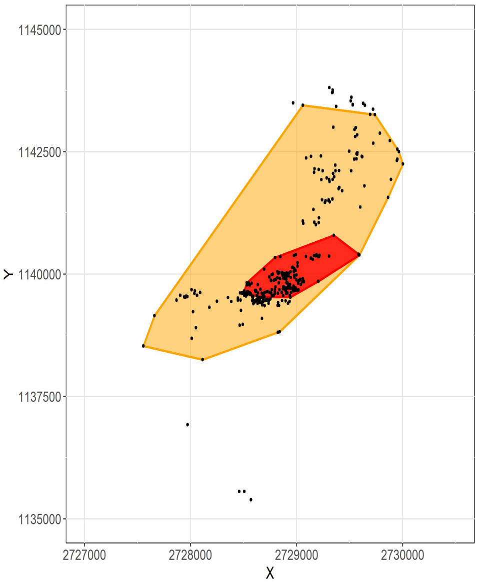


Figure 4: Minimum convex polygon for the summer home range of red deer h8. The 95% MCP is represented by the orange area, while the red area depicts the 50% MCP.

The uncomplicated use of MCP calculations enables home range analyses without a general knowledge of the point distribution or underlying parameters, such as terrain structure, of the covered area (Laver & Kelly 2008). However, there are some disadvantages to this approach which need to be taken into account as well. First of all, to derive a meaningful home range estimation at least 100 location fixes are required. If the sampling rate is lower, the error rates increase and the home ranges are getting underestimated (Seaman et al. 1999). Kolodzinski et al. (2010) even found, that studies which used under 90 data points for their analysis underestimated the area of home ranges by more than 50%. Moreover, MCP home range estimations are prone to errors since the method reacts sensitively to outliers. Such outliers promote the overestimation of home ranges because large unused areas get included into the home range calucations (Reinecke et al. 2014, Beier & McCullough 1990). In addition, topographic elements are not considered within the MCP computation. Hence, areas which an animal could not have accessed (for example lakes) get included into the home range as well (Haller 1996). Furthermore, it is not possible to derive much more information than the home range size and location of a convex polygon. This is because an MCP computation does not regard the density of the measured points. As a consequence, nothing is known about the space use intensity (but this has been addressed by the time local convex hull method by Lyons et al. (2013)). Lastly, even though extreme outliers can be eliminated through the definition of a percentage of points being used, the MCP computation remains sensitive to outliers (Beier & McCullough 1990, Haller 1996). Due to these disadvantages Nilsen et al. (2008) even advise against the use of the MCP method to derive information about home ranges. But since a lot of studies have already based their analyses on MCPs, it would make sense to use this method again for comparison purposes.

### 2.2.2. Kernel Density Estimation (KDE)

Further development of home range analyses has led to approaches whose calculations are based on probability distributions (Reinecke et al. 2014). The KDE calculates such density distributions by creating a 2-dimensional grid surface with regularly spaced cells. The cell values give an indications of the probability by which a specific individual can be found at a location within its calculated home range. This value gets estimated by computing the mean influence of the measured sites for all kernels of the grid resulting in a density surface estimate. The density surface estimate can also be used as a utilization distribution. In the end, isopleths can be derived that correspond to the probability (in percent) of which an object can be found within the specified area (see Figure 5).

Those isopleths are also known as volume contour lines (Steiniger & Hunter 2013, Hemson et al. 2005, Powell et al. 2000, Seaman et al. 1999). For the estimation of the entire home range, the 95% volume contour line is usually chosen, wherease the 50% volume contour line gets selected for the analysis of the core home range or area of intensified use (Karns & Lancia 2012, Hemson et al. 2005, Laver & Kelly 2008, Powell et al. 2000). One of the main advantages of the KDE is that it can create 3-dimensional illustrations of the utilization distribution within home ranges. The amount of time which an animal spends within a certain area, respectively the density of points within that area, is depicted as the third dimension. Such information can be used to estimate habitat selection and resource use (Seaman et al. 1999). In comparison to home range estimations using MCPs, KDEs also have the advantage of being less susceptible to sampling rates (Kolodzinski et al. 2010). However, even though home range analysis using KDE is popular, it bears the disadvantage of difficult comparability and inconsistency of results among different studies. This is due to the smoothing factor, also known as bandwidth, which has to be defined for the KDE computation (Powell et al. 2000, Reinecke et al. 2014). The distance over which a kernel can get influenced by a data point corresponds to the smoothing factor. With a larger smoothing factor, the home range estimate gets larger as well and details get blurred. In contrast, more internal structures are revealed with small bandwidths but the estimates are also smaller which again leads to disconnected utilization islands (Hemson et al. 2005). Since the smoothing factor has such a high influence on the home range estimate, several methods have been designed to find the

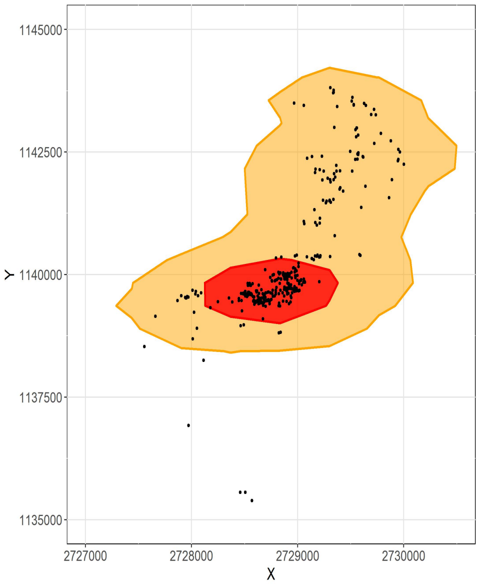


Figure 5: Kernel density estimation for the summer home range of red deer h8. The 95% KDE is represented by the orange area, while the red area depicts the 50% KDE or core home range.

most optimal smoothing factor. Three of the most commonly used functions include the normal or reference method ($h_{ref}$), the least-squared cross-validation ($h_{LSCV}$) and the plug-in technique ($h_{plug\text{-}in}$) (Gitzen et al. 2006, Hemson et al. 2005, Walter et al. 2011). According to Walter et al. (2011) $h_{ref}$ is not suitable for multimodal data which is typical for a lot of mobile species. Moreover KDE tends to over-smooth utilization distributions when using $h_{ref}$. In contrast, $h_{LSCV}$ is error prone when there is a point convergence due to high sample size or clumped distributions. Furthermore, if the samples size is <50 $h_{LSCV}$ overestimates home ranges. $H_{plug\text{-}in}$ on the other hand, is best used for animals which are less mobile and which live in small geographic areas because of the lesser smoothing than the other bandwidth estimation methods. In addition, $h_{plug\text{-}in}$ also delivers reasonable results when used on resident animals or animals with seasonal habitats where exploratory behaviour can be excluded. The preferred method of most studies however, is the LSCV method (Walter et al. 2011, Seaman et al. 1999, Gitzen et al. 2006).

Another disadvantage of the KDE is that it overlooks motion between the sample points which would be of great importance since animals usually do not move from one point to another in a straight line. Moreover, KDE does not regard temporal autocorrelation (Buchin et al. 2012). Yet, Burt (1943) defined home range to be the area which gets traversed by an individual. This means that a movement trajectory is needed in order to define a home range. In his statistical translation of movement trajectory, Otis et al. (1999, p. 1039) describes it to be a "2-dimensional, continuous, stationary, stochastic process, which, by definition, generates an associated autocorrelation function". Thus, GPS-locations of animal movement are always autocorrelated, since animals usually do not move randomly (De Solla et al. 1999, Otis & White 1999). The level of autocorrelation can be influenced by the time interval between the measured locations. A shorter sampling interval leads to an increased level of autocorrelation (Frair et al. 2010). Another possibility to reduce autocorrelation is to subsample the data set. The downside to short sampling intervals and a subsampling of the entire data set is that the biological significance of the study gets limited. Furthermore, fewer data points impede the analysis of daily movements and activities (De Solla et al. 1999, Frair et al. 2010). Due to the uncertainty which is connected to the selection of an ideal bandwidth and issues with autocorrelation, there are concerns that the KDE method might not be suitable for home range analyses with location data based on GPS-telemetry where large sample sizes are common (Gitzen et al. 2006, Byrne et al. 2014).

### 2.2.3. Dynamic Brownian Bridge Movement Model (dBBMM)

Recently, alternative methods were developed to address the issues with bandwidth selection for KDE and autocorrelated GPS data. In addition, ecologists did not only want to take the size and area of home ranges into account in wildlife research but also the temporal distribution of the measured sites (Haller 1996). Horne et al. (2007) introduced the Brownian Bridge Movement Model (BBMM) which presents an improvement compared to other utilization distribution methods such as the KDE. The BBMM incorporates time into its calculations by modelling the expected path of an individual between each consecutive pair of sampled locations. Hereby the characteristics of a conditional random walk (Brownian motion) are being used. Additionally, the elapsed time between the measurements as well as the speed of movement and location error are taken into account. This way, uncertainties in the movement path can directly be included into the computation and autocorrelation of the sample points does not represent a problem anymore (Horne et al. 2007). The result is a bimodal probability distribution with two peaks at the locations where the sample points where taken if only two GPS fixes are used for the computation (see Figure 6) (Buchin et al. 2012).

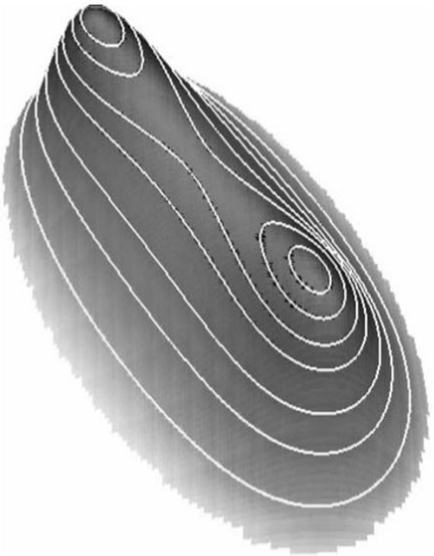
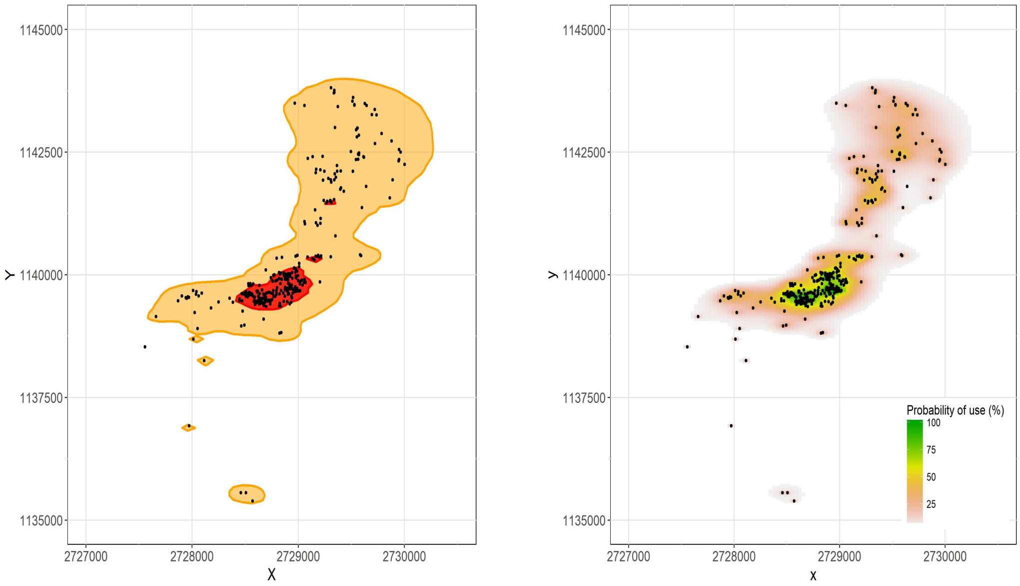


Figure 6: Bimodal probability distribution between two sample points, computed with the BBMM (Horne et al. 2007, 2356)

However, a downside of the BBMM is that it assumes a constant variance of the Brownian motion. This variance describes the regularity of an animals movement path in terms of movement scale, speed and the straightness of the path. This causes the BBMM to underestimate probability distributions in some areas and overestimate it in others, since animals have a variety of movement activities throughout the day. Especially in areas where an individual usually rests, home ranges tend to get overestimated with a fixed Brownian motion variance. This is because movement gets assumed in locations where the individual actually did not move for a prolonged period of time (Kranstauber et al. 2012, Byrne et al. 2014). Hence, Kranstauber et al. (2012) introduced the dBBMM. The dBBMM is based on the BBMM but allows the Brownian motion variance to diverge along a movement path. To do so, Kranstauber et al. (2012) incorporated a moving window as was done by Gurarie et al. (2009) in their behavioural change point analysis to find locations where a change of an animal's behaviour occurs. Likelihood comparisons are computed within the moving window in order to detect points of change and to quantify the variation of the movement parameters of an individual along its trajectory. To get stable estimates of the Brownian motion variance, larger windows should be chosen. However, this leads to a decreasing chance of finding weak changes. A window size which encompasses close to but <12 hours should be chosen if the aim is to detect diurnal changes. Apart from the advantages that the dBBMM eliminates problems with autocorrelation and can deal with varying Brownian motion variances along a track its strength lies in the ability to produce good estimates of home ranges when locations are not regularly sampled (see Figure 7) (Kranstauber et al. 2012).



(a) (b)

Figure 7: DBBMM calculation for the summer home range of red deer h8. a) The 95% dBBMM contour area is represented by the orange area, while the red area depicts the 50% dBBMM contour area or core home range. b) Utilization distribution of the individual in %. High values indicate higher probability of the animal having accessed the location.

However, uncertainties increase again with increasing sampling intervals and high mobility of the observed individual. With relatively long sampling intervals (for example one location per day), methods which rely on Brownian Bridges are not reasonable anymore and KDE might be a better choice (Buchin et al. 2012).

### 2.2.4. Net square displacement (NSD)

Bunnefeld et al. (2011) developed a novel method which enables a uniform analysis of spatio-temporal data: the use of the net square displacement. Unlike the MCP and the KDE, the NSD can be used to distinguish different forms of migrational behaviour from other movement patterns such as dispersal, stationary and nomadic behaviour. It is also possible to extract valuable characteristics of a movement path such as the timing of migration, its duration and distance. These parameters can then be used for comparisons of individuals, groups and variations between different years (Bunnefeld et al. 2011, Papworth et al. 2012). In addition, knowledge about migration parameters is essential for the understanding of an animal's movement behaviour, the plasticity of its used strategies and its conservation (Cagnacci et al. 2016). Thus, during recent years the NSD gained popularity in movement research, especially when it comes to yearly movement cycles in relation to migrating animals (Bunnefeld et al. 2011, Papworth et al. 2012). The advantage of being able to compare certain movement path parameters within a population is valuable for this master thesis in respect to the individualistic nature of red deer behaviour and the high climatic, topological and land use variability of the study area.

The NSD measures the squared Euclidian distance between the starting point of a given individual to every other GPS location point of its movement path. The squaring of the distance serves the purpose of removing directional information from the calculation (Papworth et al. 2012). When the NSD for a migrating animal is calculated, a double s-shaped function is the result. Such a curve is caused by the behaviour of the animal. Starting from its original location in the summer or winter home range, the NSD increases, as the animal migrates to its other seasonal range. At this point, the NSD reaches a stable peak, where the animal remains stationary. This pattern constitutes the first s-shaped curve. As soon as the animal starts its migration back to the original location, the NSD decreases until it reaches a value of around zero. Thus, indicating the second s-curve. Similar to this, patterns for nomadic, mixed migratory, dispersal and stationary animals exist as can be seen in Figure 8 (Bunnefeld et al. 2011, Singh et al. 2016).

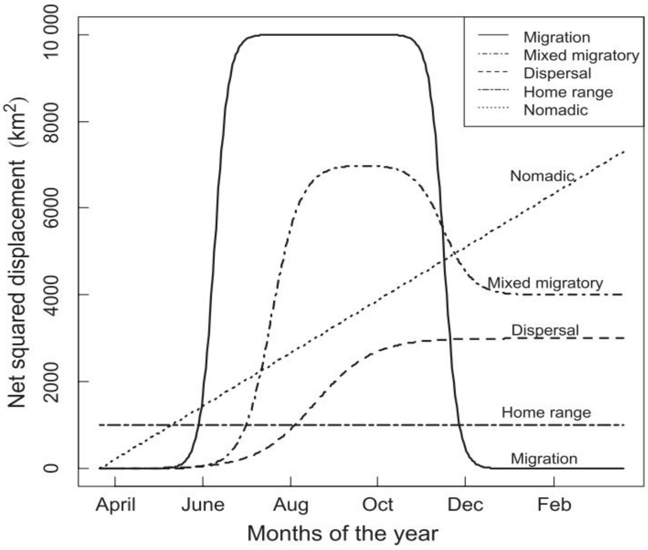


Figure 8: Different movement types analyzed with the NSD (Bunnefeld et al. 2011, 467).

One of the advantages of this method is that it is scale independent. In addition, the classification of movement patterns happens in a quantitative and objective way. However, the issue of having to define a start and end location for each movement path, in order to calculate the NSD, is a disadvantage. The correct calculation and classification of movement, as well as the estimations for migration distance and timing, is highly dependent on the choice of an appropriate start location. If, for example, the start location gets chosen during times when the individual is migrating, the time, duration and distance of migration might get estimated wrongly. Furthermore, it is important to take into consideration whether all of the GPS fixes should be included into the analyses or not. Subsampling of the data may lead to the eradication of excursions and within home range movements. The estimation of the moved distance gets affected negatively as well. On the other hand, subsampling might also constitute an advantage since daily movements get smoothed out and annual movements can be more easily differentiated

(Papworth et al. 2012, Singh et al. 2016). Another factor which influences the NSD calculations are missing locations. Especially GPS fixes which are missing during short migration phases might have an effect on migration parameter estimations (Singh et al. 2016).

### 2.2.5. Environmental Context of GPS Locations

When integrating context information into the analysis of GPS locations context data is given as raster or vector data sets. The vector data model allows for the definition of discrete points, lines and polygons. Thus, it is an ideal model for the representation of categorical features such as for example animal's nest site, rivers and home range boundaries. Field-based context refers to physical properties which are continuous in space such as precipitation and temperature and is typically represented by rasters (Gschwend 2015, Slocum et al. 2008). The question is, how meaningful information can be derived from GPS locations using such context data. Gschwend (2015) illustrates five possibilities of acquiring context values out of raster or vector data sets as can be seen in Figure 9.

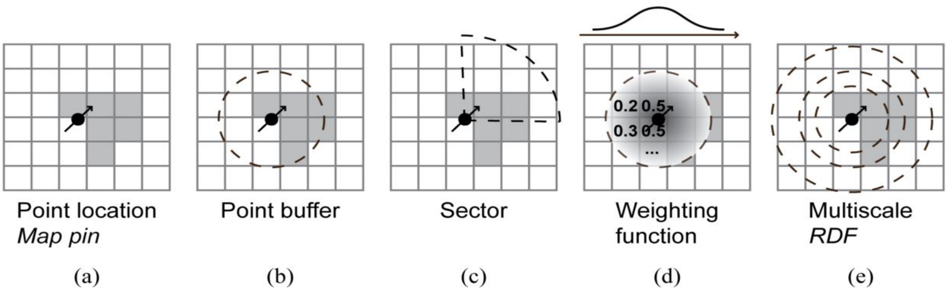


Figure 9: Different methods of acquiring context values at point locations (Gschwend 2015, 48)

The most simple and straightforward approach is to only extract the context value at the GPS point location itself. In this case, the GPS fix is treated as a map pin (Figure 9, a). This method should only be chosen if the influence of the context value has a very local impact and does not affect the rest of the movement of an individual. However, in most cases the surrounding contextual variables of an animal also have an influence on the behaviour or movement path. For this reason, methods which take the surrounding raster cells of a GPS fix into account as well by defining a buffer, sector, weighting function or multiscale radial distance function (RDF) (b - c in Figure 9) might be more suitable when analysing animal movement and behaviour. The point buffer method creates a circular buffer with a predefined radius around the GPS locations (b). In a following step, it calculates the average of all pixel values within the buffer and assigns it to the GPS point. The buffer can also be limited to a sector by selecting only a fraction or angle of view of the whole buffer (c). This method is often used for viewshed analyses but should only be chosen, when the sampling interval is small enough to estimate the actual trajectory of an individual. A distance-weighting function can be applied around the sample points to include the influence of varying importance of context values with increasing distance (d). As an alternative, buffers of different sizes can be used to evaluate various scales of context (e). Similar approaches can be applied, when context data is given in vector format. For example if a GPS location lies within a polygon, the polygon value is returned instead of a raster value.

However, context values can also be analysed with segments of a trajectory, using two or more GPS fixes instead of single points. These segments can be defined by temporal, spatial and spatio-temporal properties of the trajectory as can be seen in Figure 10 where the segments were created by time of day. In this case the segment can be interpreted as buffer as in the point buffer method of Figure 9. The shape of the buffer can be changed to create a sector and weighting functions can be applied as well. An advantage of the analysis of movement in relation to the environmental context by segments is that variations in the environment can be regarded as well (Gschwend 2015).

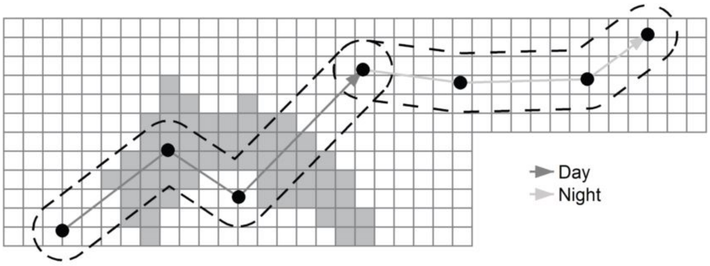


Figure 10: Acquiring context values using segment-based methods (Gschwend 2015, 48)

## 2.3. Ecological Tools

### 2.3.1. Migration Pattern Classification

Even though red deer are often referred to as migratory animals (as described in chapter 2.2.3), there are also individuals which stay within one home range all year round or where the disparity between the two home ranges is not very pronounced. In fact, in various taxa partial migration is more common than complete migration by all individuals of a population. Thus, complete migration is rather seen as an exception than the rule (Dingle & Drake 2007, Chapman et al. 2011). Partial migration seems to occur especially when the suitability of habitats varies considerably over time (Taylor & Norris 2007). To determine whether an individual executes a migration with two clearly disjoint home ranges several methods have been implemented so far in previous studies. Well known and common approaches to analyse migration patterns of animals are to check the distance respectively the overlap between seasonal home ranges and analysing spatio-temporal segregation of seasonal location clusters as was done by Patrick (2017) with the MCP and KDE methods. In addition, the NSD method can be used as well as was described in the previous section (Bunnefeld et al. 2011, Cagnacci et al. 2016, Singh et al. 2016). An advantage of the NSD method over the MCP and KDE approaches is that no specific dates have to be chosen in order to define the seasonal home ranges. In addition, the NSD method is able to distinguish a higher variety of migration patterns and can even detect daily behaviour, such as short excursions, depending on the sample size (Bunnefeld et al. 2011).

Cagnacci et al. (2016) compared those methods with each other. They found that there was a high consistency between the three methods when migration was classified at population level. As soon as migration patterns were analysed at individual level, there was less consistency. Especially partially migrating animals were not detected similarly by all methods, independently of species or migrated distance. Thus, they assume that partial migration is not uncommon and that there are different types of partial migration which again supports the division of migration types into migratory, mixed migratory and disperal by Bunnefeld et al. (2011). As a consequence, Cagnacci et al. (2016) advise to use several methods in migration pattern classification since cases with inconsistent classifications may yield interesting insights into ecological backgrounds.

### 2.3.2. Ecological Importance of the Environmental Context

GPS technology has enabled to track and map animal movement at high precision and resolution without having to be close to the monitored animal itself. The key aspect used to lie on exploring the shape, pattern and arrangements of home ranges by using geometric criteria (Gschwend 2015). However, in animal ecology it is not only of interest to know where an individual is located at which time. Some of the additional questions which are being asked are: Why is the animal at a certain location at a certain time? What is it doing at that location? And what kind of consequences might the presence of the animal have to its surroundings? Where will the animal go to in the future? To answer such questions, the GPS samples of the animal have to be related to its environment (Cagnacci et al. 2010). Mysterud & Østbye (1995) state that the inclusion of activity patterns and the environment of the animals into ungulate studies are often neglected. In addition, Laube (2014) states that to understand the behaviour which causes a movement pattern, the semantic meaning of the geometric characteristics has to be analysed. Factors which might influence animal behaviour are of environmental (e.g. resources, season and climate) as well as human nature (e.g. hunting, tourism, agriculture). Since the activity pattern of red deer is mainly based on feeding, resting and avoidance of predation, respectively avoidance of disturbance in general, especially resources where deer can feed and find cover are of interest (Adrados et al. 2008). In this sense Mysterud & Østbye (1995) distinguish between structural and non-structural cover whereas structural cover consists of physical structures such as topography and vegetation. This kind of cover cannot only be used as visual protection but also as thermal cover. Especially during times of low temperatures and strong winds, deer were found seeking shelter under dense canopy. These findings are backed up by Schmidt (1993) who found that red deer used forested areas as wind shelter during winter months. This shows that not only ground cover information is of interest but also meteorological information. Non-structural cover on the other hand, consists of factors which only provide protection through reduced visibility. Hence, the time of day or bad weather conditions can serve as non-structural cover since for example at foggy days visibility is reduced. Hence, ungulates have to balance between the two requirements of seeking cover and shelter in forest areas and feeding in more exposed areas (Mysterud & Østbye 1995). Yet, it has to be noted that cover may also constitute an advantage to predators, since it enables them to approach their prey undetected, once it is found. This may lead to a more vigilant behaviour of ungulates in areas where vegetation is dense (Goldsmith 1990). Another type of cover which was not mentioned by Mysterud & Østbye (1995) are game reserves and wildlife sanctuaries. These areas provide shelter from human recreational and hunting activities and Reimoser et al. (2014) found that such reserves and sanctuaries indeed have an influence on the space use pattern of red deer, especially during hunting and tourist seasons.

Feeding on the other hand, does not only occur in exposed areas, namely grasslands. As Putman (1996) has shown, feeding can also happen within forests where tree fruits and germinating seedlings are eaten and trees are browsed. In addition, there is also damage in agriculturally used fields by red deer, which feed on crops and pasture as was described in Section 1.1. Nevertheless, grasslands are still the main source of food and red deer movement was most often observed between forest and grassland areas (Mitchell et al. 1977, Godvik et al. 2009).

Due to the high interdependency between red deer behaviour and its environment, it is important to integrate as much environmental data as possible into the study in order to get a comprehensive knowledge of traditional key concepts of animal ecology and in this case red deer behaviour (Cagnacci et al. 2010).

### 2.3.3. Normalized difference vegetation index (NDVI)

To be able to properly judge home ranges and activity or movement patterns, it is of great value to know what kind of resources an individual accesses. Since red deer are herbivore the ground vegetation is of major interest for the study of resource use (Borowik et al. 2013). The NDVI is a suitable tool to extract vegetation from other ground cover types such as glaciers or gravel fields if vegetation data is not available. NDVI values range from -1 to 1 and are calculated by using the reflectance of vegetation in near-infrared (NIR) and red (RED) wavelengths. These wavelengths are used since vegetation transmits and reflects most of the NIR wavelengths, while the RED and visible wavelengths are mostly absorbed by the chlorophyll. This behaviour results in a distinctive pattern of the spectral signature with a low-point in wavelengths of 0.6 - 0.7 $\mu$m (RED) and a peak at wavelengths of around 0.8 - 0.9 $\mu$m (NIR), and hence showing a high absorption contrast from approximately 0.6 to 0.9 $\mu$m (see Figure 11) (Myneni et al. 1995, Jackson & Huete 1991).

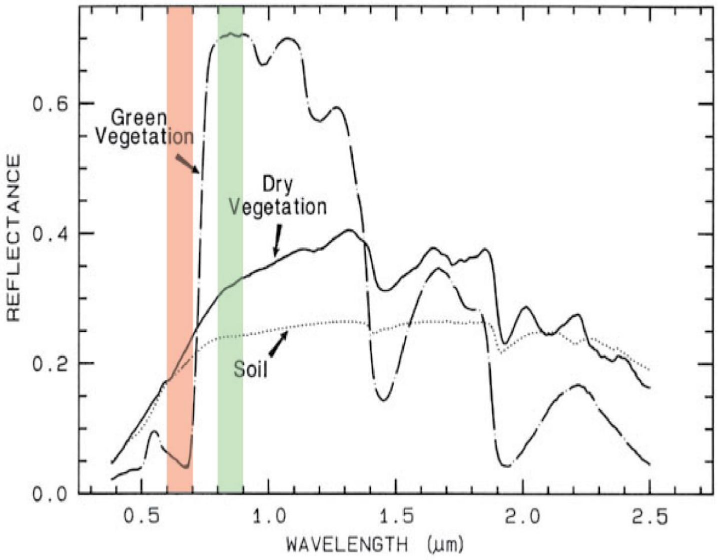


Figure 11: Reflectance spectra of soil, dry vegetation and green vegetation as described by Lillesand et al. (2008). The red bar indicates the RED spectrum and the blue bar the NIR spectrum. Figure from Patrick (2017, 20)

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Thus, satellite sensors which are used for vegetation studies are able to register the amount of NIR and RED light that is being reflected (Jackson & Huete 1991, Borowik et al. 2013). The NDVI can then be calculated using the following formula (Myneni et al. 1995):

$$NDVI = \frac{NIR - RED}{NIR + RED} \tag{1}$$

Healthy and dense vegetation generates positive values due to high *NIR* reflectance. Dry and sick or senescing vegetation, soil, water and snow on the other hand reflect considerably less *NIR*, which results in a low and negative *NDVI* value (Myneni et al. 1995). Thus, regions with an *NDVI* value > 0 have some sort of vegetation as ground cover (Mysterud et al. 2011). In addition, the *NDVI* is also of great use when vegetation dynamics are monitored. This can be done, since the vegetation density increases in spring. As a consequence, the reflection of *NIR* increases over the course of the season and reaches a peak when the soil is fully covered by vegetation (Jackson & Huete 1991, Pettorelli et al. 2005). Such information used to be acquired by laborious biomass harvest which was insufficient for studies covering large areas. The advantage of this traditional method was that information about the adaption of plants to herbivores could be gathered directly. This is not possible with the *NDVI*. Nevertheless, ecologists have increasingly turned to satellite-based methods, confirming the usefulness of the *NDVI* in animal ecology when linking animal distribution to vegetation dynamics (Borowik et al. 2013).

### 2.3.4. Jacobs Index

The Jacobs Index was first developped by Jürgen Jacobs (1974) and is a modified version of the forage ratio (FR) and the Ivlev's electivity index (IEI) which are common tools to quantify food selection. The FR and the IEI both compute food selection based on the relative abundance of different resources in the environment within an extent of selection. The downside of this method is, that biases appear when the relative abundance of the various food resources differ and the results are rendered useless. Thus, Jacobs (1974) introduced a new method, which is independent of the relative abundance of resources and calculated as follows:

$$\text{Jacobs index} = \frac{obs - exp}{obs + exp - 2 * (obs * exp)} \tag{2}$$

*Obs* constitutes the observed values, respectively the fraction of a resource which gets consumed by an individual at a specific time. *Exp* on the other hand, is the fraction of the resource which gets analysed within the entire used environment. The resulting index values range from -1 to 0 for negative selection and from 0 to 1 for positive selection. However, the Jacobs index cannot only be used to calculate preferential and non-preferential use of food resources but also to analyse the selection of land cover types as was done by Patrick (2017) and within the Rätikon Project of Reimoser et al. (2014). Similarly to the food selection analysis, *exp* corresponds to the fraction of the landcover class within the entire used environment (or home range) and *obs* to the fraction of the specific landcover which was effectively used at a certain time.

### 2.3.5. Activity Classification

In addition to knowing the environmental context of GPS locations, it is also crucial to understand what an animal is doing at a certain location and time in order to understand habitat use and irregularities. In addition, analysing spatio-temporal behaviour of animals is valuable since it allows to investigate the effect of anthropogenic activities, resource abundance and population density on activity patterns. This is especially important in areas where wildlife management and conservation meets high human (recreational) activity and tourism (Loettker et al. 2009, Coulombe et al. 2006). Before the introduction of motion-sensitive devices, animal activity was analysed using the spacing patterns of the measured GPS-locations. This method is still being implemented when GPS data is available but activity data is missing. Using the distance between two successive GPS coordinates and the curvature of the earth the speed of locomotion of an animal can be calculated as was done by Ensing et al. (2014) and Patrick (2017). The locomotion speed was then used to determine how active an animal was during a certain period of time. Despite the simple implementation of this method, it bears some disadvantages. Discrimination between different activity types is usually not possible since only statements about active or passive times can be made. In addition, animals might be active even though they do not move to different places or the displacement might be too small to be detected as activity (for example when feeding or grooming). Hence, activity bouts might not be recognised as such (Adrados et al. 2003, Coulombe et al. 2006, Gervasi et al. 2006).

With the introduction of motion-sensitive devices, however, distinctions between activity types became possible. The devices get activated by movement of the animal which is wearing the device. As soon as the animal moves, the signal mode changes. This change usually concerns the pulse rate and is being registered. The signal changes can then be used to differentiate between feeding and slow locomotion, rumination and sleeping as well as fast locomotion (Loettker et al. 2009, Georgii & Schröder 1978, Georgii 1981). The advantage to observation based activity studies is that the behaviour of the study animal is not influenced by a human standing close by when using motion-sensitive activity sensors. However, bias might be introduced through different collar tightenings between individuals and seasons. In addition, it is important not to choose a high sensitivity setting of the collar since it then becomes more difficult to differentiate between the activity types and the variations between the individuals increases (Coulombe et al. 2006). Another disadvantage is that the acceleration sensor within the motion-sensitive device is prone to head movements since the sensor is placed around the neck. As a consequence, resting periods can get misclassified as active periods due to head movements as well as moments when the animal shakes or gets up during the resting period. Moreover, choosing the correct threshold values for the activity classifications bears more risks for biases (Loettker et al. 2009). Nevertheless, Loettker et al. (2009) and Coulombe et al. (2006) were able to determine 85% - 98% of the activity types correctly by using motion-sensitive devices.

# 3. Study Area and Data

## 3.1. Study Area - the Mesolcina

### 3.1.1. Overview

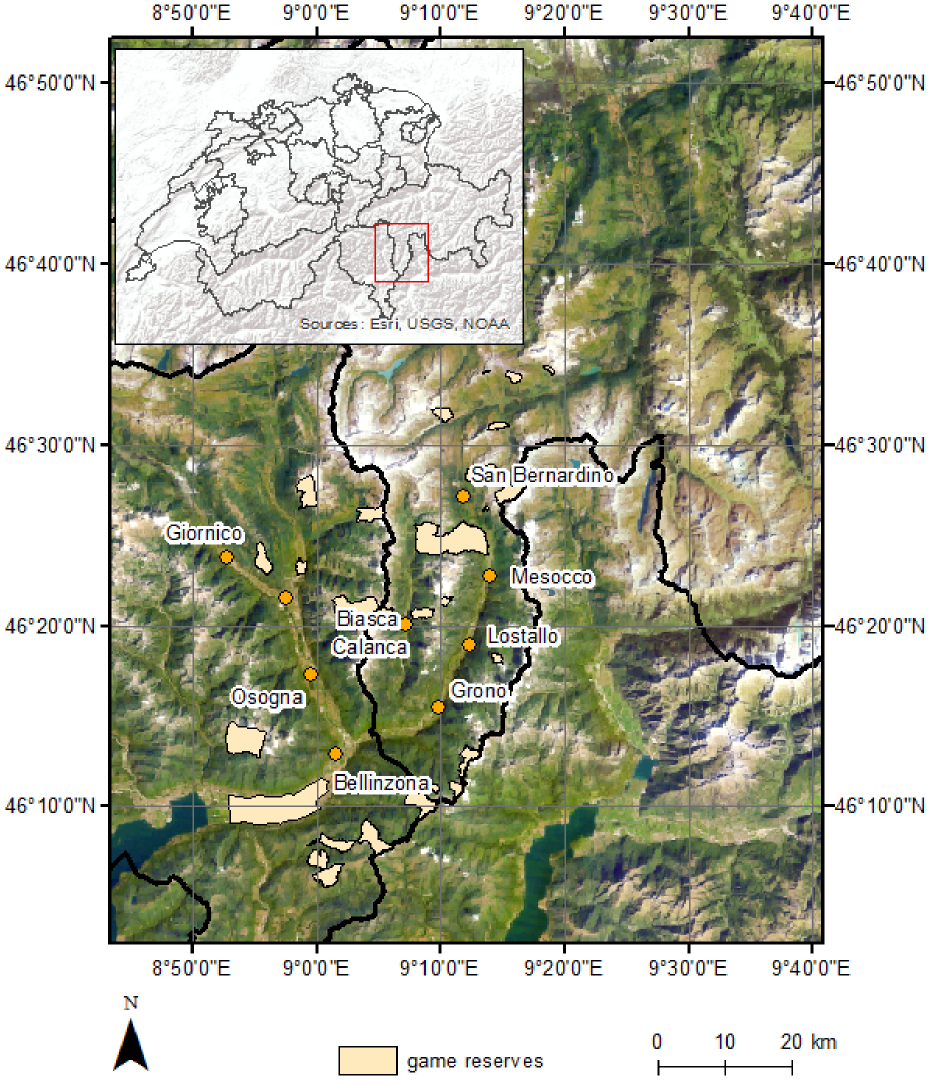


Figure 12: Overview of the study area, encompassing the Mesolcina, Calanca, Leventina and Riviera valleys.

The study area lies in the border region of the cantons of Ticino, Grisons and the Lombardy (see Figure 12). This area encompasses the Mesolcina, the Calanca and a part of the Leventina valleys and lies in the south-eastern part of Switzerland, next to Italy. The Mesolcina consists mainly of a valley adjacent to the northwards lying San Bernardino Pass and contains the municipalities of Mesocco, Soazza, Lostallo, Verdabbio, Cama, Leggia, Grono, Roveredo and San Vittore. In the south, the valley reaches out to Grono, a village of the canton of Grisons and merges with the Calanca Valley which stops shortly before the border of the canton of Ticino, close to Bellinzona. Hence, the Mesolcina ranges from 46°30'N and 9°10′E in its northern part to approximately 46°30′ N and 9°10′ E in the south. The valley itself lies between the Adula and the Tambo ridge which is located next to the border of Italy on the east and the Calanca valley in the West. This region constitutes an important connection axis between the northern and southern part of Switzerland and serves as an alternative for the Gotthard axis (Bertossa 1953). The Calanca valley is also located in the very South of the canton of Grisons and has a similar northern and southern extent as the Mesolcina Valley. However, it is situated further west and lies adjacent to the border of the canton of Ticino. It encompasses the municipalities of Calanca, Rossa, Buseno-Molina and Castenada. Contrary to the Mesolcina valley it is not a transit valley but is restricted in the north by a mountain ridge (Ciocco et al. 1998). On the eastern side of the Calanca valley the Leventina and the Riviera valleys can be found. The Riviera valley extends from Bellinzona to Biasca, encompassing amongst other municipalities Claro, Moleno, Osogna as well as Iragna and merges with the Leventina valley at Biasca. A prominent feature of the Leventina and Riviera is the Gotthard axis which runs through the valley along with the river Ticino. The slope within the valleys is relatively high with high elevations in the north and lower elevations in the south. Around the San Bernardino Pass the highest altitudes can be found reaching over 3000 m.a.s.l. In this region glaciers are common as well. However, further south in Grono and Roveredo the mountains do not exceed altitudes of 2500 m.a.s.l. (see Figure 13). The mountains which surround the Leventina reach similar heights with a decrease of height at Biasca. In the Mesolcina valley a particularly steep slope can be found between the Moesola lake with an altitude of 2063 m.a.s.l, and the valley floor at Soazza, which lies at 600 m.a.s.l. Thus, over a distance of approximately 10 km a difference of altitude of 1400 m can be found in this region. Further south the slope becomes more moderate, as is the case in the Leventina (Bertossa 1953). Moreover, while having a very distinct v-shaped valley at Mesocco in the Mesolcina valley and Giornico in the Leventina valley with steep mountain walls, such structures cannot be found at the San Bernardino Pass and further south around Lostallo and Biasca. In the region of the San Bernardino Pass the valley is relatively shallow, whereas in Lostallo a former v-shaped valley filled with sediment can be found. The sediment in this former flood plain constitutes a very fertile soil which, in combination with the warm mean annual temperatures, makes the southern part of the valley a great agriculturally used area (Bertossa 1953). A similar topography can be found in the Riviera valley between Biasca and Bellinzona where agricultural use of the land is even more common than in the Mesolcina valley. The Calanca yalley on the other hand is dominated by a v-valley throughout the entire region making agricultural use of the soil less common than in the Mesolcina and Riviera valleys. Moreover, the Calanaca valley is only around half as wide as the Mesolcina valley (Ciocco et al. 1998).

Through the entire Mesolcina valley flows the Moesa, having its spring at the Moesola lake. Especially during spring time, when the snow melt begins, the Moesa carries a lot of water and can develop into a torrent. In combination with heavy rainfall it is possible for the river to transcend its riverbank (Bertossa 1953). The Calanca valley's main river is the Calancasca, which merges with the Moesa in Grono. The river Ticino which flows through the Riviera valley later merges with the Moesa as well in Arbedo-Castione. The climate in all of the valleys is quite diverse (see Figure 14. At the northernmost locations mean temperatures rarely reach 16°C in summer but fall down to -8 degrees during winter times, showing a typical alpine climate pattern. In Grono on the other hand, the temperature hot spot of Switzerland can be found with mean temperatures reaching up to 28°C in summer. Mean temperatures below 0°C only occur very rarely, indicating a more Mediterranean climate than further north (Bundesamt für Meteorologie und Klimatologie 2013).

Influenced by the diverse weather conditions, the flora of the study area is manifold. In the North larches and Swiss mountain pines (*Pinus mugo* are the dominant tree types while horse chestnuts are common in the South and in the valley floors. Oak- and lime-mixed forests alternate with grasslands,

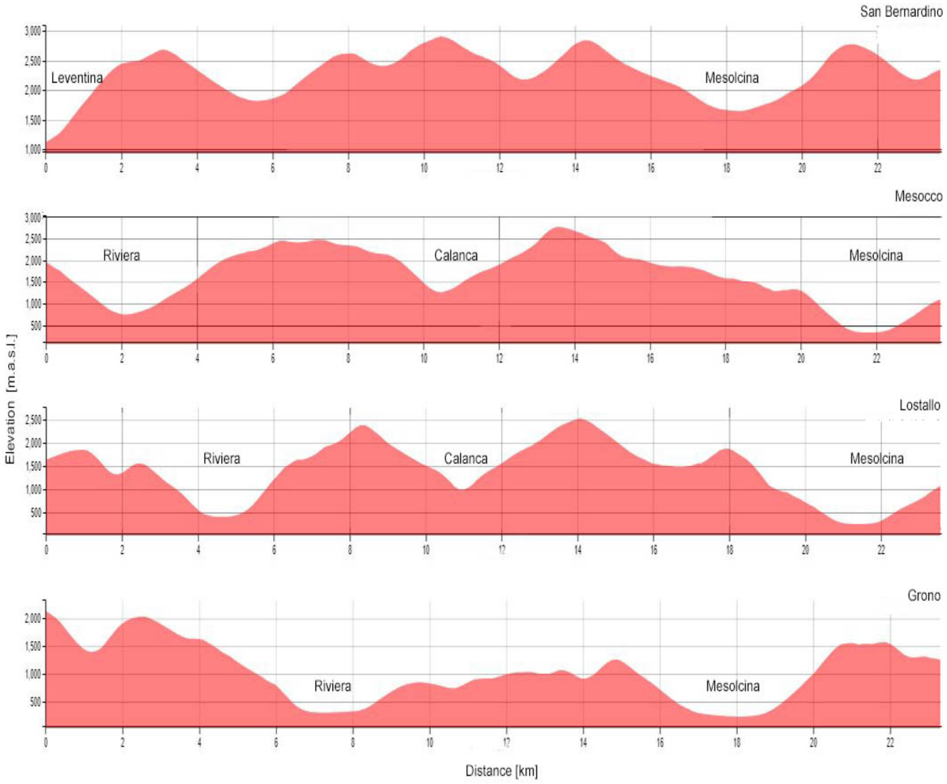
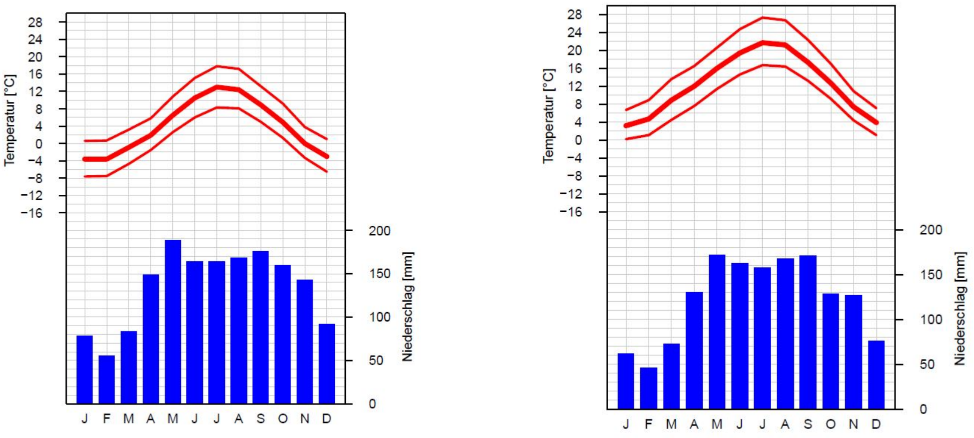


Figure 13: Cross section through the study area at the heights of the San Bernardino, Mesocco, Lostallo and Grono encompassing the Mesolcina, Calanca and the Riviera respectively the Leventina valley (Swisstopo, 2018). (Bertossa 1953).

which are often used as pasture areas. Moreover, vast wetlands such as upland bogs and fens in higher elevations and alluvial forests in the bottom of the valleys can be found. Especially the bogs around the San Bernardino Pass are of great value and belong to the biggest moor land in Switzerland, with an extent of 8 $km^2$ (Ciocco et al. 1998).

Additionally to the high climatic variations throughout the valleys, the human population density differs as well from the very north of the valleys to the south. In the northern part of the Mesolcina, only a small human population density can be found. On the other hand, the highly agriculturally used south inhabits a higher population density. A similar pattern can be observed in the Calanca Valley but with a generally lower population density than in the Mesolcina. Especially the sparse population density makes the two valleys popular for outdoor activities such as hiking and mountain biking during summer times and skiing in winter. In the Calanca Valley one ski resort can be found in Rossa and three ski resorts are located in the Mesolcina Valley at the San Bernardino Pass and northwards of Mesocco.

To protect wild animals from such human disturbances the wildlife sanctuary (Wildruhezone) Trescolmen was set in place between Mesocco and the San Bernardino Pass. It also encompasses the eastern hillside of the Calanca Valley at the north of Rossa. In the wildlife sanctuary Trescolmen, animals are protected all year round (Bundesamt für Umwelt 2017). This is especially of great importance during harsh weather conditions in winter when the availability of food is low and energy loss has to be minimized. Especially disturbances caused by skiers and snowboarders which do not stay within the designated ski slopes can constitute a threat to wild animals. In addition, wildlife sanctuaries are also able to channel animal movement patterns and behaviour and hence guarantee an ideal dispersion of



(a)

(b)

Figure 14: Mean monthly temperature and precipitation for a) the San Bernardino and b) Grono meteo station at 1639 m.a.s.l. respectively 324 m.a.s.l. from 1981 - 2010. The thick red line indicates monthly mean temperature. Thin red lines represent minimum and maximum temperature. Blue beams indicate mean monthly precipitation sum (Bundesamt für Meteorologie und Klimatologie 2013)

the animals. However, hunting in wildlife sanctuaries is still allowed (Bundesamt für Umwelt 2017).

### 3.1.2. Hunting in the Study Area

Today, a two-level hunting concept is in use in the whole canton of Grisons, with which a sustainable regulation of the red deer population should be supported. This concept is linked to an annual animal-monitoring where the health, population size and the condition of the animals' habitat are evaluated. In addition, conflicts between red deer and forestry as well as agriculture are analysed. Based on these factors the number of red deer which can be culled is determined. The first level of the hunting concept is then constituted by a coarse regulation (Hochjagd) in September, which lasts 21 days, with a break of 4 - 7 days. During this time, the animals are expected to be located in their summer home ranges and lactating hinds, young animals, brockets with antlers that are longer than their ears, as well as stags with surroyals are protected. The protection of these animals during the coarse regulation serves the purpose of preserving animals with the best body condition and those which most probably contribute to reproduction cycles. Moreover, the protection of lactating hinds and their offspring aims at the maintenance of a good dispersion of the animals by providing them a sense of security through which they stay in the hunting grounds. Hunting during this time is permitted to any hunter, as long as they are in possession of a valid hunting license (Jenny et al. 2011).

However, in the following fine regulation (Sonderjagd), lasting from November to December until the hunting plan is reached or over a maximum of 10 half days (7 a.m. - 2 p.m.), female and young deer are hunted as well, in order to comply with regional needs. It is expected that the animals reside in their winter home range during this time of the year. The hunting plan stipulates that the hunted number of red deer has to be the same for hinds and stags. The hunting plan is reached, if enough hinds are culled. However, while the coarse regulation starts and ends at the same date in the whole canton of Grisons, the timing of the fine regulation may vary throughout canton. During this time, the number of hunters, the number of deer which are allowed to be culled as well as the hunting grounds are limited. Moreover, financial fees and rewards ensure that only young, sick and weak animals are hunted. However, a problematic factor of the fine regulation is the correct timing. On the one hand, the animals have to be located in their winter home ranges. Yet, most often the animals only migrate to their winter home ranges following the first snow falls in the mountains. On the other hand, if the snow falls deep down to the valley, the animals stay close to villages where hunting is prohibited (Jenny et al. 2011).

In addition to the wildlife sanctuary, game reserves (*Wildschutzgebiete*) can be found as well in the region of the Mesolcina and the Calanca Valley. Those are divided into game reserves during the coarse regulation (coarse regulation asylum) and for the time during the fine regulation (fine regulation asylum), as well as game reserves which exist all year round (Jenny et al. 2011). Fine regulation asylums exist between the San Bernardino Pass and Mesocco as well as on the eastern hillside of Soazza, in Lostallo and between Leggia and Grono. Coarse regulation asylums, on the other hand, are located between the San Bernardino Pass and Mesocco, on the eastern and western side of Soazza, eastward of Lostallo and in Roveredo. Another relevant game reserve can be found north of Mesocco (Geogr 2018). In these areas, not only recreational activities are restricted but hunting also faces strong limitations. Hence, they play a crucial role in guaranteeing a species-appropriate dispersion of red deer. At the same time, they contribute to the preservation of a healthy population structure (Jenny et al. 2011).

## 3.2. Data

### 3.2.1. GPS and Activity Data

All movement data was gathered by the Offices of Hunting and Fisheries of the canton of Grisons[3] and of Ticino[4] and supplied as CSV data files. In total 52 animals (24 stags and 28 hinds) were captured in the winter 2014/2015, 2014/2016 as well as at 2016/2017 and equipped with GPS collars which collected data about the location of the individuals at a 3h interval. At times where the animals had to be located physically, the sampling interval was increased to 15 minutes[5]. Since it was not possible to capture all deer within one day, 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. However, for 13 animals sampling duration was shorter than a year. Especially for home range estimations and yearly activity patterns, such short sampling durations pose a problem. The data sets of another three animals were too patchy to be used. Thus, only 36 animals fulfilled the criteria of having a sampling duration of an entire year and no missing coordinates over a prolonged timed period. For the sake of consistency the starting date of the 1st April was used during the whole analysis. In addition, four animals were monitored for a time span of two years. Unfortunately, with the definition of the cut off date of the 1st April the second year of study did not reach a full second year anymore. In addition, during the last weeks of the sampling period of these animals, a sampling interval of 15 minutes was implemented, meaning that attempts to capture the animal occurred over a prolonged period of time, possibly altering the behaviour of the animals within this period. As a consequence, the second year was not included into the analysis.

The GPS collars were provided by VECTRONIC Aerospace GmbH and were also equipped with a motion-sensitive acceleration sensor to gather information about the activity of an individual. The GPS and the acceleration sensor stored various variables including the coordinates of the deer fixes in

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[3] Amt für Jagd und Fischerei

[4] Ufficia della caccia e della pesca

[5] Personal notice of Nicola de Tann, gamekeeper and chief of hunting district VI Moesano, 01.05.2017

the coordinate systems WGS84 and CH1903+/LV95 as well as the height of the locations in meters. Timestamps of the stored GPS fixes were saved in the UTC and LMT format. Furthermore, the dilution of precision (DOP) describes the satellite geometry quality which influences GPS location accuracy. The DOP value gets calculated by using the number of visible satellites and their position in relation to each other and the observed point of interest (resp. the GPS collar). As a rule of thumb, the DOP value and thus the accuracy increases with the number of satellites which are included in a measurement, with a low DOP indicating good accuracy. However, unfavourable constellations of the satellites lead to a decrease of accuracy and the DOP value (Langley 1999, Adrados et al. 2002). In addition, information about the fix type (2D, 3D and validated 3D) was stored as well, which also provides information about the GPS location accuracy. 3D locations get saved when at least four satellites are measured and are considered to be more accurate than 2D fixes where only three satellites are visible (Adrados et al. 2002, Rempel et al. 1995). Validated 3D locations are fixes where the DOP is better than 10 and no less than five satellites were visible for the calculation of the position (Vectronic Aerospace 2017). In order to filter error prone data, the fix types could be used to eliminate 2D fixes. An overview of the data of the study period 2014 - 2015 is shown in Figure 15. For the overviews of the study periods 2015 - 2016 as well as 2016 - 2017 see Appendix A.1.1.

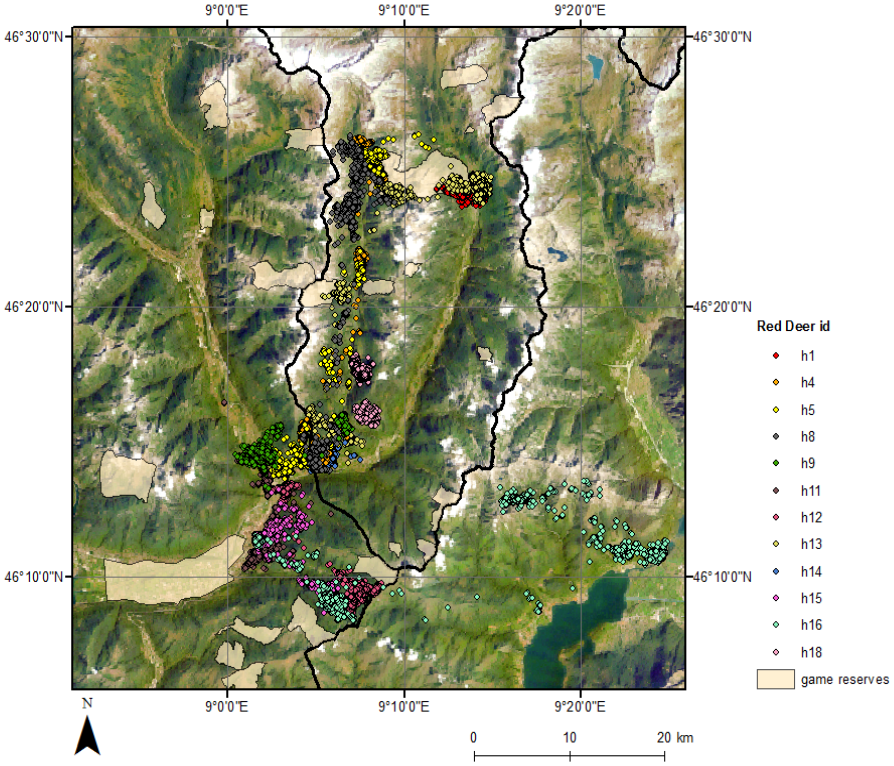

Figure 15: Overview of the red deer individuals during the study period 2014 - 2015

The activity sensor measured the true acceleration continuously four times per second on the x, y and z axes (back-forth, right-left and up-down) for 16 animals whereof only 10 animals fulfilled the required criteria for analysis which were mentioned above. As a consequence the time periods which could be used for the activity analysis got reduced to 2014 - 2015 and 2015 - 2016. For the time period 2015 - 2016 unfortunately only two data sets of hinds were available. No activity data was available for the period of 2016 -2017 because the activity sensors were not yet retrieved and still in use. The scale of the activity values ranges from 0 to 255 indicating no to maximum measurable acceleration. These values then got averaged into 5 minute intervals. In addition, the temperature inside the upper housing of the collar was stored as well. However, the stored number does not necessarily represent the surrounding ambient temperature, since the heat of the animal as well as the solar radiation can warm up the collar as well. Hence, the measured temperature always has a positive bias.

**Pre-processing**

In a first step, failed GPS position records had to be removed from the data sets. Extreme outliers were detected and removed manually upon visual inspection of the data. Zweifel-Schielly & Suter (2007) illustrated that topographical ruggedness as well as vegetation cover have a strong influence on the acquired proportion of 3D positions. However, they advise against the omission of data fixes of lower accuracy such as 2D points due to unnecessary loss of data. DeCesare et al. (2005) also found that high canopy cover leads to approximately 27.5% of GPS track length error. They argue that especially the cumulative effect of location errors can add a substantial bias to track length estimations and tortuosity and that the error could be even larger if a lot of forested areas and a rough topography is involved. Moreover, Zweifel-Schielly & Suter (2007) found that GPS accuracy decreases when red deer are resting since the collar of lying animals is near to the ground level which makes it more likely that the GPS signal gets obstructed by micro-topographical structures, rocks or even the animal's body itself. Another source of bias can result from the comparison of positions within open (e.g. grasslands) and closed habitats (e.g. forests) due to different position error rates. Due to these findings and the fact that the collared animals of this thesis mainly moved in regions with a high amount of forests and a rugged topography, all analyses were conducted by using only validated 3D GPS positions and unvalidated 3D fixes with a DOP value < 10. Table 1 shows that a majority of 78% accounts to validated 3D GPS fixes, whereas in total only 16% of the entire data set is classified as 2D and invalidated 3D fixes. In 4% of all local acquisition attempts no fix could be generated. Even though the overall number of unvalidated fixes only accounts to 16% the data set of some individuals was reduced to under 50% when all unvalidated fixes were deleted. That is the reason as for why unvalidated 3D GPS with DOP < 10 were included into the analysis as well.

Table 1: Number and percentage of 2D, unvalidated 3D as well as validated 3D GPS fixes and the number of failed GPS position acquisition for the entire red deer data set.

| **GPS-2D** | **GPS-3D** | **val. GPS-3D** | **no fix** |
|---|---|---|---|
| 13297 (6%) | 20886 (10%) | 162149 (78%) | 10245 (4%) |

As mentioned above, a 15 minute sampling interval was implemented when an individual deer had to be physically located and caught. In most cases, these periods were eliminated automatically by the limitation of the data sets to one year, starting from April 1st. Laube & Purves (2011) state that movement parameters such as turning angle, speed and sinuosity are sensitive to the temporal sampling interval of the GPS fixes. For example an increase of speed can be observed with increasing sampling rate. Thus, the 15 minute intervals which remain after filtering the data might introduce a bias to the mentioned parameters. However, the remaining sampling rates of 15 minutes only concerned two days. Additionally, since no method which is used in this thesis relies on the calculation of speed, angle or sinuosity of an animal's track and directly incorporates temporal sampling differences into the analysis, the periods with 15 minute intervals where not subsampled or deleted. An overview of the used data can be seen in Table 2.

Table 2: Overview of all undividuals which were included in the study and their respective GPS collar id, sex, start and end date of data acquisition, total number of fixes, the number of validated 3D fixes and invalidated 3D fixes with a DOP < 10 (unv. 3D fixes DOP < 10), percentage of the used fixes in relation to the total number of fixes (% used fixes) and information whether activity data is available or not (activity data).

| id | collar id | sex | start date | end date | total number of fixes | validated 3D fixes | unv. 3D fixes DOP <10 | % used fixes | activity data |
|---|---|---|---|---|---|---|---|---|---|
| h1 | 7508 | f | 10.03.2014 | 16.12.2015 | 5938 | 3559 | 671 | 71.23 | yes |
| h4 | 7522 | m | 11.03.2014 | 15.12.2015 | 5167 | 2427 | 535 | 57.32 | yes |
| h5 | 7528 | f | 10.03.2014 | 24.03.2016 | 11313 | 9399 | 624 | 88.6 | no |
| h8 | 7590 | m | 19.03.2014 | 12.01.2016 | 7253 | 5503 | 606 | 84.23 | yes |
| h9 | 7501 | f | 19.03.2014 | 17.09.2015 | 4382 | 2258 | 404 | 68.4 | yes |
| h11 | 7591 | m | 19.03.2014 | 15.10.2015 | 5135 | 4007 | 462 | 87.03 | no |
| h12 | 7599 | f | 19.03.2014 | 16.12.2015 | 5494 | 4489 | 421 | 89.37 | no |
| h13 | 7512 | m | 27.03.2014 | 24.09.2015 | 4374 | 2947 | 425 | 77.09 | yes |
| h14 | 7532 | f | 27.03.2014 | 05.05.2015 | 3417 | 1961 | 395 | 68.94 | yes |
| h15 | 7535 | f | 27.03.2014 | 04.11.2015 | 4831 | 3313 | 503 | 78.99 | yes |
| h16 | 7598 | m | 27.03.2014 | 28.09.2015 | 4108 | 3304 | 332 | 88.51 | no |
| h18 | 7504 | f | 31.03.2014 | 27.10.2015 | 4601 | 3176 | 391 | 77.52 | yes |
| h19 | 7497 | f | 04.03.2015 | 14.12.2016 | 6827 | 5540 | 496 | 88.41 | yes |
| h20 | 7498 | f | 04.03.2015 | 09.12.2016 | 6067 | 4493 | 632 | 84.47 | yes |
| h22 | 16974 | f | 10.03.2015 | 26.03.2017 | 10567 | 9112 | 443 | 90.17 | no |
| h23 | 16975 | f | 10.03.2015 | 20.01.2017 | 10059 | 9613 | 189 | 97.44 | no |
| h24 | 16981 | f | 10.03.2015 | 07.04.2017 | 9558 | 8736 | 395 | 95.53 | no |
| h25 | 16977 | f | 11.03.2015 | 09.11.2016 | 4890 | 4386 | 251 | 94.82 | no |
| h26 | 16979 | m | 11.03.2015 | 24.11.2016 | 4025 | 2812 | 318 | 77.76 | no |
| h27 | 16976 | m | 18.03.2015 | 22.09.2016 | 3738 | 2899 | 309 | 85.82 | no |
| h28 | 16978 | m | 18.03.2015 | 02.11.2016 | 4774 | 3785 | 411 | 87.89 | no |
| h29 | 16980 | f | 18.03.2015 | 10.04.2017 | 12101 | 11438 | 345 | 97.37 | no |
| h31 | 7533 | m | 20.03.2015 | 19.05.2016 | 2828 | 2209 | 238 | 86.52 | no |
| h32 | 9975 | m | 20.03.2015 | 30.01.2017 | 10510 | 9349 | 480 | 93.52 | no |
| h33 | 7507 | m | 24.03.2015 | 07.04.2017 | 7120 | 5861 | 599 | 90.73 | no |
| h35 | 16973 | m | 24.03.2015 | 13.12.2016 | 6639 | 5836 | 336 | 92.96 | no |
| h38 | 7610 | m | 27.12.2015 | 11.04.2017 | 3599 | 2097 | 538 | 73.21 | no |
| h39 | 7527 | m | 24.02.2016 | 11.04.2017 | 3065 | 2182 | 343 | 82.38 | no |
| h40 | 7535 | m | 24.02.2016 | 11.04.2017 | 3109 | 2337 | 325 | 85.62 | no |
| h41 | 7504 | f | 01.03.2016 | 11.04.2017 | 3052 | 2480 | 276 | 90.3 | no |
| h42 | 7591 | m | 01.03.2016 | 10.04.2017 | 3002 | 2550 | 197 | 91.51 | no |
| h44 | 7512 | f | 02.03.2016 | 11.04.2017 | 2997 | 2344 | 224 | 85.69 | no |
| h47 | 7525 | f | 03.03.2016 | 10.04.2017 | 2971 | 2230 | 215 | 82.3 | no |
| h48 | 7508 | f | 16.03.2016 | 10.04.2017 | 2930 | 2490 | 168 | 90.72 | no |
| h49 | 7590 | m | 19.03.2016 | 10.04.2017 | 2870 | 2008 | 306 | 80.63 | no |
| h50 | 7599 | f | 18.03.2016 | 11.04.2017 | 2942 | 2688 | 123 | 95.55 | no |

### 3.2.2. Context Information

**Vector Data**
The landcover data of the types forest, vineyard and urban areas were extracted from the swissTLM$^{3D}$ data set, which is provided by Swisstopo. The swissTLM$^{3D}$ data set is a three dimensional topographic landscape model which covers the entire Switzerland as well as Liechtenstein and is also used for the production of the Swiss topographic maps. The objects have an accuracy of 1 - 3 m and are stored in the Swiss reference system CH1903 LV03 (Bundesamt für Landestopografie 2015). In addition, the features do not overlap and are thus exclusive of each other. For the canton of Grisons, data sets of game reserves and agriculturally used areas were provided by www.geogr.ch. The data set of agriculturally used areas for the canton of Ticino was provided by the Department of Spatial Development.

**Raster Data**
Since no usable data for grasslands for the whole study area was available, the Swissimage FCIR data set of the Bundesamt für Landestopografie (2015) was used to extract grasslands with the NDVI value. The Swissimage data set basically is a color orthophotomosaic with a spatial resolution of 25 cm and the projection Swiss reference system CH1903+ LV95. By using band 1 (NIR) and band 2 (RED) the NDVI could be computed for the entire study area. In a following step, raster cells with values > 0.3 were assigned to be areas covered by vegetation, since values lower than < 0.3 correspond to areas where no or only sparse vegetation cover can be found (ESRI 2018). To extract only areas with grasslands the vegetation raster was then intersected with layers of other ground cover data such as forests and shrublands from the swissTLM data base and agriculturally used fields. The remaining areas were saved as a grassland vector data set.

In addition, temperature data was used to relate movement patterns to climate conditions. Data of daily mean temperature was accessed from Meteo Swiss. This data was saved as a gridded data set and in the WGS84 projection coordinate system with a spatial resolution of 0.0208 decimal degrees which corresponds to approximately to 2.3 km (Bundesamt für Meteorologie und Klimatologie 2013). In order to analyse animal movement in context of temperature, the daily mean temperature was calculated for the area where the animal had been present during the first three days of the analysis period and thus before the onset of migration. For the area in which the deer could be found within that period the 95% probability contour was calculated using the dBBMM. The reference temperature for an individual deer was then always taken from that starting area before migration.

### 3.2.3. Data Limitations

Since the temporal resolution of the dataset is rather coarse (3 hour sampling interval) it is difficult or even impossible to extract information from the data about relocations that happen in a short time frame. For example resting and grazing periods cannot be reliably identified with a sampling interval of three hours. Especially grazing bouts, which usually last 10 - 200 minutes, as was described in Section 2.2.2, cannot be detected with the given GPS data. In addition, the low sampling rates lead to a decrease of accuracy in the movement patterns. However, the fine sampling interval of the activity data enables the detailed analysis of activity patterns. Yet, there might be inaccuracies in the GPS data due to the presence of mountains and vegetation cover in the study area, which may disturb satellite signals and lead to a deteriorated dilution of precision (DOP). The uncertainty even increases since not only validated but also unvalidated 3D fixes had to be used in the analysis. Moreover, the absence of 2D and 3D error estimates hinders the incorporation of inaccuracies into the analysis which again supports the decision of excluding 2D fixes.

The used swissTLM$^{3D}$ data set was updated in the year 2015. Hence, it can be expected that a majority of the ground cover classifications was accurate for the study period of this thesis. Yet, changes in ground cover within the study period are not incorporated. In the data of agriculturally used fields information about the cultured crops, seed and harvest time as well as seasonal variations are missing. As a consequence, it can only be observed when an animal might access such a field. but detailed conclusions about what makes the accessed area attractive cannot be drawn. Furthermore, the extraction of grasslands by using the NDVI and intersection with the swissTLM$^{3D}$ data may have led to imprecise results with no information on ground truth.

Unfortunately there was no information available on wildlife sanctuaries in the canton of Ticino. Yet, wildlife sanctuaries play an important role for wildlife animals in regions with high tourist activity, which is the case in certain regions of the study area (see section 3.1). For this reason, the influence of wildlife sanctuaries on red deer behaviour cannot be analysed and it remains unclear to what extent and at what times the sanctuaries are used.

# 4. Methodology

The computations were performed using the open source software R version 1.0.136 (R Development Core Team 2010).

## 4.1. Migration Pattern Classification

In order to classify the migration behaviour of the red deer individuals two approaches were chosen. One approach uses the net squared displacement (*NSD*) to measure the squared Euclidian distance between the starting point of an animal's path to each subsequently measured GPS fix (Bunnefeld et al. 2011). To avoid inconsistent sample sizes and to reduce the impact of one-time exploration behaviour, the mean NSD, also called mean squared displacement (*MSD*), per day was calculated. Compared to the NSD, MSD calculations result in smoother trajectories (Börger & Fryxell 2012, Singh et al. 2016). To determine the migration class of the MSD patterns of each red deer individual, the movement models of Bunnefeld et al. (2011) were then used (see Figure 8). Each of these models was fitted to the red deer MSD calculations. Depending on the model fit, the individuals received different Akaike Information Critera (AIC) weights and thus the best model for each individual could be selected, as was done by Bunnefeld et al. (2011). Generally, movement models have a higher fit to MSD trajectories than to NSD trajectories since daily movements get blurred and annual movement can be detected more easily in MSD trajectories (Singh et al. 2016). The square root of the MSD values then returned the estimated distances from the first location to every displacement location. In the next step, the migration pattern classification was adjusted manually by taking into account natural deer behaviour. For this, the difference between the mean displacement distance of the first and the mean displacement distance of the last day was subtracted. If the difference was smaller than 2.5 km and the individual was originally classified as mixed-migratory it was reclassified as being purely migratory. This threshold value was chosen according to Georgii & Schröder (1983) who argue that the average distance between summer and winter home range of red deer is 2.5 km. Moreover, if the maximum distance of all fixes did not exceed 5 km the individual was reclassified as a residential animal since Filli & Suter (2006) found a minimum migration distance of 5 km between seasonal home ranges.

The second approach is similar to the method which Patrick (2017) chose in his master thesis. In a first step, the minimum convex polygons (MCP) for the summer home ranges in July and August and the winter home range from January to February were calculated. If the two home ranges did not overlap the individuals were classified as migratory and otherwise as possibly stationary. In order to deal with possible bias, the classification was improved by a subsequent kernel density estimation (KDE) through which the distance of the core areas (50% KDE) could be measured. In regard to the comparability of the results between this and Patrick's (2017) thesis, $_{\text{ref}}$ was chosen as the smoothing function. If the maximum distance between the centre of the core areas exceeded 2500m the respective red deer individuals were classified as migrating animals. Animals with a distance below 2500 m between the centre of their core area were classified as residential, as can be seen in Figure 16 (Patrick 2017). The centroids were calculated by taking the mean location of the points of the 50% KDE. In the case of this work, however, the summer home range was defined to lie within the months of June and July due to the onset of the migration to the winter home ranges in August, which were found through the NSD analysis (see Appendix A.1.2). The net squared displacement values show rapid increases during April and May for deer h4, h5, h8, h9 and h12 in the period of 2014 - 2015. H4 and h8 are stags whereas h5, h9 and h12 are hinds. In the following year such increases occurred for deer h31 (male), h32 (male) and h33 (male) and again for deer h47 (female) as well as h50 (female) in the period of 2016 - 2017. Since most of the non-resident individuals showed this increase in NSD, it was assumed that the months April and May were times of starting and ongoing migration to the summer home ranges. On the other hand, in some cases (for example deer h9) the NSD values decreased again as early as late August and early October, which implies that migration to winter home ranges had already started by then. The winter home range was thus set to January and February as was done by Patrick (2017) (see Appendix A.1.2).

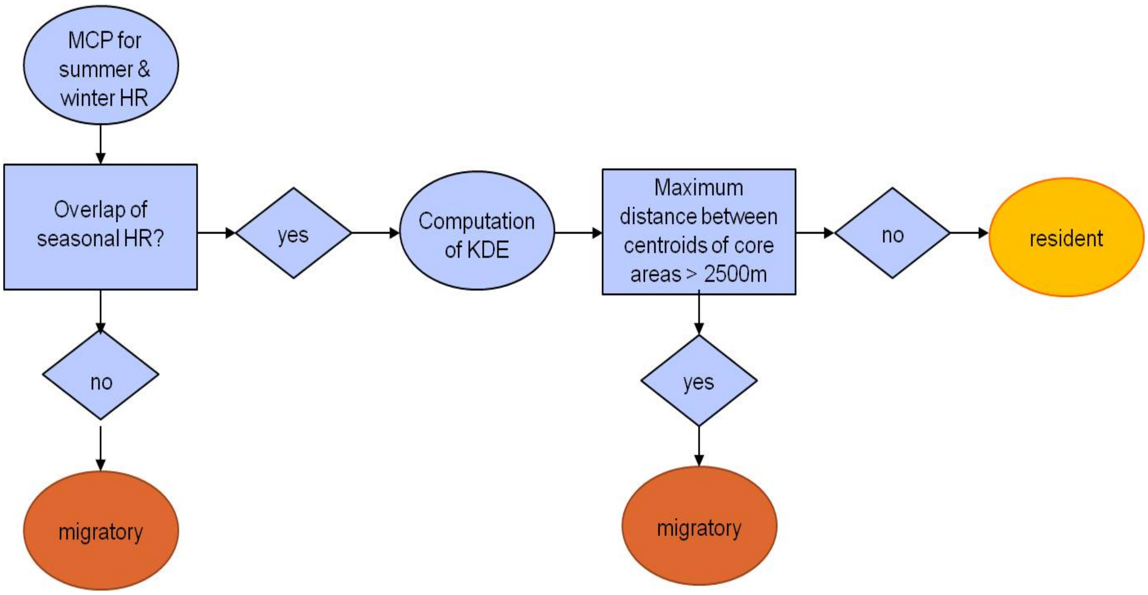

Figure 16: Schematic representation of Patrick's (2017) methodology of migration classification. The term home range is abbreviated as HR.

To analyse to what degree temperature changes are able to explain movement patterns, linear regression models were applied to temperature and NSD values as well as temperature and elevation data of the respective deer.

## 4.2. Home Range Size Analysis

As was described in Section 2.1.3, migrating animals have a summer and a winter home range which do not only lie in different locations but which can also vary in size. And even though residual individuals stay within a specific range all year round the sex, age and season might have an influence on the home range size as well. According to Burt (1943) what is not part of the home range is the migratory route between summer and winter home ranges. Hence, only the summer and winter months (same as in Section 4.1) were chosen for analysis where red deer were least likely to migrate back and forth to the summer and winter home range. The home range sizes of the red deer individuals were estimated using the MCP, KDE and dBBMM methods. For the KDE estimation of the home range size the 95% - KDE was chosen. The same applies to the dBBMM analysis where the 95% probability contour was chosen as the home range. Since no information about the mean location error estimate of the GPS device was available an error estimate of 20 m was assumed, following the findings and recommendations of Di Orio et al. (2003) and Frair et al. (2010). The parameters which were chosen to fit the dBBMM to the red deer tracks are a window size of 9, a margin of 3 and a raster size of 35 m. These parameters were chosen based on recommendations of Hengl (2006) and Kranstauber et al. (2012). In a next step, it was investigated whether significant differences between the winter and summer home ranges of the MCP, the KDE and the dBBMM methods could be found. This was done by using one way analysis of variance (ANOVA). The same method was used for the analysis of significant differences between residents and non-resident (nomadic, dispersal, migratory, mixed-migratory) individuals when using the different home range size estimation methods. Both of the variance analyses encompass the whole study duration from 2014 to 2017.

### 4.3. Temporal Activity Pattern

To analyse the activity in relation with time, the diurnality and crepuscularity index were computed as was done in Patrick's (2017) work. The values of the diurnality and crepuscularity index always lie between -1 and 1. In the diurnality index, negative values indicate nocturnal activities whereas positive values stand for diurnal activities. The diurnality index ($I_D$) is computed by taking the sum of activity during night ($A_N$) and day ($A_D$) as follows:

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

On the other hand, the crepuscularity index ($I_C$) is calculated by using the sum of twilight activity ($A_T$) in contrast to times of non-twilight:

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

In the crepusclarity index negative values stand for non-crepuscular activity and crepuscular activities get assigned positive values (Ensing et al. 2014). For the crepuscularity index the dawn and dusk times got defined as the twilight hours which lie between the start of nautical twilight and sunrise respectively sunset and the end of nautical twilight. In this case, the start of nautical twilight is the moment when the sun is located 12° under the horizon. However, contrary to the work of Patrick (2017), the values of the x-axis of the activity sensor were used instead of locomotion speed. The reason as for why only the x-axis values were used for the analysis will be given further below. The measured activity values were classified into the three activity types "fast locomotion", "feeding / slow locomotion" and "resting". The threshold values for this classification scheme were set according to the findings of Löttker et al. (2009). Feeding and slow locomotion constitute a single category since Georgii & Schröder (1978) argue that the two behavioural types are closely linked to each other. Moreover, Löttker et al. (2009) were not able to find a significant difference between slow locomotion and feeding in the activity values. Due to the fact that the percentage of accurately assigned values was highest for the x-values (horizontal sensor), Löttker et al. (2009) recommend to only use the x-values for the assignment of activity types. The threshold value which they found for the classification of resting behaviour in the horizontal sensor is $\leq 15$. Feeding / slow locomotion corresponded to x-values of $> 15$ and $\leq 189$. Values $> 189$ were assigned to fast locomotion. According to these findings only the x-axis values were used in this work as well. The data was then split into summer (June and July) and winter (January and February), since those are the months where daily activity patterns are assumed to be most constant due to missing influence of migration and rut. Furthermore, the hunting season (September, November and December) was analysed as well to be able to detect changes of behaviour triggered by human activity.

## 4.4. Resource Use

The resource use analysis was conducted in three steps. First, the utilization distribution between every GPS fix and its consecutive fix was calculated using the dBBMM method. Thus, the utilization distribution of the red deer between two consecutive GPS fixed could be computed. For these computations the same dBBMM parameters were chosen as in Section 4.2 in the home range size estimation. The results were raster layers, where each raster value implied the probability of use between two consecutive GPS fixes. For the following procedures, only rasters were selected, where the probability of occurrence of a red deer was higher than 5%. The remaining raster fields then constitute the area within which a deer can be found with a probability of 95%. In order to minimize the data volume, these raster fields were converted into points, whereas each point represents the centre of a raster. In the second step, the resource use within these stepwise 95% probability areas was analysed by counting all raster points between two consecutive GPS-locations. After that the raster points which lie within a certain resource type were counted. The following land cover types were used for this analysis: forest, grassland, agriculturally used land, vineyards, urban areas and game reserves. Using this method, the percentage of each used landcover type or resource between two consecutive GPS fixes could be calculated. The percentage of the respective resource type uses were then aggregated by season (summer: June / July, winter: January / February, hunting: September / November / December), time interval as well as resident and non-resident (nomadic, dispersal, migration and mixed-migration) animals or sex respectively, so that the resource use over the course of a day could be analysed. The third step consisted of calculating the Jacobs index in order to analyse the preference of a certain resource, respectively land cover type, in relation to its relative occurrence within the entire study area. To do so, the expected (exp) value of each resource type was calculated. This was done by calculating the area of a resource type within the MCP of the entire data set and dividing this value by the total area of the entire MCP. The exp value then represents the contribution of a resource to the entire study area, which was derived from the calculation of the MCP using the GPS fixes of all individuals, covered by all the investigated red deer individuals. To compute the observed (*obs*) values, the total number of raster points within each 95% dBBMM step contour was calculated (*tot*). Next, the raster points which lie within a certain resource type within the 95% probability area of two consecutive GPS fixes were counted (*resource point*). The observed values were then calculated by dividing the *tot* by the *resource point*. The Jacobs index was then computed using Formula 2.

Since no ground cover data was available for Italy, the individuals h16, h22, h31, h44 and h50 were not included in the analysis because they crossed the Swiss border to Italy.

## 4.5. Resource Use and Activity

In this step it was analysed which activity types occurred within each resource type. Since GPS fixes were only available for three hour intervals and coordinate information was missing in the activity data, the GPS and activity data sets were connected via the timestamps, which were stored in both data sets. Each activity value was assigned to the GPS fix which was taken most recently before the activity was measured. In other words, each GPS fix received activity values which were taken at the same moment or within the time stamp before the next location point was measured. For the analysis the same behavioural types were used as in Chapter 5 where the temporal activity patterns were studied. Thus, there are only two hinds for the time period of 2015 - 2016, one of them with a resident migration pattern and the other one conducting a dispersal (non-resident) pattern. The resources agricultural fields, forest, grasslands, urban areas and vineyards add up to 100% since other soil cover types were excluded from the study because it is assumed that red deer can only be rarely found on the remaining ground cover types such as glaciers, water bodies and industrial areas.

# 5. Results and Discussion

## 5.1. Migration Pattern Classification

### 5.1.1. Migration Pattern

The results of the migration pattern classifications are shown in Table 3. When an individual was reclassified from a resident to a non-resident individual or the other way round by the NSD migration classification, the respective classification is marked red. If the migratory pattern of an individual was reclassified to one of the finer migration differentiations of Bunnefeld et al. (2011) (dispersal, migratory, mixed-migratory and nomadic) the classification was marked in a brown colour.

When migration patterns were solely classified with the MCP method four animals were declared to have overlapping summer and winter home ranges and are thus classified as residential animals during the sampling period 2014 - 2015. On the other hand, eight animals were classified as migratory individuals. With the incorporation of the distance between the core areas of the KDE, h15 was reclassified in its migration pattern from resident to a migratory. The longest distance between the centroids of the seasonal home ranges holds h16 (male) with 23'694 m. H18 (female) was classified as a resident animal with the shortest distance between seasonal core area centroids of 1067 m. The classification of the migration patterns with the NSD method resulted in two resident, five migratory one mixed-migratory and four dispersal animals. Using this method, h18 got re-classified as a mixed-migratory animal. The maximal distance was travelled by h16 (male) with 29'982 m which also has the highest distance between the seasonal KDE centroids. The lowest maximum travelled distance is 3'015 m which belongs to the as stationary classified h1. The smallest difference between mean summer and winter elevation can be found in h14 (female) with only 51 m. On the other hand, h5 (female) has the largest difference with 1332 m.

In the sampling period of 2015 - 2016 a total of 14 animals was analysed, with ten resident and four migratory animals according to the MCP migration pattern classification. With the second criterion of the distance between the 50% KDE centroids h19, h23, h24, h27 and h29 got reclassified as migratory animals, reducing the number of resident animals to five. The largest distance between the center KDE core areas is 11'093 by h31 (male). The maximal distance is hence approximately 12.6 km shorter than in the period of 2014 - 2015. The NSD migration pattern classification resulted in four resident, five migratory, one mixed-migratory, three dispersal animals and one nomadic animal. H29 (female) was reclassified from a migratory to a resident animal, h32 (male) was reclassified from a resident to a dispersal animal and h35 (male) was classified as a mixed-migratory animal instead of a resident animal. The highest maximum travel distance was reached by h33 (male) with 12'767 m. This value is also lower than in the period of 2014 -2015 with the furthest travelled distance of 29'982 m. The lowest maximum travel distance in this time period was travelled by h20 (female) with 2639 m. This value is lower than in 2014 - 2015. H28 has the smallest difference between mean winter and summer elevation with 72 m whereas h33 has the largest difference with 1241 m.

Five deer were classified as migratory animals and five as residents during 2016 - 2017 out of a total of 10 animals with the pure MCP migration pattern classification. The integration of the KDE distance criterion resulted in h41 (female) and h47 (female) being reclassified from a resident to a migratory animals. The longest distance between the KDE centroids is 15'036 m for h48 (female). This lies between the values of 2014 - 2015 and 2015 - 2016. The migration pattern classification with the NSD resulted in three resident animals, four migratory, two mixed migratory and one dispersal animal. The largest travel distance in this case is 16'001 m which was travelled by h48 (female). This value is lower than in 2014 - 2015 but higher than in 2015 - 2016. Deer 39 (male) reached the lowest maximum travel distance with 2270 m, which is higher than the lowest distance reached in 2014 - 2015. The biggest hight difference can be found in h44 (female) with 928 m. H49 (male) has the lowest difference between summer and winter mean elevation of 36 m.

All of the animals which were classified as resident by the NSD migration pattern classification method, have their home range in the mountain valley ranging from Mesocco to Bellinzona (Mesolcina Valley) as well as between Serravalle and Biasca and are living in the proximity of or even within villages (see Appendix A.1.1).

Two sample t-tests for all three time periods revealed that there is no significant difference of the maximum migration distance between stags and hinds which were classified as non-resident and thus are either migratory, mixed-migratory, dispersal or nomadic. In all cases, the mean distance of hinds is smaller than that of the stags. The mean maximum travelled distance of stags is 20.9 km and 11 km for hinds in the period 2014 - 2015 with a p-value of 0.09. The stags of the year 2015 - 2016 have a mean distance of 9.5 km and the hinds reach a value of approximately 7.2 km. In this case, the p-value is 0.19. During the last year of sampling the p-value was 0.4 with stags having the mean maximum NSD-value of 13.7 km and hinds 11 km. Overall the males of all three study years have a higher range of maximum mean travel distance than hinds.

In Figure 17 boxplots illustrate the mean travel distance per migration pattern. In all time periods the mean of travelled distance of resident animals is low and the maximum travelled distance does not exceed 5 km. The overall variance of travelled distance in resident animals is also small. Migratory animals have a higher variance and the maximum distance does not fall under 5 km.

Table 3: Results of the classification (*class.*) of the migration patterns of all 38 animals. The classes of the NSD classification are the same as were defined by Bunnefeld et al. (2011). Maximum travelled distance (*Max. distance [m]*) was derived from the squared distances of the NSD computation.

| Year | id | sex | MCP migration pattern class. | Distance between KDE Centroids | MCP and KDE migration pattern | NSD migration pattern class. | Max. distance [m] | Summer mean elevation [m.a.s.l] | Winter mean elevation [m.a.s.l] |
|---|---|---|---|---|---|---|---|---|---|
| **2014 - 2015** | **h1** | f | resident | 1278 | resident | resident | 3015 | 1224 | 970 |
| | **h4** | m | migratory | 21945 | migratory | migratory | 23015 | 1766 | 614 |
| | **h5** | f | migratory | 22373 | migratory | migratory | 24337 | 1976 | 644 |
| | **h8** | m | migratory | 17074 | migratory | migratory | 22710 | 1955 | 757 |
| | **h9** | f | migratory | 6276 | migratory | migratory | 7477 | 758 | 470 |
| | **h11** | m | migratory | 4865 | migratory | **dispersal** | 6450 | 286 | 511 |
| | **h12** | f | migratory | 8911 | migratory | migratory | 9913 | 1468 | 342 |
| | **h13** | m | migratory | 6045 | migratory | dispersal | 22242 | 1982 | 960 |
| | **h14** | f | resident | 1278 | migratory | **resident** | 3747 | 448 | 499 |
| | **h15** | f | migratory | 6768 | migratory | **dispersal** | 8037 | 1289 | 475 |
| | **h16** | m | migratory | 23694 | migratory | **dispersal** | 29982 | 1790 | 460 |
| | **h18** | f | resident | 1067 | resident | **mixed-migratory** | 5168 | 1326 | 1327 |
| **2015 - 2016** | **h19** | f | resident | 4292 | migratory | **dispersal** | 4833 | 1309 | 542 |
| | **h20** | f | resident | 1250 | resident | resident | 2639 | 1574 | 1342 |
| | **h22** | f | migratory | 8685 | migratory | migratory | 10237 | 1705 | 674 |
| | **h23** | f | resident | 7138 | migratory | **nomadic** | 8470 | 1359 | 870 |
| | **h24** | f | resident | 5637 | migratory | migratory | 5089 | 1690 | 822 |
| | **h25** | f | resident | 1618 | resident | resident | 2863 | 417 | 1049 |
| | **h26** | m | migratory | 1919 | migratory | **dispersal** | 6724 | 995 | 559 |
| | **h27** | m | resident | 8550 | migratory | migratory | 9638 | 1321 | 690 |
| | **h28** | m | resident | 1666 | resident | resident | 3394 | 673 | 745 |
| | **h29** | f | resident | 5503 | migratory | **resident** | 3687 | 1378 | 944 |
| | **h31** | m | migratory | 11093 | migratory | migratory | 12267 | 1856 | 563 |
| | **h32** | m | resident | 141 | resident | **dispersal** | 6972 | 1175 | 948 |
| | **h33** | m | migratory | 8463 | migratory | migratory | 12767 | 1774 | 533 |
| | **h35** | m | resident | 1122 | resident | **mixed-migratory** | 8718 | 951 | 617 |
| **2016 - 2017** | **h38** | m | migratory | 8827 | migratory | **mixed-migratory** | 13577 | 1794 | 1052 |
| | **h39** | m | resident | 676 | resident | resident | 2270 | 752 | 660 |
| | **h40** | m | resident | 2114 | resident | resident | 3282 | 1501 | 1304 |
| | **h41** | f | resident | 5823 | migratory | migratory | 6970 | 1781 | 1489 |
| | **h42** | m | migratory | 5070 | migratory | **dispersal** | 13732 | 1874 | 1381 |
| | **h43** | f | resident | 2767 | migratory | **resident** | 3444 | 379 | 720 |
| | **h44** | f | migratory | 10428 | migratory | **mixed-migratory** | 14466 | 1570 | 642 |
| | **h47** | f | resident | 7074 | migratory | migratory | 7724 | 1581 | 697 |
| | **h48** | f | migratory | 15036 | migratory | migratory | 16001 | 1613 | 1160 |
| | **h49** | m | resident | 122 | resident | resident | 2969 | 999 | 963 |
| | **h50** | f | migratory | 6869 | migratory | migratory | 10163 | 1771 | 1224 |

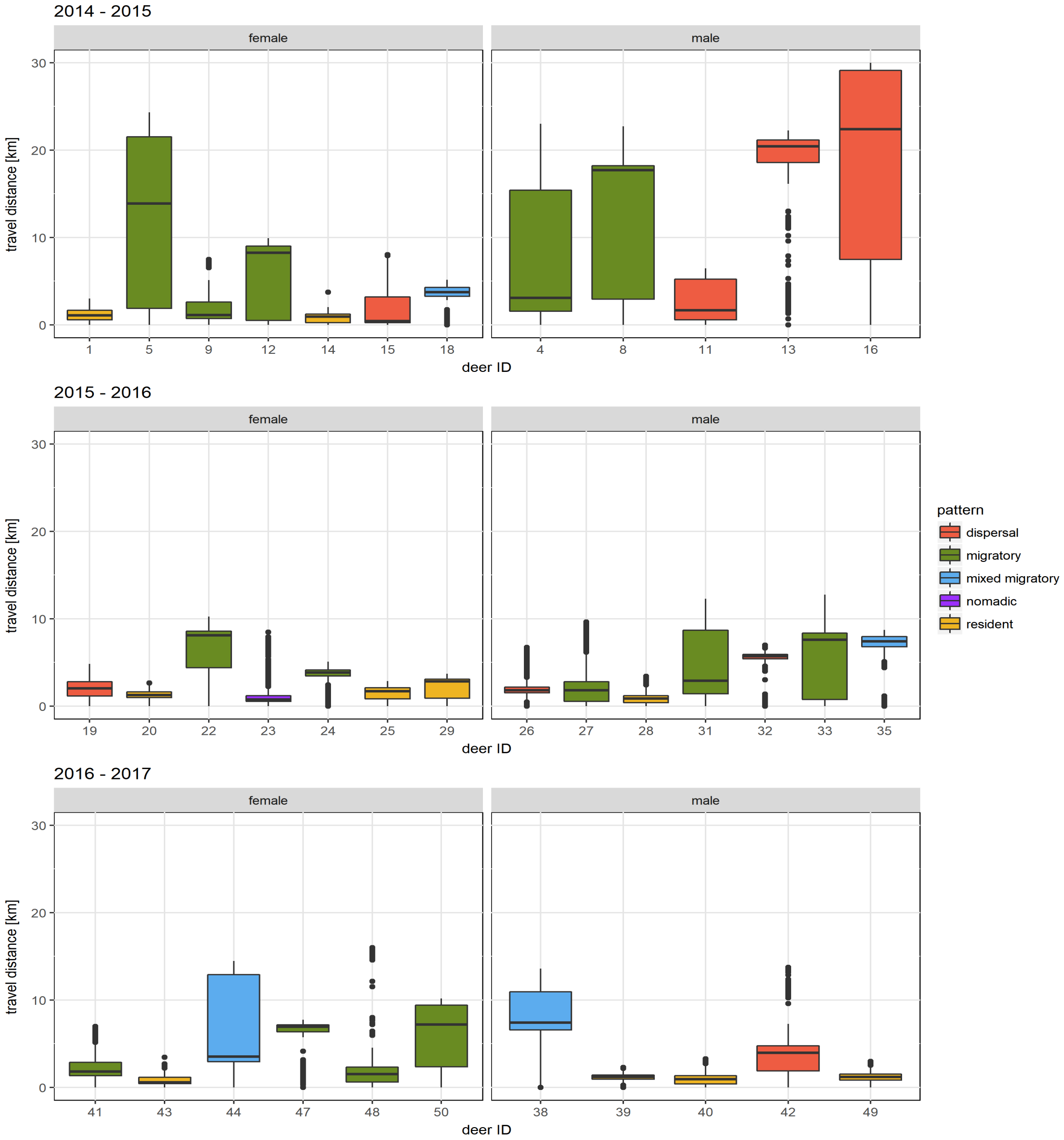

Figure 17: Mean travelled distance sorted by migration pattern (as defined by Bunnefeld et al. (2011)) and sex.

The monthly mean elevations of each individual (Figure 18) show that the difference of mean elevation between summer and winter periods is higher in dispersal and migratory animals in the period of 2014 - 2015. The resident animals (h1 and h14) did not undertake such a distinct change in elevation as did the dispersal and migratory animals of the respective year. Similar to the elevation pattern of the resident deer is the pattern of the mixed migratory deer (h18). The dispersal and mixed migratory animals mostly display a pattern that is similar to a double sigmoid curve, meaning that they return to the elevation from which they started. Only h9 shows a pattern which is unlike the other migratory animals. Contrary to this observation the resident animals (h20, h25 and h29) of the period 2015 - 2016 show a higher variance of elevation except for h28. The dispersal and migratory animals, however, also show the double sigmoid shaped elevation migration pattern, although the maximum elevation is not as high as in the period of 2014 - 2015. In the period of 2016 - 2017 the migratoy and dispersal animals show a distinct change in elevation again. Other than in the previous years the mixed migratory individuals migrate over larger elevation differences. In fact, the two mixed migratory animals (h38 and h44) show a very similar pattern. And while the two residential animals 40 and 49 exhibit quite distinctive changes in elevation, deer 30 seems also to be stationary from the perspective of height differences. Overall the migratory and dispersal animals of the period 2014 -2015 reached the highest average monthly elevation, whereas no animal of the other two time periods reached an average elevation of over 2000 m.a.s.l.

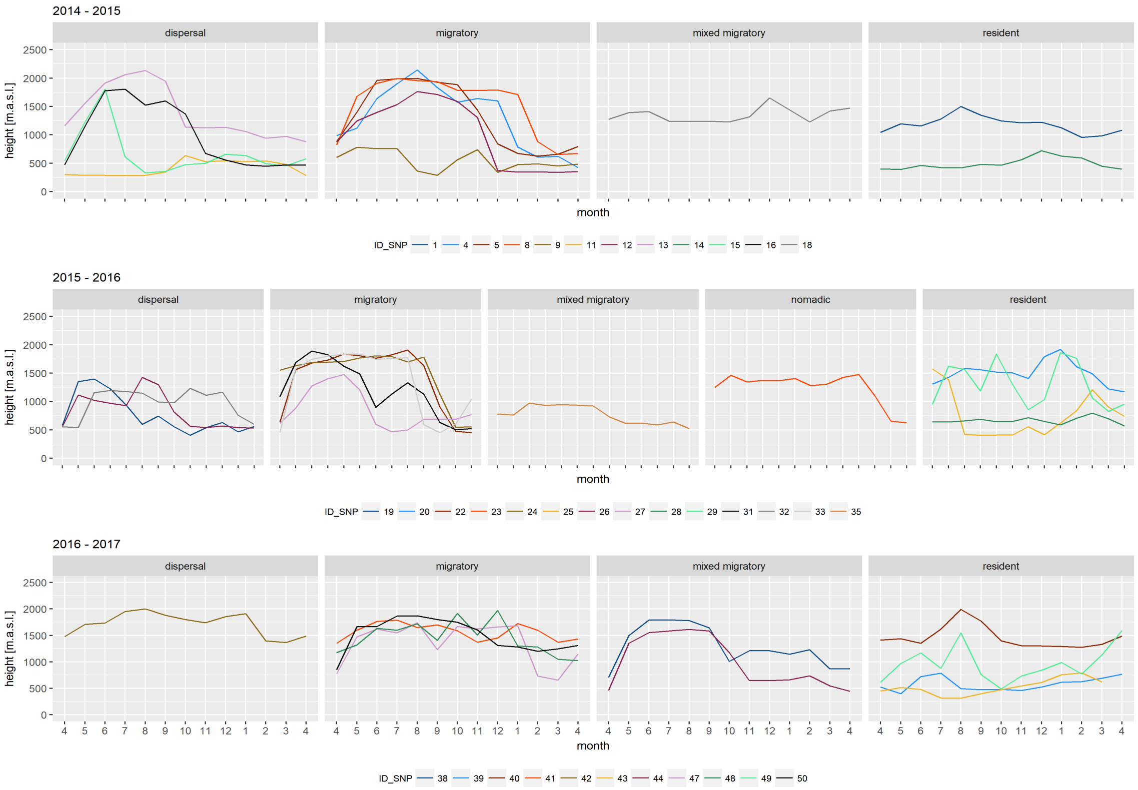

Figure 18: Mean monthly elevation sorted by study period and migration pattern

### 5.1.2. Migration Pattern and Temperature

Additional calculations of the travel distance in combination with temperature data show that a temperature change cannot always explain the pattern of the NSD values. Table 4 shows the p and the $R^2$

values of regression analysis between the temperature and the NSD curve of each individual. In the period of 2014 -2015 all of the p-values are much smaller than the significance level of 0.05 and thus it can be assumed that there is a relationship between the temperature and the NSD. However, the $R^2$-values are rather low except for the individuals h4, h5, h12 and h11 where over 50% of the NSD curve could be explained by temperature changes. This can also be seen when looking at Figure A.3 which shows the temperature curve in relation to the travelled distance. The mean $R^2$ is 0.35 and thus yields the highest value of the three studied time periods. The NSD patterns of the red deer individuals in 2015 - 2016 can be even less explained by temperature changes. For h19, h20, h26, h28, and h32 the null hypothesis cannot be rejected and it can be assumed that no relation between the temperature and the NSD could be found. Only h27 reached an $R^2$ value of over 50%. On average only 15% of the NSD variation can be explained by temperature alone. In the period of 2016 - 2017 only h39 reached a p-value higher than 0.05 which means that its NSD pattern cannot be explained by temperature changes. For deer 44 and 50 temperature explains over 50% of the NSD variance. However, on average only 25% of the total variance can be explained with temperature changes.

Table 4: Result of regression analysis between mean daily temperature and mean daily NSD. "***" depict p-values which are < 0.001.

| 2014 - 2015 | | | 2015 - 2016 | | | 2016 - 2017 | | |
|---|---|---|---|---|---|---|---|---|
| **id** | **p-value** | **R squared** | **id** | **p-value** | **R squared** | **id** | **p-value** | **R squared** |
| h1 | *** | 0.26 | h19 | 0.07 | 0.01 | h38 | *** | 0.21 |
| h4 | *** | 0.66 | h20 | 0.89 | 0.00 | h39 | 0.91 | 0.00 |
| h5 | *** | 0.71 | h22 | *** | 0.17 | h40 | *** | 0.45 |
| h8 | *** | 0.14 | h23 | *** | 0.15 | h41 | *** | 0.09 |
| h9 | *** | 0.27 | h24 | *** | 0.14 | h42 | 0.024 | 0.01 |
| h11 | *** | 0.74 | h25 | *** | 0.10 | h43 | 0.92 | 0.00 |
| h12 | *** | 0.57 | h26 | 0.056 | 0.01 | h44 | *** | 0.56 |
| h13 | *** | 0.06 | h27 | *** | 0.54 | h47 | *** | 0.07 |
| h14 | *** | 0.14 | h28 | 0.348 | 0.00 | h48 | *** | 0.49 |
| h15 | *** | 0.09 | h29 | *** | 0.03 | h49 | *** | 0.07 |
| h16 | *** | 0.50 | h31 | *** | 0.60 | h50 | *** | 0.53 |
| h18 | 0.008 | 0.02 | h32 | 0.64 | 0.00 | | | |
| | | | h33 | *** | 0.31 | | | |
| | | | h35 | *** | 0.05 | | | |
| | | mean: 0.35 | | | mean: 0.15 | | | mean: 0.23 |
| | | max: 0.74 | | | max: 0.6 | | | max: 0.56 |
| | | min: 0.02 | | | min: 0.0 | | | min: 0.0 |

Table 5 shows the p and $R^2$-values of the regression analysis between the temperature and elevation data of each individual observed animal. In the period of 2014 - 2015 the significance level of 0.05 is smaller than all of the p-values, which means that all the elevation variances can partly be explained by temperature. However, $R^2$ is fairly small for deer h9, h15 and h18, making it questionable whether the elevation variances really can be described by temperature. The overall mean of explainable elevation variation during this period is 33%, with the highest percentage of h13 with 66%, which is both lower than the NSD variation which can be explained through temperature in the same year. The mean and the maximum $R^2$-values in the period of 2014 - 2015 are both higher than the values from 2015 - 2016. However, the elevation variation of h28, h29 and h32 cannot be explained by temperature data. So, for deer 32 the temperature changes cannot explain its movement pattern. Overall the $R^2$-values of 2016 - 2017 are rather low. The maximum $R^2$-value has h44 as was the case in the temperature-NSD analysis. Deer 47 has a p-value of approximately 0.1 by which the null hypothesis cannot be rejected and it can be assumed that the temperature had no influence on the migration pattern of this individual.

Table 5: Result of regression analysis between mean daily temperature and mean daily elevation. "***" depict p-values which are < 0.001.

| 2014 - 2015 | | | 2015 - 2016 | | | 2016 - 2017 | | |
|---|---|---|---|---|---|---|---|---|
| **id** | **p-value** | **R squared** | **id** | **p-value** | **R squared** | **id** | **p-value** | **R squared** |
| h1 | *** | 0.22 | h19 | *** | 0.49 | h38 | *** | 0.35 |
| h4 | *** | 0.37 | h20 | 0.11 | 0.01 | h39 | 0.005 | 0.02 |
| h5 | *** | 0.64 | h22 | *** | 0.10 | h40 | *** | 0.40 |
| h8 | *** | 0.18 | h23 | *** | 0.07 | h41 | *** | 0.10 |
| h8 | *** | 0.04 | h24 | *** | 0.13 | h42 | *** | 0.10 |
| h11 | *** | 0.31 | h25 | *** | 0.06 | h43 | *** | 0.52 |
| h12 | *** | 0.61 | h26 | *** | 0.21 | h44 | *** | 0.53 |
| h13 | *** | 0.66 | h27 | *** | 0.52 | h47 | 0.12 | 0.01 |
| h14 | *** | 0.20 | h28 | 0.22 | 0.00 | h48 | *** | 0.04 |
| h15 | *** | 0.05 | h29 | 0.06 | 0.01 | h49 | *** | 0.08 |
| h16 | *** | 0.62 | h31 | *** | 0.38 | h50 | *** | 0.27 |
| h18 | 0.008 | 0.05 | h32 | 0.18 | 0.00 | | | |
| | | | h33 | *** | 0.29 | | | |
| | | | h35 | *** | 0.51 | | | |
| | | mean: 0.33 | | | mean: 0.20 | | | mean: 0.22 |
| | | max: 0.66 | | | max: 0.52 | | | max: 0.53 |
| | | min: 0.04 | | | min: 0.0 | | | min: 0.01 |

Another factor which might have an influence on the migration pattern are the hunting seasons. Visual inspection of the travelled distance and temperature graphs in Appendix 1.2 suggests that the decrease of the distance values stands in connection with hunting seasons for deer h5, h12, h26, h22, h38, h42 and h50 since their travelled distance pattern changes shortly before, during or after hunting periods.

### 5.1.3. Discussion

The three used methods to analyse and describe migration patterns of red deer are all still commonly used nowadays. Yet, especially the use of the MCP method is questionable since it does not take the underlying structure of the poits (such as density or temporal order) into account and because it is prone to errors caused by outliers (Nilsen et al. 2008, Beier & McCullough 1990). By using the second criterion of the distance between core areas of the KDEs the first movement pattern classification of the MCP can be adjusted without having to necessarily inspect the data visually and the risk of bias through outliers gets reduced (Kolodzinski et al. 2010). However, since the KDE does not regard temporal autocorrelation and a bias can be introduced by the unfavourable choice of the time periods in which animals are expected to be in their summer respectively winter home range, it is advised to use several methods for migration pattern classification (Cagnacci et al. 2016). For example if all points of August are assumed to lie within the summer home range, a bias occurs if the animal had already started it's migration to the winter home range at that time of the year. As a consequence, a priori knowledge is required in order to derive meaningful information about migration patterns.

In the study period of 2014 - 2016 one individual which was classified as a resident animal was reclassified as migratory animals when the KDE was included into the computation. In the study period of 2015 - 2016 this accounted to five individuals and also occurred to the individuals h41 and h47 in the study period 2016 - 2017, suggesting that migratory behaviour is more difficult to detect for the MCP method. This might account to the fact that home ranges are often overestimated with the MCP method and hence it might be more likely for them to overlap or to be too close to each other in order to be classified as migratory when compared to other home range analysis tools (Beier & McCullough 1990). The final migration pattern classification with the NSD shows that only nine out of 36 animals are resident animals, suggesting that it is more common for red deer to show some sort of migratory behaviour. Cagnacci et al. (2016) states that it is more popular for animals to migrate partially than completely with two distinct summer and winter home ranges. 13 out of the 27 deer which were not classified as resident animals indeed do show dispersal, mixed-migratory and nomadic behaviour instead of purely migratory behaviour. This underlines Cagnacci's (2016) statement that migration patterns which are not resident or purely migratory are common as well. All in all, three animals (h18, h32 and h35) were reclassified from resident to non-resident animals. For h29 this happened the other way round and it was reclassified as a resident animal instead of migratory by the NSD method. Interestingly, there is quite a distinct difference between mean summer and winter elevation (434 m). This corresponds to a change of the alpine altitude from high montane (*Hochmontan*) in summer to upper montane (*Obermontan*) in winter according to Frehner et al. (2005). Such a distinctive change of altitude between the summer and winter home range can also be observed for 21 other individuals whereas only h25 and h29 are classified as resident by the NSD method. However, Figure 17 shows that not only the individuals h25 and h29 of the resident animals exhibit high changes in elevation but also the individuals h20, h44 and h49. Yet, there is no clear pattern of the elevation change as is the case in migratory animals where seasonal structures are visible. The migration from lower to higher altitudes or the other way round without horizontal relocation constitute a form of migration as well and should not be neglected in migration pattern analysis especially in a mountainous region as in the study area of this work. In such cases, elevation data can serve to verify the migration classifications in an additional step. Like this, the mentioned individuals might be identified as non-resident animals even if the NSD method classified them as residents.

In general, the summer mean elevation is higher than the winter elevation which can be seen in Figure 18 and coincides with the description of the annual migration cycle of Georgii & Schröder (1983). The individuals h4, h5 and h8 show very clear migrations with big distances between the northern region of the study area to the south. The summer home ranges are chosen in the cooler north whereas they travelled to the warmer south for the winter months. Resident individuals generally tend to stay in lower elevation all year round than non-resident animals. However, h14, h25 and h28 exhibit an inversed migration pattern with increased mean elevation during winter compared to summer. The difference of elevation is especially high for h25 where the winter home range is located approximately 632 m higher in elevation than the summer home range. Figure 14 and A.1 show that h14 and h28 have their home range in the very south of the study area around Roveredo, Bellinzona and Giubiasco. H25 on the other hand is located in the very north between Biasca and Serravalle. All three animals remain within or close to populated areas. It got assumed that these animals might seek out hollows in the populated valleys where temperatures are colder during summer[6]. Upon close inspection of the

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[6] Personal communication with Flurin Filli (Swiss National Park) and Hannes Jenny (AJFGR), 04.01.2017

Figures A.3 and A.5 this theory can most probably be rejected due to the collar temperature remaining similar to the temperature which was calculated for the starting area. If the theory was true, the collar temperature of the respective deer should fall below the reference temperature. Another explanation for this uncommon behaviour might be that these individualls especially target the nutritious agricultural fields during summer times and then retreat back into higher altitudes after the crops are harvested as was described in section 1.1 and 2.1.5. In addition, h9 does not exhibit such a strong migration in regard to elevation as is the case for the other migratory animals as can be seen in Figure 17 and A.1.1. It has its home range in the south of the study area around Claro and Roveredo. However, no obvious reason can be found as for why h9 exhibits a smaller change in elevation than for example h5 and h8 who have their summer home ranges in a similar area. On the other hand, it shows that red deer do not always stick to population patterns but also show individual habits and preferences which cannot be explained on population level.

The migration pattern of red deer in the study area of this thesis cannot be explained solely through temperature as is shown in Table 4. and 5. This indicates that the cause for migration is multi layered and not just caused by a single factor. For the individuals h4, h5, h12, h26, h27, h31, h48 and h50 the hunting seasons could be a direct cause for the start of migration since the timing of the migration coincides with the hunting seasons (see Figures A3, A5 and A7). As was described by Jarnemo (2008), red deer also follow low snow cover levels when migration between different elevations. Another factor which might trigger migration is the growth of fresh vegetation (Mysterud et al. 2011). However, Figure 16 shows that the travel distance as well as its variance in the period of 2015 - 2016 was distinctively lower than in the other study periods of the migratory animals. This might be explained by the increased monthly mean temperature during summer where it was 3° warmer than in the period of 2014 - 2015.

For the comparison with the results of Patrick (2017) it was noticed that instead of the described months for summer (July and August) and winter (January and February) Patrick (2017) used the months June, July and August as well as January, February and March. When these dates were corrected to the ones which were described in his thesis, only two individuals (12.5%) were classified as resident after the inclusion of the KDE criterion, which stands in contrast to the 28% of resident deer within the study area of this thesis. Moreover, the mean distance between the KDE centroids in Patrick's (2017) work changed to 8070 m. This values is higher than the values which was computed for the deer in the region of the Mesolcina, which reach a mean distance between the KDE centroids of approximately 6964 m. In addition, Patrick's (2017) migratory animals generally migrated to higher grounds in summer and the winter home ranges also remained in higher altitudes. This difference can partially be explained by the fact that the lower Engadin valley generally lies in a higher altitude than in the region around the Mesolcina where for example Bellinzona has only an altitude of 230 m.a.s.l. As a consequence deer from this study can travel to lower altitudes than those of the lower Engadine valley. However the animals of both studies migrate to higher altitudes during the summer months.

## 5.2. Home Range Size Analysis

### 5.2.1. Home Range Size Estimation

During the period of 2014 - 2015 the largest estimated MCP summer home range size was found for h13 (male) with 11.81 km$^2$ whereas h8 (male) has the larges MCP winter home range with 30.31 km$^2$ (see Table 6). When the home range size was estimated with the KDE method, h8 had the largest summer and winter home ranges with 2.68 km$^2$ respectively 3.02 km$^2$. The dBBMM method again resulted in h8 having the biggest summer (5.94 km$^2$) and winter (5.73 km$^2$) home range. On the other hand, the smallest MCP and KDE home ranges are occupied by h9 (female, summer) with 0.18 km$^2$ respectively 0.34 km$^2$ and h12 (female, winter) with 0.51 km$^2$ and 0.65 km$^2$. H9 has the smallest summer dBBMM home range (0.43 km$^2$). The smallest dBBMM winter home range was estimated for h18 (female) with 0.4 km$^2$. The largest MCP summer home range for the period 2015 - 2016 was found for the individual h27 (male) with 13.26 km$^2$. The largest winter home range on the other hand, was inhabited by h22 (female) with 17.13 km$^2$. H19 (female) and h22 have the largest summer respectively winter KDE home range. With a total area of 5.2 km$^2$ deer h19 also has the largest dBBMM summer home range. The biggest dBBMM winter home range is occupied by h23 (female) with 6.9 km$^2$. In contrast, h26 (male) has the smallest home ranges for both MCP and KDE summer and winter home range and the dBBMM summer home range. In the study period of 2016 - 2017 h48 (female) had a MCP summer home range of the size of 54.98 km$^2$ and thus by far the largest MCP home range of all animals during the three study periods. H47 (female) had the largest MCP winter home range with 14.33 km$^2$. H41 (female) and h47 also had the largest summer and winter KDE with 3.19 km$^2$ and 3.44 km$^2$. With 7.04 km$^2$ h42 (male) has the biggest dBBMM summer home range. The biggest dBBMM winter home range can be assigned to h49 (male) with 5.73 km$^2$. The smallest home range for all methods and seasons during this time period has h38 (male). Generally the mean home range size estimation for the summer period is higher than the winter home range size estimation except for the KDE computation.

### 5.2.2. Home Range Variance Analysis

Looking at the mean of the winter home ranges of the MCP, KDE and dBBMM computations (Table 6) it gets visible that the mean size of the MCP winter home ranges (4.55 km$^2$) is higher than those of the KDE (1.85 km$^2$) and dBBMM (2.2 km$^2$) calculations. The MCP winter estimations also have a higher standard deviation (6.09 km$^2$). Moreover, with a p-value of 0.003 there is a significant difference between the various winter home range size estimates. During the summer months the mean home range size of the MCP was also higher than the mean of the KDE and dBBMM estimates. The p-value of 0.01 denotes a significant difference between the mean home range sizes of the various seasons. Upon closer inspection of pairwise differences the significant difference can be found between the mean KDE and MCP home range size estimates with a p-value of 0.02. However, there is no significant difference between the MCP and dBBMM as well as dBBMM and KDE home range size estimates. The largest mean of the summer home range estimate was reached by the MCP method with a size of approximately 5.08 km$^2$. The KDE computed the smallest mean home range size (1.56 km$^2$). The MSD method also resulted in the highest standard deviations (9.19 km$^2$), followed by the dBBMM (1.69 km$^2$) and the KDE (0.85 km$^2$). The difference between the summer home range sizes of the various study periods is significant with a p-value of 0.01. However, as was the case for the winter estimates, the significant difference only exists between the KDE and MCP home range sizes. No significant difference could be found between the dBBMM and MCP as well as the dBBMM and KDE home ranges.

Table 6: Home range sizes in km$^2$ computed by the MCP, KDE and dBBMM methods.

| Year | id | MCP summer | MCP winter | KDE summer | KDE winter | dBBMM summer | dBBMM winter | pattern |
|---|---|---|---|---|---|---|---|---|
| 2014 - 2015 | h1 | 1.46 | 1.93 | 1.37 | 1.52 | 1.61 | 1.31 | resident |
| | h4 | 7.31 | 1.21 | 1.04 | 1.08 | 1.28 | 1.53 | migratory |
| | h5 | 2.28 | 1.59 | 1.42 | 1.37 | 4.4 | 3.73 | migratory |
| | h8 | 6.19 | 30.31 | 2.68 | 3.02 | 5.94 | 5.73 | migratory |
| | h9 | 0.18 | 2.18 | 0.34 | 1.00 | 0.43 | 2.07 | migratory |
| | h11 | 0.25 | 1.88 | 0.44 | 1.27 | 0.64 | 3.14 | dispersal |
| | h12 | 1.53 | 0.51 | 1.63 | 0.65 | 1.95 | 0.93 | migratory |
| | h13 | 11.81 | 1.11 | 1.94 | 1.10 | 3.85 | 0.43 | dispersal |
| | h14 | 0.86 | 0.86 | 0.55 | 1.02 | 0.73 | 1.16 | resident |
| | h15 | 6.55 | 8.79 | 0.80 | 1.32 | 1.19 | 3.19 | dispersal |
| | h16 | 2.45 | 1.08 | 2.26 | 1.14 | 3.36 | 2.26 | dispersal |
| | h18 | 0.91 | 0.85 | 0.61 | 0.83 | 0.66 | 0.4 | mixed migratory |
| 2015 - 2016 | h19 | 6.35 | 3.51 | 4.39 | 3.40 | 5.2 | 2.63 | dispersal |
| | h20 | 1.72 | 1.96 | 1.66 | 1.56 | 1.74 | 1.21 | resident |
| | h22 | 1.49 | 17.13 | 1.51 | 4.96 | 2.21 | 2.61 | migratory |
| | h23 | 1.00 | 16.83 | 1.23 | 3.61 | 1.27 | 6.9 | nomadic |
| | h24 | 1.47 | 10.55 | 1.74 | 3.27 | 1.95 | 2.37 | migratory |
| | h25 | 1.20 | 6.09 | 1.36 | 3.81 | 2.16 | 2.84 | resident |
| | h26 | 0.41 | 0.53 | 0.65 | 0.79 | 0.54 | 1.15 | dispersal |
| | h27 | 13.26 | 1.81 | 2.21 | 1.84 | 2.99 | 1.53 | migratory |
| | h28 | 2.10 | 3.60 | 1.51 | 2.74 | 1.9 | 2.24 | resident |
| | h29 | 1.58 | 5.22 | 1.00 | 1.59 | 1.03 | 2.01 | resident |
| | h31 | 8.33 | 3.09 | 2.56 | 2.32 | 5.18 | 4.16 | migratory |
| | h32 | 0.99 | 2.04 | 1.10 | 1.83 | 1.26 | 0.82 | dispersal |
| | h33 | 1.46 | 1.62 | 1.54 | 1.57 | 1.86 | 1.48 | migratory |
| | h35 | 0.85 | 0.62 | 1.13 | 0.93 | 1.07 | 1.11 | mixed migratory |
| 2016 - 2017 | h38 | 0.53 | 0.54 | 0.70 | 0.83 | 0.51 | 0.45 | mixed migratory |
| | h39 | 1.93 | 0.93 | 0.74 | 1.09 | 0.8 | 1.17 | resident |
| | h40 | 4.21 | 1.13 | 2.41 | 1.21 | 3.53 | 1.45 | resident |
| | h41 | 15.41 | 4.40 | 3.19 | 1.82 | 4.05 | 3.08 | migratory |
| | h42 | 9.81 | 5.95 | 2.78 | 2.05 | 7.04 | 1.77 | dispersal |
| | h44 | 0.74 | 1.21 | 0.76 | 1.46 | 1.42 | 1.66 | mixed migratory |
| | h47 | 1.69 | 14.33 | 1.50 | 3.44 | 1.95 | 2.43 | migratory |
| | h48 | 54.98 | 1.23 | 2.34 | 1.39 | 5.69 | 0.98 | migratory |
| | h49 | 2.05 | 3.75 | 2.04 | 2.87 | 2.62 | 5.73 | resident |
| | h50 | 3.27 | 1.74 | 1.79 | 1.84 | 2.41 | 2.35 | migratory |
| | | mean: 5.08 | mean: 4.55 | mean: 1.56 | mean: 1.85 | mean: 2.38 | mean: 2.20 | |
| | | sd: 9.19 | sd: 6.09 | sd: 0.85 | sd: 1.02 | sd: 1.69 | sd: 1.47 | |

The mean summer home range size which was estimated for both the resident and the non-resident animals is highest for the MCP method with 1.9 km$^2$ for resident animals respectively 5.97 km$^2$ for non-resident animals (see Table 7). However, no significant difference between the MCP home range sizes of resident and non-resident animals was detected (p-value 0.27). The same accounts for the winter home ranges where resident animals have a mean home range size of 2.83 km$^2$ and non-resident animals 5.06 km$^2$. The difference of the KDE home range sizes between the migration patterns is not as pronounced as those of the MCP computation. The mean summer home range is 1.4 km$^2$ for resident animals and 1.64 km$^2$ for non-resident animals during summer. During winter the home range size accounts to 1.93 km$^2$ for resident and 1.86 km$^2$ for non-resident animals. No significant difference between the resident and the non-resident animals could be found as well. Similar results were found for the dBBMM estimation with a mean homerange size of 2.21 km$^2$ for resident and 2.26 km$^2$ for non-resident animals. The p-value is 0.23 and hence, there is no a significant difference between the dBBMM winter home range estimates.

Table 7: Mean estimated home range size [km$^2$] for the home range analysis methods MSD, KDE and dBBMM aggregated by season and migration pattern type.

| **Season** | **Migration Pattern** | **MCP** | **KDE** | **dBBMM** |
|---|---|---|---|---|
| **summer** | resident | 1.90 | 1.40 | 1.79 |
| | non-resident | 5.97 | 1.64 | 2.60 |
| **winter** | resident | 2.83 | 1.93 | 2.21 |
| | non-resident | 5.06 | 1.86 | 2.26 |

### 5.2.3. Discussion

The mean home range size estimations of the MCP analysis are considerably bigger than the estimations of the other used methods. This underlines the findings of Reinecke et al. (2014) and Beier & McCullough (1990) that the MCP method often overestimates home range sizes due to the inclusion of unused areas. Especially individual h48 shows an extreme difference in MCP home range size from the summer to the winter months. Since this difference cannot be observed for the other methods, it can be assumed that an outlier caused the large MCP summer home range size. In addition, for h8, h22, h23, h24, h25, and h29 the winter MCP home range sizes are considerably larger than the summer home range sizes. This finding stands in contrast to Georgii & Schröder (1983) who claims that winter home ranges are generally smaller than summer home ranges. However, the KDE and dBBMM analysis resulted in much smaller differences of the home range sizes for these animals so that the seasonal home ranges are very similar, or even inversed the situation of the MCP estimate by estimating larger summer than winter home ranges. Those individuals which still have winter home ranges that are larger than the summer home range by more than 0.5 km$^2$ are h15, h23, h25, h26, h29 and h49. H25, h29 and h49 are resident animals which do not show distinctive seasonal home ranges. H15 and h26 are dispersal animals. H15, h23, h29 and h49 are located in the very south of the study area (see Figure 14, A.1 and A.2) where the climate is relatively mild even in winter without temperatures falling below 0° as was shown in section 3.1.1. Georgii & Schröder (1983) describe snow cover to be one of the main reasons for the decrease of home range sizes in winter. Yet, since there barely is any snow cover in the south of the study area in winter, there is also no obvious reason as for why winter home ranges of the respective animals should be smaller during this time of the year. H25 and h26 on the other hand, are both located north of Biasca. While h25 mainly stays within the valley all year round, h26 comes down to the valley bottom as well during the winter months. Here, snow cover is lower than in higher elevations and thus might also have a smaller impact on the winter home range size.

The home range variance analysis shows that the difference of the MCP estimations to the KDE estimation is significant. The overestimation of home range sizes and the high differences between the summer and winter months compared to the KDE and dBBMM estimates underline the statement of Nilsen et al. (2008) that the MCP method is not suitable for the analysis of home range sizes. Yet, with dBBMM summer home range sizes lying between 0.43 $km^2$ and 7.04 $km^2$ (mean: 2.2 $km^2$) as well as dBBMM winter home range sizes of 0.4 $km^2$ to 5.73 $km^2$ (mean: 2.38 $km^2$) the mean home range sizes are generally smaller than the mean size of 4.5 $km^2$ found by Reinecke et al. (2014) and those which Filli & Suter (2006) observed in the Swiss National Park. The smaller mean home range sizes within the study area might be explained by the high quality of the habitat with a lot of possibilities for seeking cover intertwined with high forage quality.

Table 7 shows that the home ranges of the resident animals are generally smaller than those of the non-residents except for the winter home ranges of the KDE computations. Especially when the home range size is calculated with the MCP method, the difference between resident and non-resident animals is high. However, for both summer and winter home range these differences are not significant. As a consequence, it can be assumed, that the home range size is not dependant on the migration type.

## 5.3. Temporal Activity Pattern

### 5.3.1. Monthly Activity Pattern

A distinctive bimodal activity pattern with peaks before, during and shortly after dawn and dusk can be observed during all months and for both sexes (Figure 19). In addition, night time activity is generally higher than day time activity. Moreover, the activity levels are higher during March, April, May, June, July and August and decrease again from September onwards. This decrease is more pronounced for stags where mean activity values of 40 are not reached anymore in July while hinds still reach higher mean activity values than 40 in August. Minimal activity is reached in January for the animals of the study period of 2014 - 2015. The activity during twilight is lower compared to the other months and activity values are below 30. Animals of the study period 2015 - 2016 are least active a month later in February. During times of low activity, the difference between the highest and lowest activity level is not as distinct as during summer where activity levels are higher. Interestingly, night time activity increases before daytime activity (March vs. April) when the overall activity level increases again in spring. All in all, The activity patterns of both sexes are relatively similar.

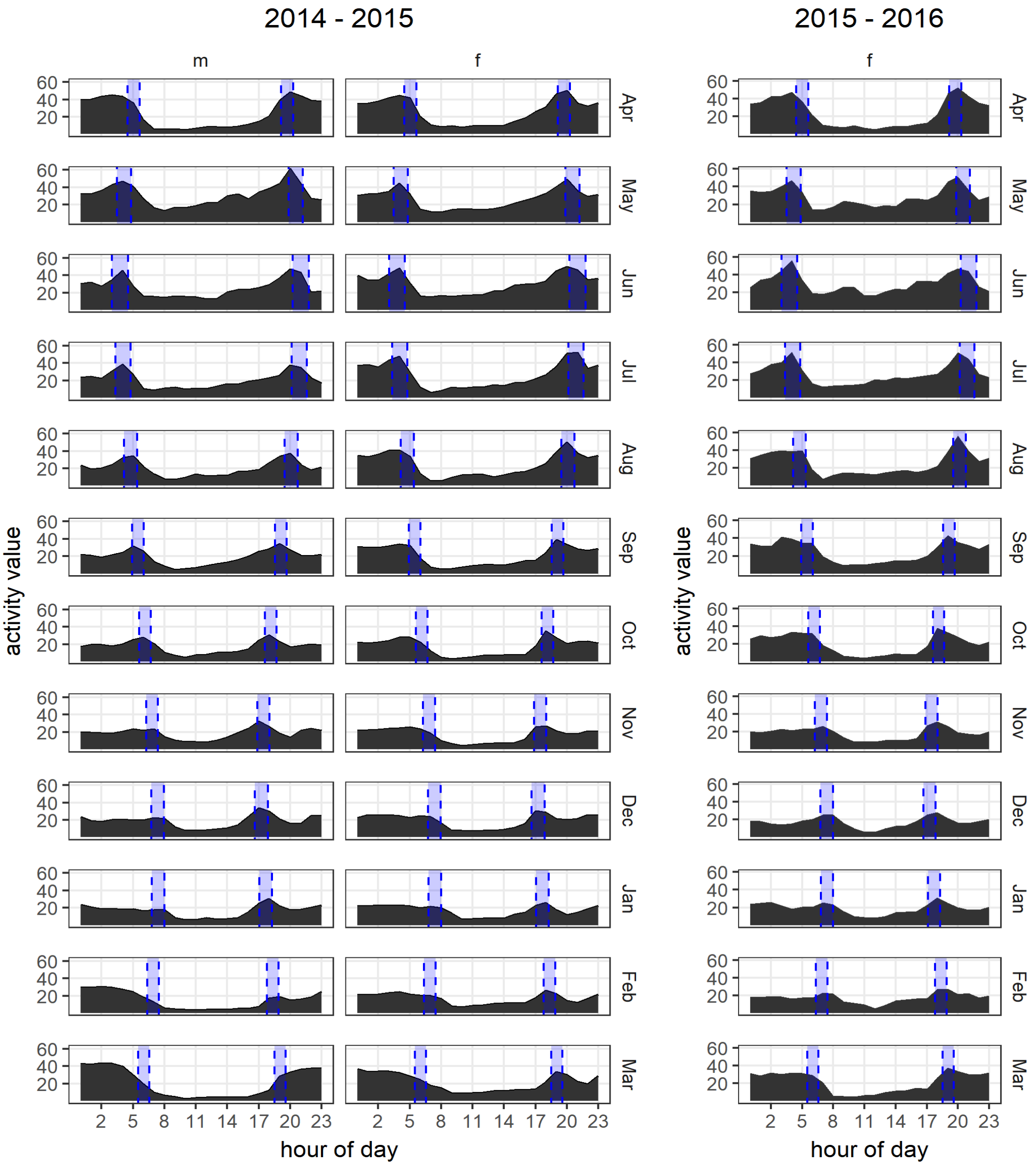
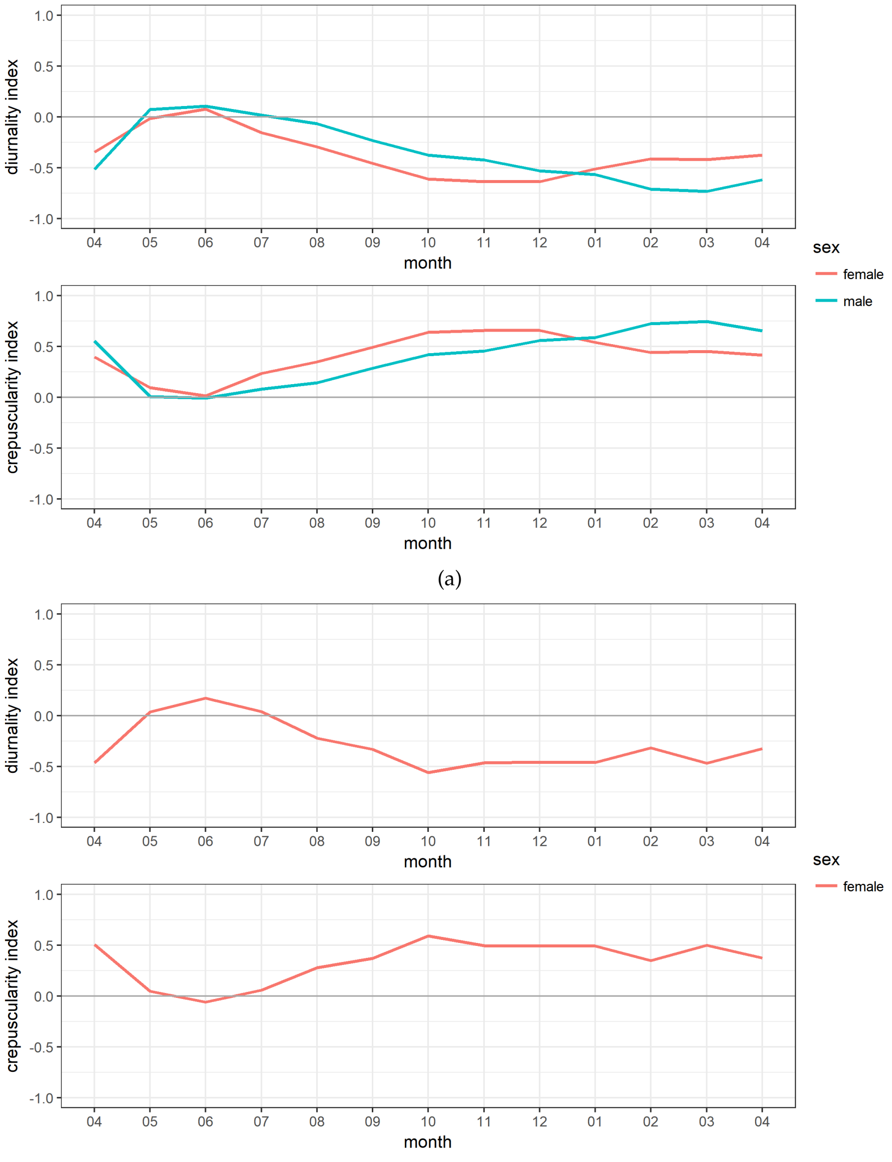


Figure 19: Mean monthly activity values for female and male deer. No males were recorded in 2015 - 2016. Start of nautical twilight, sunrise, sunset and end of nautical twiligh are represented by the blue dashed lines.

The diurnality index of Figure 20a underlines the assumption, that red deer are more active during the night. This seems to be true for both hinds and stags. However, during May and June the activity shifted towards a more diurnal pattern which lasted longer for stags. Generally, hinds showed a stronger tendency to nocturnal activity than stags except for the months January, February, and March in the time period 2014 - 2015. The crepuscularity index of both time periods show, that deer are most active during twilight hours. But here a change from crepuscularity to a non-crepuscular activity during May and June can be observed as well.



(a)

(b)

Figure 20: Diurnal and Crepuscularity index for the study periods 2014 - 2015 (a) and 2015 - 2016 (b).

### 5.3.2. Daily Activity Pattern

In Figure 21 the mean daily distribution of the activity type feeding/slow locomotion aggregated over the two study years 2014 - 2015 and 2015 - 2016 is illustrated. Fast locomotion occurred only for an insignificant number of times compared to the amount of feeding/slow locomotion and resting. Hence, the amount of time spent for resting is approximately complementary to the time spent for feeding and slow locomotion.

During the summer period a crepuscular feeding/slow locomotion behaviour can be observed with the highest feeding/slow locomotion activity during dusk, followed by dawn (Figure 21). During the day the time spend for feeding/slow locomotion decreased which means that resting behaviour is more common during the day. At night more time is spent again for slow locomotion and feeding than for resting. During the winter months the crepuscular feeding/slow locomotion pattern gets blurred due to decreased feeding / slow locomotion activity at dawn and dusk in comparison to summer. Overall, resting behaviour increased during all times in winter. However, most of the time that is spent for resting occurs during the day. In addition, during dawn and night feeding / slow locomotion behaviour is shown nearly as often as resting behaviour which was not the case during the summer months. In addition, the individuals are quite consistent in their activity type distribution showing only little variance. Generally, higher variances occurred at summer with the highest variance of activity at night. During the hunting season variances are also higher than in winter but lower than in summer. Moreover, feeding/slow locomotion activity is higher again during the hunting season at dawn, dusk and night in expense of resting behaviour.

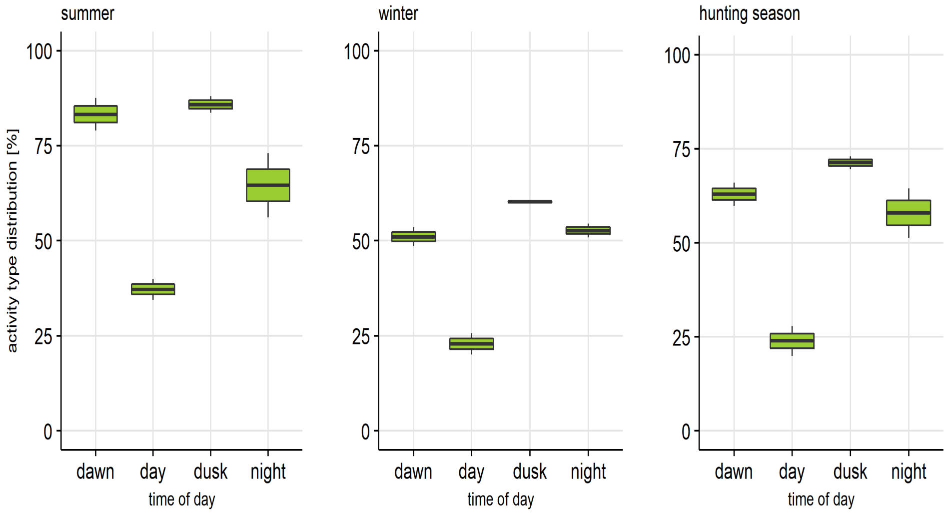


Figure 21: Distribution of the activity type feeding/slow locomotion over the course of a day, categorised into dawn, day, dusk and night.

### 5.3.3. Discussion

The results of the mean monthly activity values illustrate a distinctive bimodal activity pattern for every month of the year with activity peaks before, during and shortly after dawn and dusk. These findings correspond with the observations of Ensing et al. (2014), Georgii (1981), Georgii & Schröder (1978). Georgii (1981) and Georgii & Schröder (1978) conducted research about female red deer in the Bavarian Alps. From winter to early summer Georgii (1981) was able to observe an increase of activity, followed by a high activity in summer and early autumn. The activity then decreased at November. Figure 19 shows a very similar pattern, where the activity values start to increase at February and remain high until September. However, the decline of activity already seems to happen in October and not in November as was found by Georgii (1981). The highest values were found for May and June for both study periods of this thesis. This rise of activity may be explained with the increased energy demand of hinds due to gestation and birth of the calves as is described in section 2.1.1. Contrary to this, it would be expected to find an increase of activity during the rutting season at August and September for stags. Surprisingly no such pattern can be observed for unknown reasons. However, Georgii (1981) also found that the activity at night is higher than activity at day during autumn and winter which is also the case for the red deer in the Mesolcina area.

In addition, Hofmann & Nievergelt (1972) who did research on red deer in the Upper Engadin in Switzerland found that red deer leave their resting grounds between 6 - 8 o'clock and move from forested areas to more open grazing grounds. Feeding activity increased until the evening shortly before dusk. At around 18 - 19 o'clock the animals moved back into the forests to rest. The increased activity during the twilight hours thus stands most probably in accordance with the migration between resting and feeding grounds. The crepuscularity index and its result Figure 20 underline the observation, that red deer are mainly active during twilight hours. This preference for twilight hours decreases during April and May but remained relative constant for the rest of the year. The values of the diurnality index on the other hand, suggest a preference for nocturnal activity which changes to a more diurnal activity with increased index values in May. However, Kamler et al. (2007) did not detect crepuscular peaks in his study of activity patterns of red deer in the Biolowieza National Park. They argue that the missing crepuscular activity pattern might be the cause of the absence of human hunting activities, only little human recreational activities and the presence of large carnivores. Consequently, the crepusuclar activity pattern of red deer around the Mesolcina might be the result of high human activity in red deer habitats. Closer inspection of the individual crepuscularity indices (see Figure A.9) show that individual h1, h14 and h19 only show crepuscular activity and barely any activity outside of the twilight hours. These individuals mainly live in the valley floor of the Mesolcina. In addition, the crepuscularity index values range between -0.14 - 0.81 with a mean of 0.39 and peaks during the winter months (November - February) and a low at summer around June and July. Hence, crepuscular activity occurs more often in winter with a decrease during the summer months. The reason for this might be increased human activity during the winter months (for winter activities such as skiing) as is going to be illustrated further below. The decrease of the diurnality index at winter underlines this assumption. Unfortunately the relationship between migration pattern and crepuscular index as well sex and crepuscular index can not be investigated more thoroughly with statistical methods due to the small sample size.

Kamler et al. (2007) observed that at winter red deer have a higher activity level during the day which increases with progressing daylight hours. Hence, deer were affected by the daily temperature and were most active before sunset when the temperature reached its daily peak. During the cold morning hours just before sunrise only little activity was observed. This stands in contrast with the diurnality indices of the animals in this study. The diurnality indices illustrate higher nocturnal activity during the winter months and diurnal activity at summer. Moreover, Arnold et al. (2004) found that red deer have a nocturnal hypometabolism which prevents them from using too much energy during harsh winter months. This again might be the reason for the low activity at night and just before sunrise in the study of Kamler et al. (2007). On the other hand, Ensing et al. (2014) found peaks of activity at night for red deer in the Netherlands. They found human disturbance to be the main cause of this behaviour pattern since a lot of people used their study area for recreational activities during the day. As was discussed in Section 2.1.5 this theory got backed up by Kitchen et al. (2000) and Frank & Woodroffe (2001) who found similar changes of behaviour in other animals. Jayakody et al. (2008) describes that red deer especially perceive recreational activities and hunting as a predation risk. As a consequence, it is reasonable that the red deer which were monitored for this work prefer nocturnal activity due to a high amount of human disturbance since they live in an area where human activity is high (see Section 3.1). Under inspection of the individual diurnality indices the most distinctive unimodal pattern is shown by the individuals h1, h4, h8, h13, h15 and h19 with diurnal activity peaks around 6 O'clock in the morning (Figure A.9). H1 is a resident animal and has its home range in the valley of Mesocco. Its home range also covers the wildlife sanctuary Trescolmen which at the same time serves as a game reserve where hunting is prohibited. When comparing the diurnality index with the elevation values of Figure A.4 and A.6 it gets visible that for h4, h8, h13, h15 and h19 the nocturnal activity corresponds well to times when they can be found in lower elevations and are thus closer to urban areas. For individual h1 this behaviour is less explicit since the change of elevation is smaller. Only individual h14 does not show diurnal activity at all. The home range of H14 lies between Roveredo and Bellinzona and hence lies in an area with increased human activity compared to other areas of the study region. H9, h18 as well as h20 have their home ranges in elevated heights within forests all year round and especially h18 only rarely gets close to urban areas for an extended period of time as some of the other individuals did. This might explain why their nocturnal activity already decreases again in October and November.

As Clutton-Brock et al. (1982) and Bützler (2001) observed the main activity of red deer is grazing and foraging which stands in contrast to the rumination and resting bouts. This is also the case in this work where red deer spend most of the time with feeding/slow locomotion and resting. The third activity category, fast locomotion, occurred so rarely that it can almost be negligible. It is interesting that fast locomotion does not occur more often during the hunting seasons and indicates a high habitat quality for red deer with plenty of possibilities to seek cover. Furthermore, the study of the daily activity pattern of Section 5.3.2 confirms the findings of the monthly activity pattern analysis. During dawn and dusk feeding and slow locomotion are shown most often, corresponding with the findings from the monthly activity analysis and the crepuscularity index that activity is highest at twilight hours. Figure 21 illustrates that during the summer months June and July feeding and slow locomotion behaviour is higher than during the winter and hunting season and occurs more often during twilight hours than during day and night. Clutton-Brock et al. (1982) and Mitchell et al. (1977) also found a seasonal trend in red deer feeding behaviour with a maximum around July when calves are being born and food is most abundant. During the hunting seasons the activity at dawn and dusk is still higher than di- and nocturnal activity but the overall amount of time spent for feeding and slow locomotion decreased. Since the behaviour type of resting is complementary to feeding/slow locomotion this means that the amount of resting increases parallel to the decrease of feeding and slow locomotion. This corresponds well with Figure 19 where a decrease of activity can be observed from September until January with a large decrease of daytime feeding/slow locomotion than at night. This difference between feeding/slow locomotion at day and at night is visible in the diurnality index since generally activity still occurs more often at night than during the day. During the winter months feeding/slow locomotion overall decreases even more compared to the hunting season. The generally lower amount of feeding/slow locomotion activity again corresponds with the findings of Clutton-Brock et al. (1982) and Mitchell et al. (1977) and can be explained by the lack of forage availability as well as the bad digestibility of winter foods as is described in Section 2.1.4. However, feeding and slow locomotion still occurs most often during dusk closely followed by dawn and night.

All in all, the results conform quite well to the findings of James Patrick (2017). In his work, Patrick (2017) was able to observe increased energy demands of hinds starting in March until August with peaks of activity during the twilight hours. The animals of this thesis showed a very similar pattern.

However, there are also some inconsistencies for the analysed mean monthly activity for which Patrick (2017) calculated the locomotion speed between fix points to derive information about the activity level. In his work, the increase of activity before dusk happens in a relatively short period of time until the maximum activity (or locomotion speed) is reached. On the other hand, the results of this study indicate a steadier increase of activity, which during the summer months already starts in the morning hours. This behaviour suits the description of Hofmann & Nievergelt (1972) that the activity increases all day long until the maximum is reached in the evening. It might be that Patrick (2017) was not able to detect this more subtle decrease in activity due to the coarse sampling size of one hour of his data. Because of this sample size short bursts of activity respectively increases of locomotion speed get smoothed out and it seems that the deer was not active. Furthermore, since only position within the environment and no head movement was recorded, an animal which was barely moving but feeding, could not be detected as an active animal. Another discrepancy is that the decrease of activity of the animals in the Unterengadin valley already occurs in August whereas the activity of the deer in the region of the Mesolcina started to decrease approximately one month later. In addition, in Patrick's (2017) results stags show increased locomotion speed during September and October, indicating increased activity during the rutting season. Surprisingly, no such pattern could be found for the stags of this thesis. The crepuscularity indices of both studies show that the investigated animals were most active during dawn and dusk with a decrease of the index values in summer months. This decrease was smaller in Patrick's (2017) study. Similar patterns can be found for the diurnality indices as well with positive values at summer (diurnal activity) and negative values (nocturnal activity) during spring, autumn and winter. Yet, as was the case for the crepuscularity indices, the fluctuation of the values is more distinct in this work than in that of Patrick's (2017). This difference probably also accounts to coarse the sampling rate of 1 hour and that the activity has to be much stronger to be detected as such, since only position information and no head movement information is being stored for the red deer of the Unterengadin valley. Nevertheless, the method to use locomotion speed as a proxy for activity levels works well and can certainly be used to detect activity patterns, especially when only GPS location data and not activity data per se is given.

## 5.4. Resource Use

For the resource analysis it was crucial that the animals did not cross the border to Italy, since no ground cover data outside of Switzerland was available. Thus, individuals with ID 16, 22, 31, 44 and 50 had to be excluded from the resource analysis and hence, from the time periods of 2014 - 2015 eleven, from 2015 - 2016 twelve and from 2016 - 2017 nine animals were analysed. In total activity data of 16 animals was available, whereof only 10 animals fulfilled the required criteria for analysis.

### 5.4.1. Relative Resource Use Analysis

#### Natural Resources and Areas Used by Man

Figure 22 shows the mean values of the relative resource use of all the animals which were included in the analysis for all three study years. The use of forest areas increased in all seasons during the day, reaching a maximum value around noon for both resident and non-resident animals and thus, showing a unimodal pattern. For both migration types, forest use is slightly higher during the winter months than in summer, reaching a maximum mean value of 83% for non-resident and 79% for resident animals. The lowest use of forest occurs during the hunting seasons where only approximately 74% of all the resources accounted to forest for the non-resident animals and 75% for the resident animals. The increased use of forests during daytimes corresponds with a decrease in the use of grassland. Hence, the highest use of grasslands occurs at night and reaches a low point around noon. Overall, agricultural areas are only used rarely in context of other resources. The use of vineyards is also small but an increase of use at night during the hunting season can be observed for non-resident (1.8%) and resident (1.86%) animals. Of the man made structures, the urban areas were used most often. Here maximum use can be observed during night times. In Figure 23 a difference in resource use can be observed between hinds and stags at summer. During summer, the maximum use of forested areas is around 75 % for hinds and higher for stags with 85%. During winter and the hunting seasons the difference between the amount of forest use of hinds and stags is smaller. Use of forest increases and reaches a maximum value of around 80% in winter for hinds with lower values during the hunting seasons. The same account to stags where maximum values of 85% were reached at winter around noon. Both sexes show a unimodal relative forest use pattern. While forest use intensifies during the day until noon, use of grasslands is lowest at that time and highest during the night as is the case when the use of the resident and non-resident animals are compared. Another difference between the resource use of stags and hinds is given for the use urban areas. Stags use such areas up to 11 % (highest value in winter) of the entire resource use while urban areas account to approximately 9.9% of the entire resource use for hinds (highest value in summer). Both hinds and stag use urban areas more often during night times in all seasons.

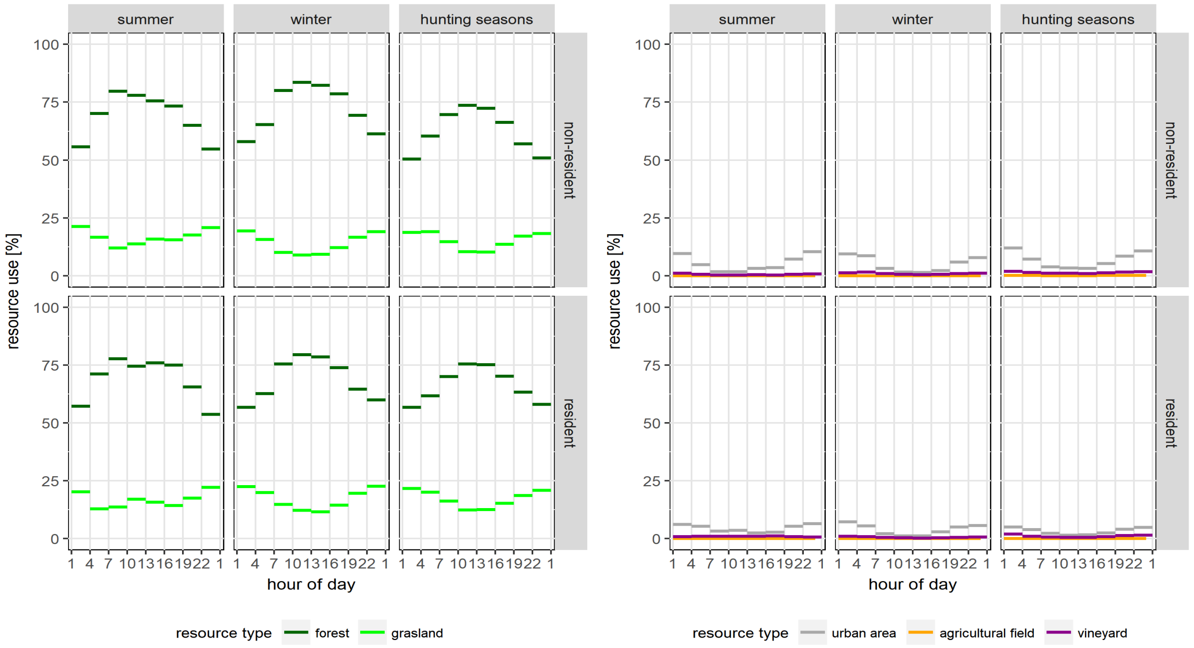


Figure 22: Relative use of the resources forest, agricultural fields, urban areas and vineyards in % from the study period 2014 - 2015, 2015 - 2016 and 2016 - 2017 aggregated by migration type (resident and non-resident). Beams depict time intervals of three hours.

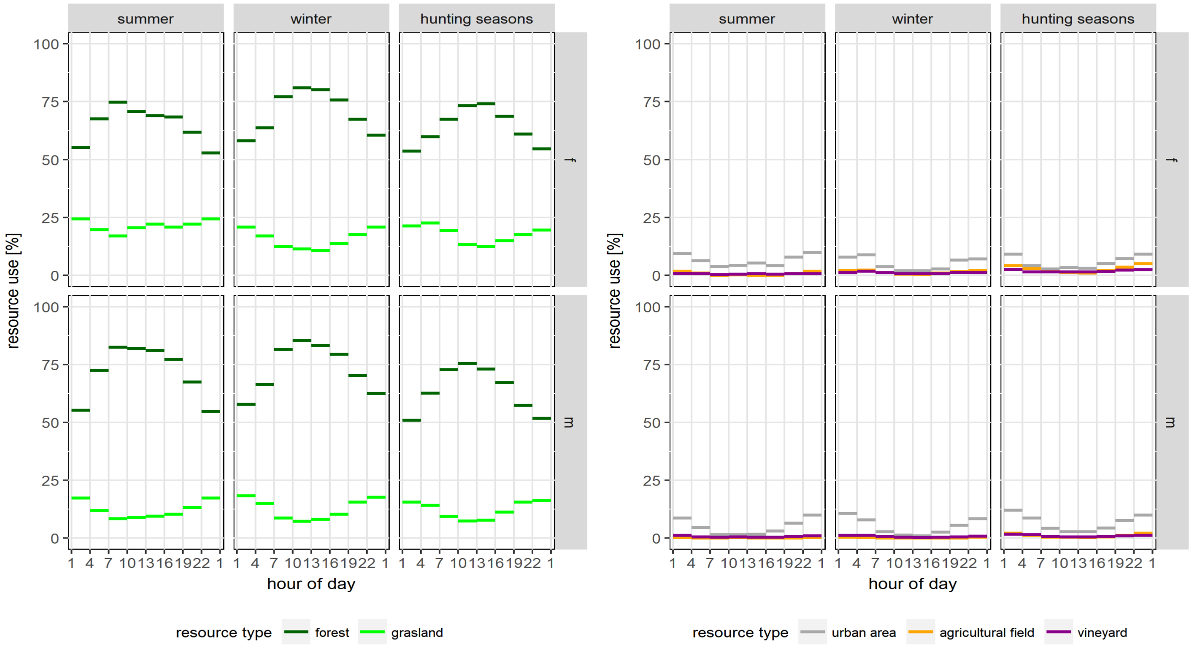


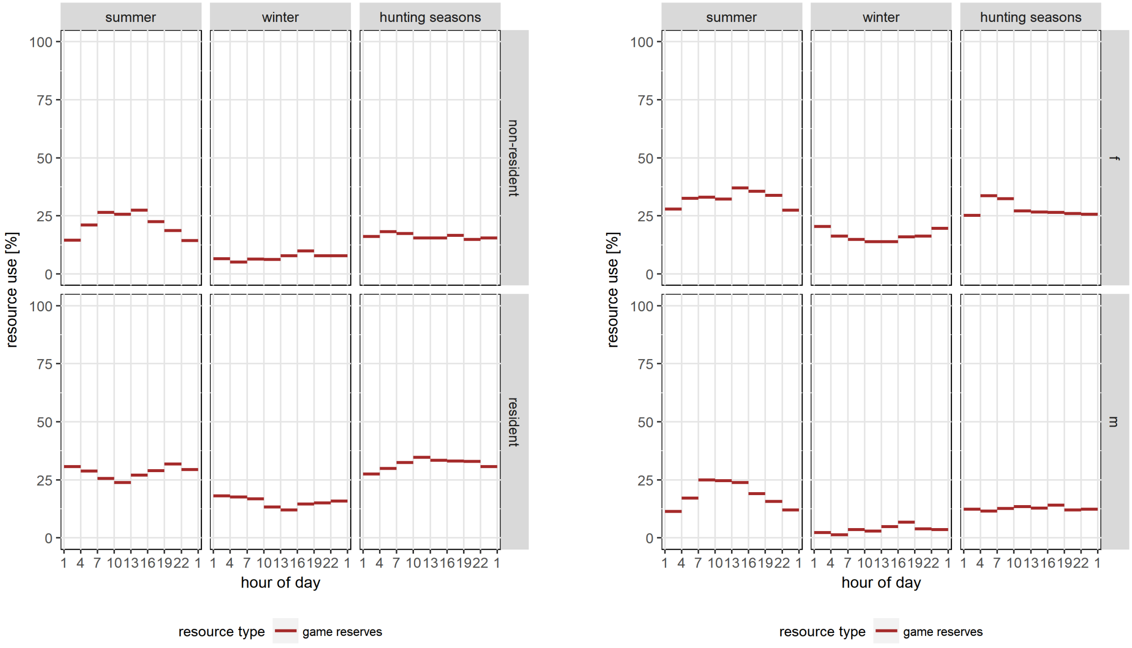
Figure 23: Relative use of the resources forest, agricultural fields, urban areas and vineyards in % from the study period 2014 - 2015, 2015 - 2016 and 2016 - 2017 aggregated by sex. Beams depict time intervals of three hours.

### Game Reserve

Figure 24 shows the mean relative use of game reserves for all individuals. It has to be noted, that game reserves include ground cover types such as forest and grasslands. As a consequence, the use values have to be seen as use of game reserves in contrast to the use of areas which are no game reserves.

Non-resident animals used game reserves most often during the summer period where the highest value (26%) was reached at noon, showing a unimodal use pattern. During the hunting seasons this unimodal pattern disappeared and game reserves were more regularly accessed throughout the day with values ranging around 16%. Lowest use of game reserves can be observed during the winter months. Resident animals on the other hand, access game reserves more often at night than during the day. Compared to the summer months, the maximum mean use values increased with the highest value of 35% compared to 32% at summer. As was the case for non-resident animals, the use of game reserves is lowest during the winter months.

Differences can be observed in the access of game reserves between hinds and stags. Game reserves are most often used by hinds at summer, reaching values up to 37%. Hereby a unimodal pattern can be observed, where the highest values occur shortly after noon. During winter this pattern gets inverted and game reserves are most often accessed at night yet still less often than at summer with mean maximum values only reaching 20%. Maximum values of 34% are reached during the hunting season whereas the values remain more constant than during the summer period. For stags similar patterns as for hinds occur during the summer and hunting season. However, game reserves are generally accessed less often by stags during this periods, reaching maximum values (25%) around noon at summer. During the winter months the access is low with a maximum value of around 7% but stays relatively constant throughout the day.



(a) (b)

Figure 24: Relative use of game reserves (%) during the combined study periods 2014 - 2015, 2015 - 2016 and 2016 - 2017. Values were aggregated per migration type (resident and non-resident) (a) and sex (b). Beams depict time intervals of three hours.

### 5.4.2. Jacobs Index

#### Natural Resources and Areas Used by Man

Even though the results of the relative resource use analysis implied a preferred use of forest areas at any time, the Jacobs index (see Figure 25) reveals that a positive preference for forest areas is only given during the day in every season of the study year 2014 - 2015 for resident and the non-resident animals alike. At night there is a negative preference for forests which becomes positive during the twilight hours and hence describing an unimodal pattern. While the forest preference is lowest during the hunting season with a mean maximum index value around noon of 0.18 for non-resident animals and at summer with an index value of 0.23 for resident animals forest use is most post preferred at winter. This is also the case for resident animals except that during summer forest preference decreases at noon. In terms of grasslands, red deer show a mirrored behaviour to forests. Even though the preference is negative at all times for all animals, the negative index values increase during the twilight hours and reach a minimum around noon. Complementary to the pattern of forest use, grasslands are least preferred at winter where negative index values of -0.78 (non-resident) and -0.72 (resident) are reached.

For both resident and non-resident animals the preference for urban areas, agricultural fields and vineyards stays negative during all times. Although negative, the preference for urban areas of non-resident individuals is highest during winter times, reaching maximum values at night. Generally urban areas are least preferred during the day except for resident animals at summer where the negative preference for urban stays relatively constant with an outlier at late afternoon / evening. In addition, the index values of resident animals for urban areas are elevated during the hunting seasons. The use of vineyards has a similar pattern like the urban use, although overall the preference of vineyards is lower. Agricultural areas seem to have been used only occasionally and at some points even nearly reach a value of -1. Interestingly non-resident animals use agricultural areas more often in winter whereas the lowest negative preference for residents can be found in summer.

When aggregating the Jacobs index by sex (see Figure 26) the forest and grassland preferences are similar for the summer and winter months as when the values were aggregated by migration type. Forest preferences were always positive for hinds during the day with negative selection at night. This is the case for stags as well during summer and winter but surprisingly, the preference for forests is negative during hunting season and only reaches a maximum values of -0.02. On the other hand, the use urban areas, agricultural fields and vineyards is similar as in Figure 25 except during the summer season of stags where index values for all resource types do not exceed -0.6. Hence, stags frequent those areas less often than hinds. In addition, the use of urban areas is highest at winter for stags where maximum values of -0.05 are reached. This accounts also to hinds where maximum index values of -0.13 are reached during winter months. Contrary to expectations the use of vineyards is higher for both hinds and stags during winter.

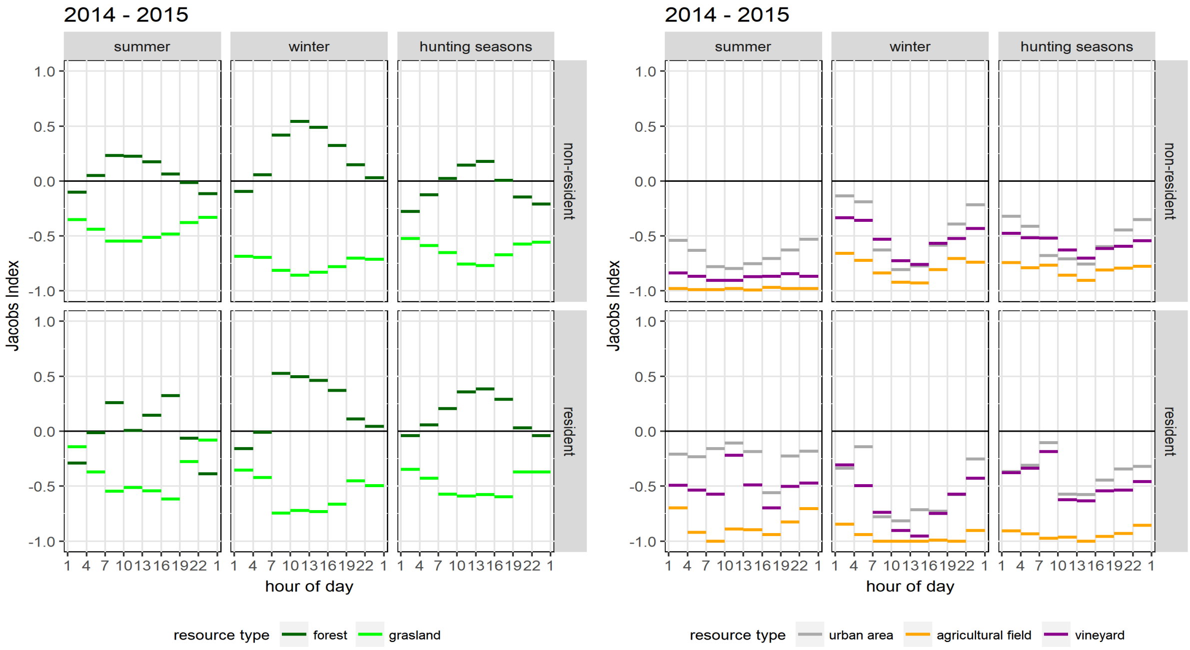


Figure 25: Jacobs Index (1973). Temporal preference during 2014 - 2015 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per migration type (resident and non-resident). Beams indicate time intervals of 3 hours.

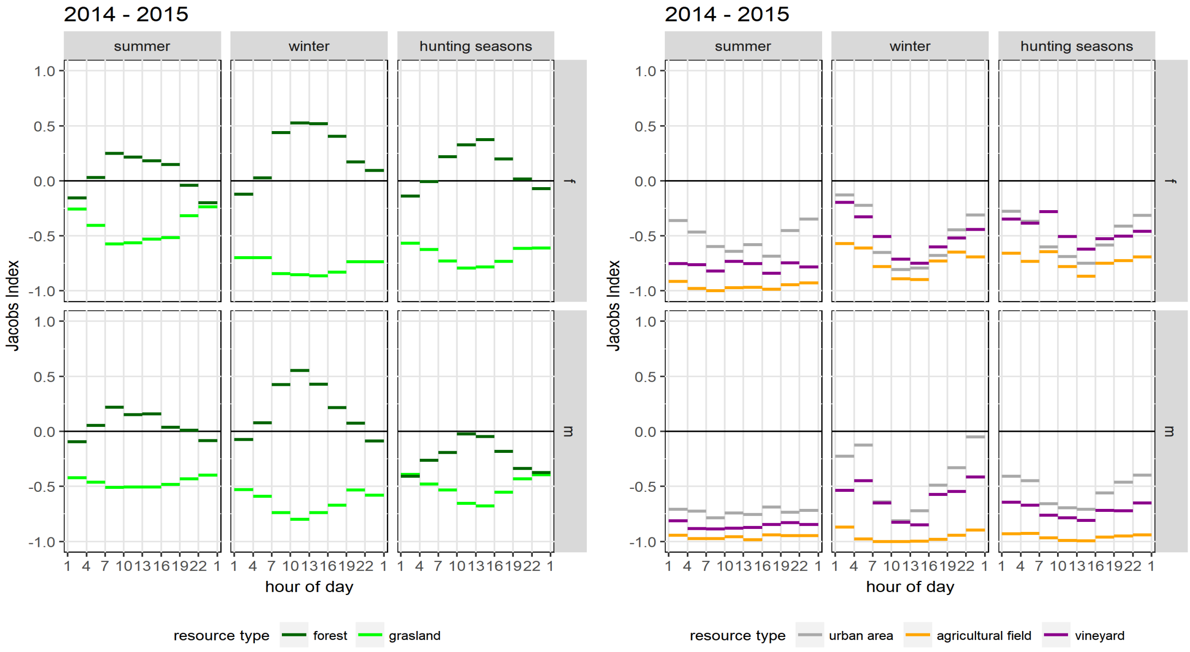


Figure 26: Jacobs Index (1973). Temporal preference during 2014 - 2015 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per sex. Beams indicate time intervals of 3 hours.

During the study year of 2015 - 2016 forest preference patterns of non-resident and resident animals were similar to the previous study year showing a bimodal structure with peaks around noon (see Figure 27. During the night, the preference for forests decreased again with a complimentary decrease of the negative preference of grasslands. During the summer and hunting seasons, there is even a negative preference of forests at night. Generally, there is not much variation between the different seasons within the study year. Forest preference is a little bit lower during the hunting seasons with a maximum index value of 0.37 and a minimum of -0.8 for non-resident animals. These values were lower during the study period of 2014 - 2015. On the other hand, the highest index values of the entire study year for non-resident animals can be found at winter with a maximum mean value of 0.52. Contrary to this, the most negative preference for grasslands (-7.1) can be found during the winter months as well. Resident animals too show a bimodal forest preference pattern as do the non-resident animals with positive selection of forests during the day and negative preferences of grasslands during the day. But during this study period, the forest preference is generally lower for resident animals than for non-resident animals. Negative index values are reached during all seasons and not only during summer and the hunting times. The maximum index for forest preference, on the other hand, is reached at winter with a value of 0.34.

The Jacobs index of urban areas, agricultural fields and vineyards remains negative during all seasons for both non-resident and resident animals. Urban areas have the lowest negative preference which reach maximum values during the hunting season. The preference for these areas is most negative during the day. The index values for urban areas of resident animals are higher during summer and winter compared to the values of the non-resident animals but remain negative. The highest value reached at summer is -0,27 for resident animals compared to -0.47 for non-resident animals. However, contrary to the non-resident animals, resident animals have the most negative preference of urban areas during the hunting seasons where the highest value is -0.51 compared to -0.32 for non-resident animals. Contrary to the previous study year the index for agricultural areas during summer for non-resident animals is -1 which means that agricultural areas were not accessed at all. The same thing is the case for vineyards. Agricultural area is accessed slightly more often during winter although the index values still nearly reach -1. On the other hand, negative selection decreased visibly for vineyards during winter and the hunting seasons. Agricultural areas are also more accessed during the hunting season but the preference remains negative.

As can be seen in Figure 28 the preference for forests of female deer is lower in the study period of 2015 - 2016 than in 2014 - 2015. Again the highest preference for forest areas is reached during the winter months with the highest index value of 0.3 compared to 0.52 in the previous year. In addition, the preference for grasslands is less negative than in the period of 2014 - 2015. Yet, the overall unimodal pattern of increased forest preference during the day with the complementary negative preference of grasslands is still the same. In addition, while the stags of the previous study year showed a negative preference for forest areas, this is not the case for the stags of the period 2015 - 2016. However, even though there is a negative preference for forest areas at night during the summer months, which does not exist at winter, the maximum Jacobs index of summer and winter for stags are very similar with the values 0.63 respectively 0.64. Especially the value of the summer months is higher than that reached by the stags of the previous study year. On the other hand, the preference for grasslands is more negative for the stags of the study year 2015 - 2016. Overall, the preference for agricultural areas and vineyards is more negative for hinds of the study period 2015 - 2016 than during 2014 - 2015. Only the indices for urban areas reach similar values as in the previous study year during the summer months. On the other hand, the values for the preference of urban areas are higher during summer and the hunting season for the stags of 2015 - 2016 than in the previous study period, but still indicating a strong negative preference. For all seasons preference is less negative during the night than during the day and the maximum value of all seasons is reached during the hunting season with a value of -0.06. In addition preference for urban areas is also more negative for hinds than for stags as is the case for vineyards at winter and during the hunting seasons.

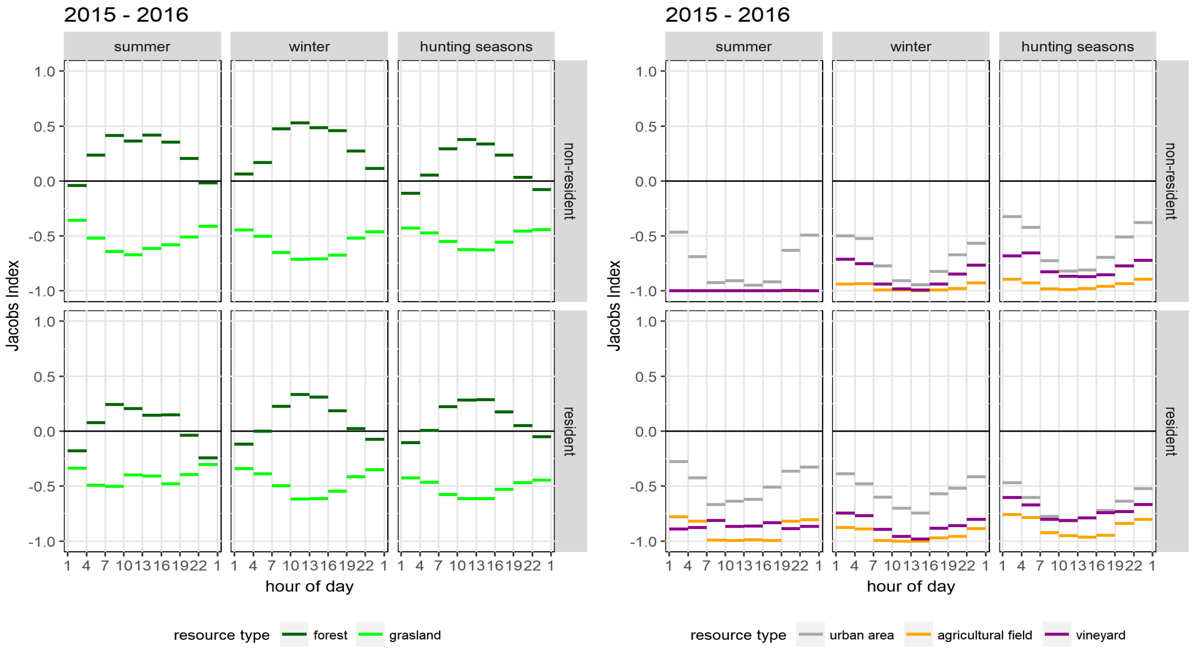


Figure 27: Jacobs Index (1973). Temporal preference during 2015 - 2016 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per migration type (resident and non-resident). Beams indicate time intervals of 3 hours.

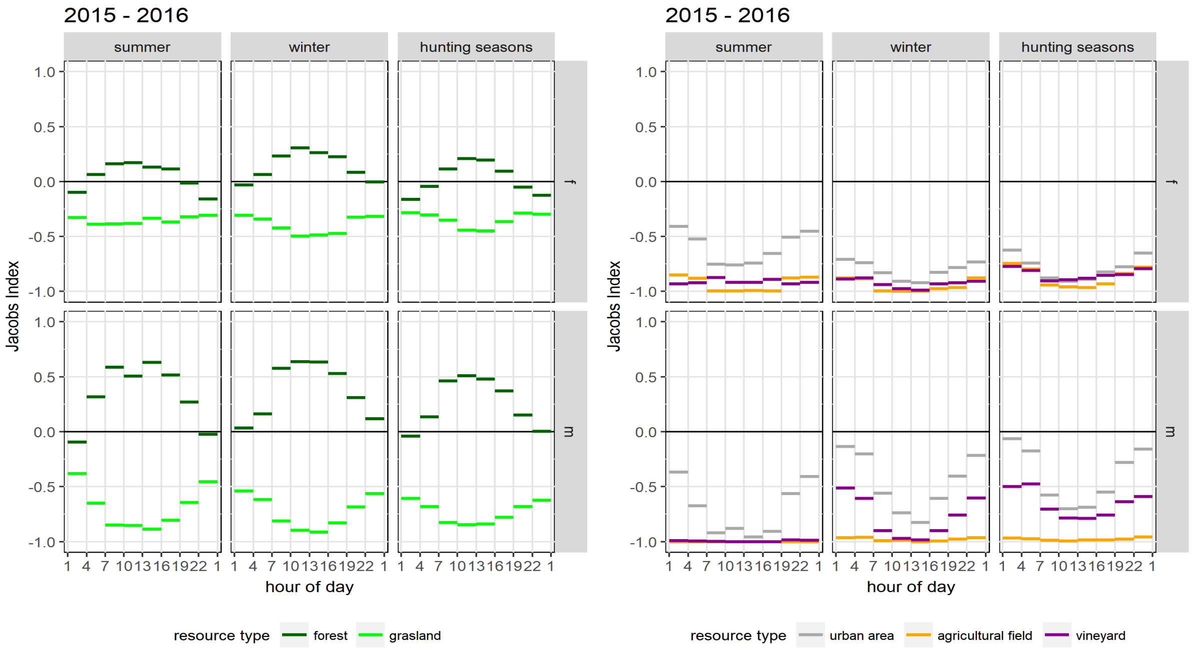


Figure 28: Jacobs Index (1973). Temporal preference during 2015 - 2016 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per sex. Beams indicate time intervals of 3 hours.

Figure 29 shows that the non-resident animals only have a weak preference for forest areas during winter and the hunting seasons in the study period 2016 - 2017. With a maximum value of 0.1 at winter and 0.09 during the hunting seasons, the preference is lower than compared to the previous study periods. For summer and the hunting season the unimodal pattern of high preference during the day and lower or even negative preference during the night remained as well. But for the winter months Jacobs index values at night can be observed which are higher than the values during twilight. Moreover, for the first time the forest index values are lower than the grassland index values which can be observed at night during the winter months. At summer, the preference for grasslands is lowest at night and increases throughout the day until dusk, yet staying negative at all times. Such a pattern cannot be observed in the previous two study years. The negative preference for grasslands during the hunting seasons remains relatively constant at around 0.3. On the other hand, the index pattern of resident animals is more similar to those of the study periods 2014 - 2015 and 2015 - 2016. Here again, forests are most preferred at winter, reaching a maximum mean value of 0.47. The maximum indices for forests at summer and during the hunting seasons are relatively similar whereas the negative values are lower at summer. In addition, the typical pattern of Jacobs indices for grassland with increased values at night and decreased values during the day are shown as well. Non-resident animals did not access agricultural fields and thus, the index value for this resource is -1 for all seasons. Vineyards were not used during the winter months as well. However, as was the case in the previous two study periods, negative preferences for urban areas were observed during all seasons with higher index values during the night than during the day. Vineyards also show a negative preference during summer and the hunting seasons but the values are lower than those of the urban areas. During the study period of 2014 - 2015 and 2015 - 2016 non-resident animals showed a less negative preference for urban areas with values > -0.5 being reached which is not the case in the study period of 2016 - 2017 for any season of the non-resident animals. On the other hand, index values of urban areas for resident animals are higher in this study period and are similar to the values of the period 2015 - 2016, reaching a maximum mean index value at summer of -0.2. Vineyards and agricultural fields have a negative preference as well. For agricultural areas, the values are more negative during the day for all seasons, whereas the pattern is relatively constant during the winter months. The highest value for all seasons of resident animals for agricultural fields is reached during the hunting season with a maximum mean index value of -0.65. Lower index values during the day are also shown for vineyards, with a maximum mean value of -0.47. at summer.

Hinds and stags both show similar index patterns as in the previous two study periods with the highest forest preference during the day and around noon (see Figure 30). At winter, no negative preference is reached by hinds at winter where also the highest mean index value of 0.42 of all seasons is reached. Stags also have the highest preference of forests at winter with a maximum mean value of 0.34. In addition, the preference of grasslands again remains negative as was the case in the two previous study years with lowest values at the day and higher values at night. The values are relatively similar for both hinds and stags during all the seasons. No agricultural fields were accessed by hinds during the winter months resulting in index values of -1. Contrary to the other study periods however, the values for agricultural preference of hinds are on par with the values for the urban areas although the preference remains negative. Especially at summer hinds have a higher index value for agricultural areas with a maximum mean value of -0.6 at night and lower values during the day. During the hunting seasons the values remain relatively constant at -0.85 as is the case for the index values of vineyards at winter and during the hunting seasons. For both sexes and during all seasons, index values for urban areas are highest at night and lower at day. Especially stags show a high fluctuation of negative preference for urban areas at summer and winter with values ranging from -0.15 to -0.68 respectively -0.31 to -0.87. At summer and winter negative preferences for agricultural fields are observed which nearly reach values of -1. On the other hand, vineyards also have a negative preference but the values are higher especially during the night, reaching maximum mean values at summer of -0.58.

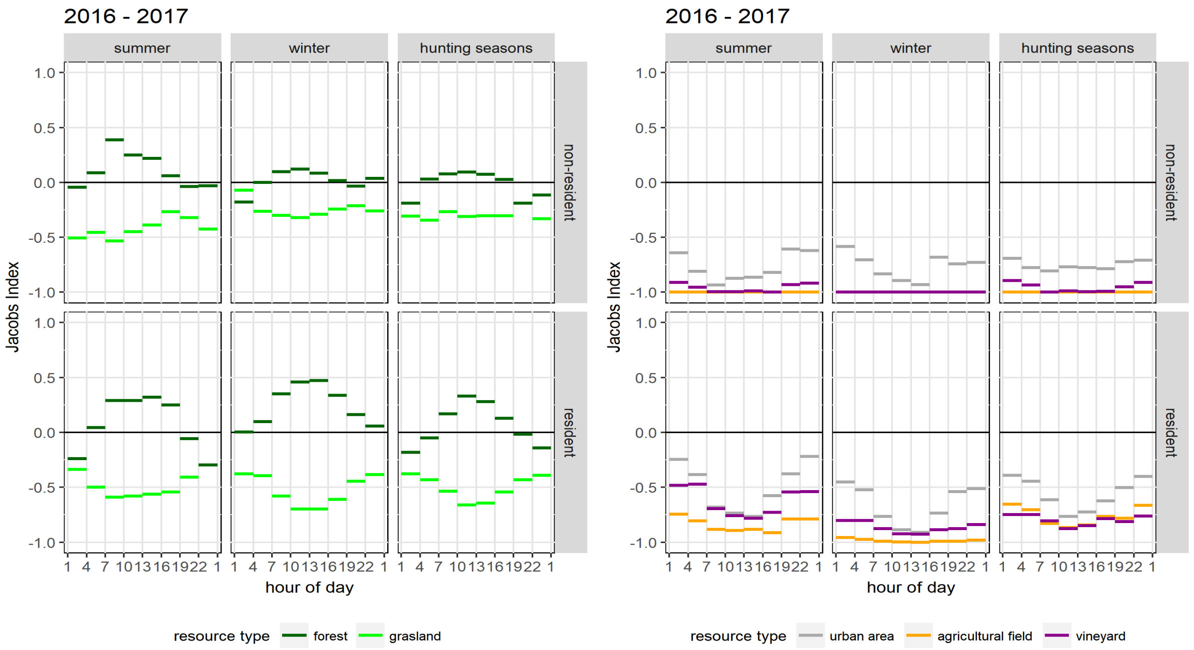


Figure 29: Jacobs Index (1973). Temporal preference during 2016 - 2017 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per migration type (resident and non-resident). Beams indicate time intervals of 3 hours.

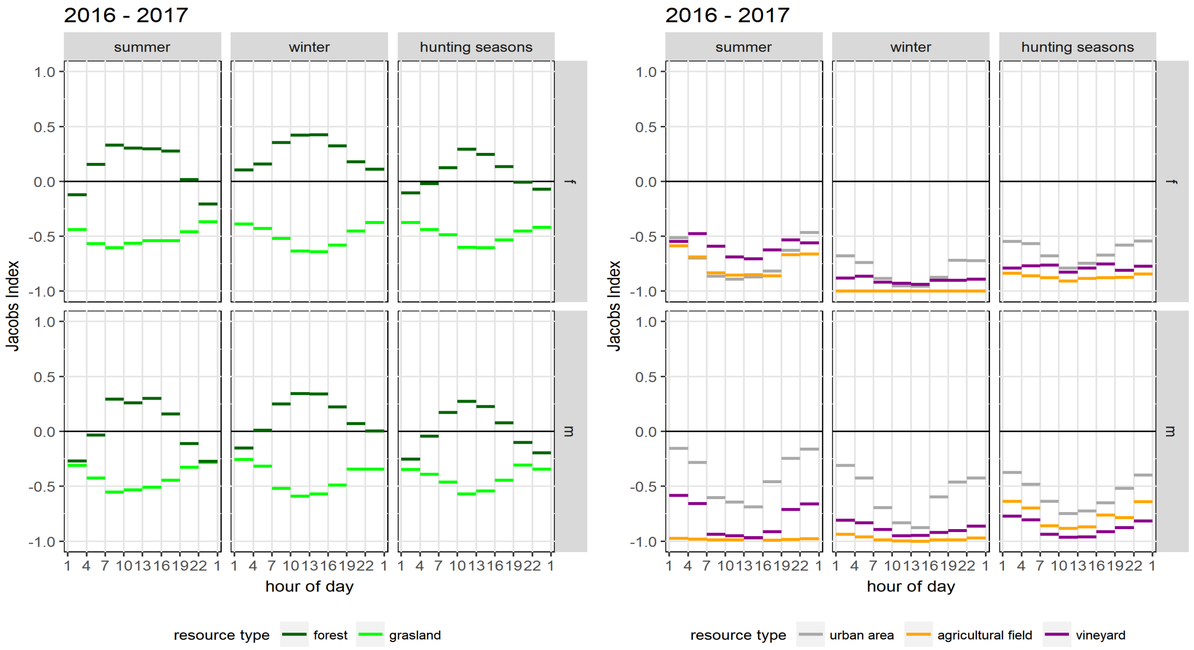


Figure 30: Jacobs Index (1973). Temporal preference during 2016 - 2017 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per sex. Beams indicate time intervals of 3 hours.

### Game Reserves

Figure 31 shows the mean Jacobs index values for the game reserves aggregated by season and migration type. For all three study periods the index values remained negative during winter and the hunting seasons regardless of the migration pattern. Only the resident animals of the study period 2014 - 2015 as well as the non-resident animals of 2016 - 2017 show positive preferences at summer. During the study period of 2014 - 2015 non-resident animals do not access game reserves. As a consequence, the index values are -1. Highest values of non-resident animals are reached at summer, even though they remain negative with the highest mean index value of -0.61. The positive preference which occurs for the resident animals at summer have a maximum mean index value of 0.04 and are reached at night while a minimum mean value of -0.47 is reached at day. During the hunting season the preference remains negative. However, the mean index values are higher than in winter even though they stay lower than during the summer months and reach a minimum during the day. This is also the case for non-resident animals of the study period 2014 - 2015. In the period of 2015 - 2016 the mean index values for non-resident animals all remain below -0.5 during all seasons and stay relatively constant. The values of the resident animals are higher and staying constant at around -0.5 during the winter and hunting seasons. However, at summer the values are higher with a maximum mean value of -0.04. Non-resident animals of the time period 2016 - 2017 show a distinctive positive preference for game reserves at summer with increased values in the morning. The maximum mean value reaches 0.63 with a minimum of 0.39. Lowest vales are reached at winter with a maximum mean value of -0.82. However, the index values are higher during the hunting season but remain negative and reach a minimum of at night. The resident animals only show negative preferences for game reserves. While the index values remain below -0.5 during summer and winter, the value increases to a maximum mean value of -0.47 at day and during the hunting season.

As can be seen in Figure 32 all the mean Jacobs index values for hinds and stags concerning game reserves remain negative during the season 2014 - 2015. For stags even values of -1 are reached at winter for the entire day. Both sexes reach the highest mean values at summer where hinds have a highest maximum mean value of -0.48 and stags -0.57. The preference for game reserves is also negative during the hunting season but reaches higher values than at winter with maximum mean values (-0.68) during the day and the minimum (-0.82) at night for hinds and -0.73 respectively -0.87 for stags. Although the hinds of the study period 2015 - 2016 have higher mean index values compared to the hinds of the previous study year, a positive preference is not reached at summer since the maximum values only reach -0.01. At winter the values remain relatively constant for hinds at around 0.4 while slightly increased values can be observed during the hunting season with a maximum mean index value of -0.29 in the morning hours. The least negative preference for stags occurs during the hunting seasons where the index values are around -0.8 with a slight increase at night. At summer, game reserves are barely accessed and thus a maximum mean index value of only -0.99 is reached. At winter the negative preference of stags also falls down to -0.99 during the day but increase again at night to reach a value of -0.82. During the time period of 2016 - 2017 the preference for game reserves remains relatively constant negative for hinds at summer and winter with values around -0.8 respectively -0.75. The values at summer are lower than during the summer months of the previous study periods. During the hunting season, the preference increases but still remains negative with constant values around -0.5. On the other hand, stags show a positive preference for game reserves at summer where a maximum mean value of 0.07 is reached in the morning. At night the index values decrease again to a negative preference. At winter and during the hunting seasons similar patterns of negative game reserve preference can be observed for stags where the values are highest at day and lowest at night. However, during the hunting seasons the preference is less negative and a maximum mean value of -0.45 is reached.

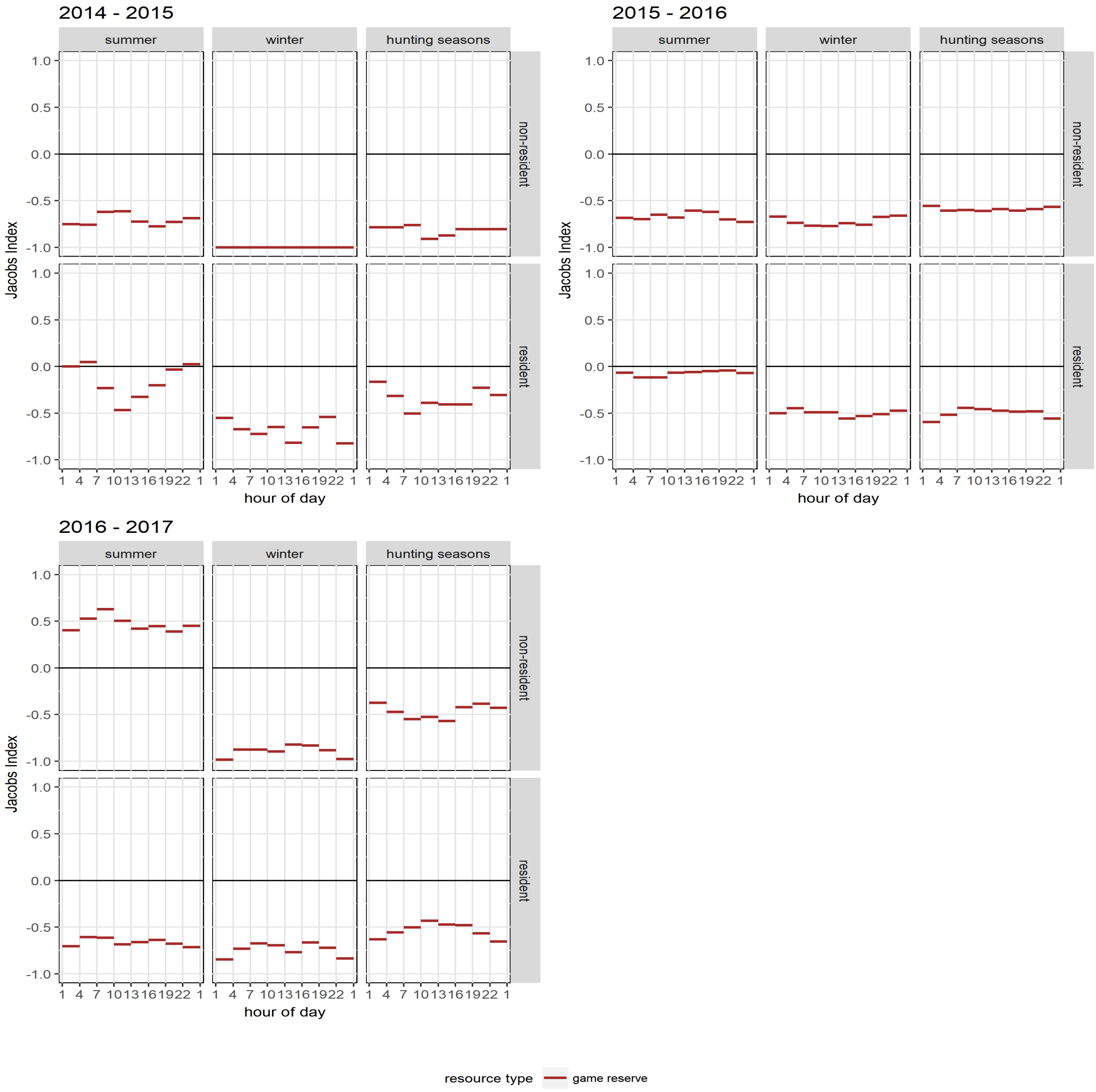


Figure 31: Jacobs Index (1973). Temporal preference during 2016 - 2017 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per migration type (resident and non-resident). Beams indicate time intervals of 3 hours.

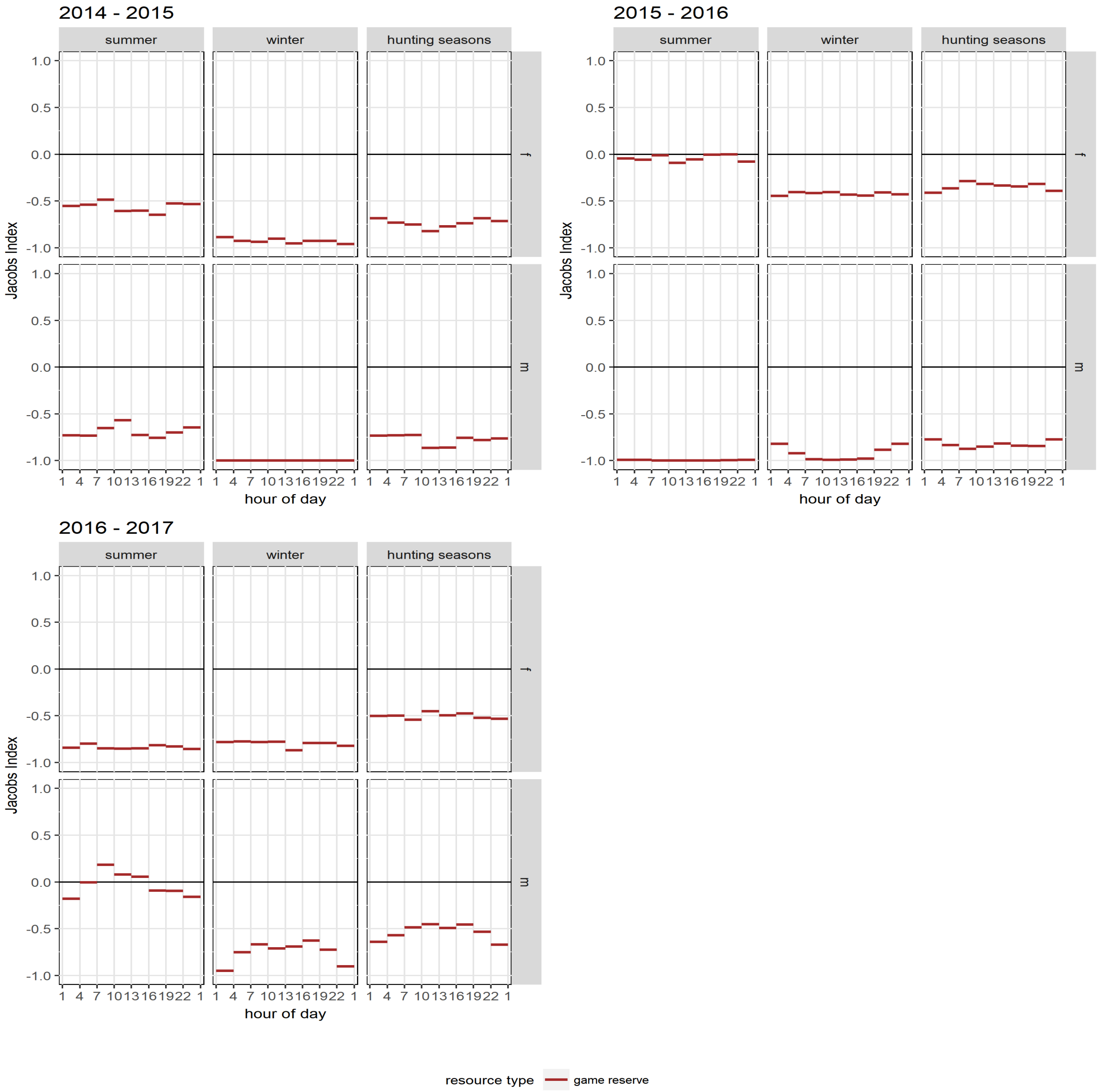


Figure 32: Jacobs Index (1973). Temporal preference during 2016 - 2017 of the resources forest, grassland, agricultural land, urban area and vineyards aggregated per sex. Beams indicate time intervals of 3 hours.

### 5.4.3. Discussion

As a first note it must be mentioned that the use of classified land cover areas might introduce a bias especially for the use of grasslands since dividing grasslands from other vegetational ground cover by using the NDVI comes with an uncertainty.

The relative resource analysis revealed a distinctive diurnal pattern for the use of forests where red deer individuals access forests more often during the day and less frequently at night. This pattern stands in contrast to the use of grasslands where peaks of use generally occur at night with a decrease during daytimes. Considering the findings of Mysterud et al. (1999) that grazing bouts are carried out in open habitats and resting / rumination bouts usually in areas with higher structural cover, the findings of the relative resource use analysis can be interpreted as such that the animals are mostly inactive at day and become most active at night, showing a constant trade-off between resting and ruminating under cover and foraging in open areas. When looking back at the results of the temporal activity patterns of section 5.3 indeed an increased activity level at night with lower activity levels at day were observed. However, peaks in activity were found during the twilight hours. Following the statement of Mysterud et al. (1999) a perfect matching resource use pattern would show lowest use of forests respectively highest use of open habitats such as grasslands during the twilight hours. However, in this study this is not fully true. Forest use is increasing, respectively decreasing, during dawn and dusk. But the minimal use is reached at hours of darkness. The reversed pattern accounts for grasslands where use is decreasing at dawn and increasing at night with maximum values at night, even though the pattern is not as distinct as for forest use. The reason as for why the animals already seek shelter when activity values are still high might be increasing human disturbance starting from the morning hours. As is described in section 2.1 a retreat into forests does not necessarily mean that the animals stop foraging. They might as well continue feeding from trees and bushes instead of grass. Another reason for this result might lie within the data structure and the coarse temporal resolution of three hours which. As a consequence of the low temporal resolution it might be that peaks of forest use at dawn and dusk cannot be detected properly in the first place. However, the exact cause for this discrepancy cannot be detected without additional information on the studied animals or ground-based observations. The results of the relative resource use analysis also show an increased use of urban areas at night regardless of gender and migration pattern. This behaviour might have several reasons as well, startin from the findings of Burcham et al. (1999) and Etter et al. (2002) that high forage quality such as gardens and fertilized lawns might attract animals during summer months as well as in winter. An additional factor which might influence this behaviour at winter is that the urban areas of the study area are located at the valley floors where snow cover is usually lower than up in the mountains (see section 2.1.3 for further explanations). Moreover hunting is restricted in urban areas, by which safe zones outside of the game reserves are created unintentionally during the hunting seasons. In fact, a higher use of urban areas was observed during hunting seasons, indicating, that the animals really did make use of urban areas to seek cover. On the other hand, no increased use during hunting seasons could be detected for non-resident animals and stags, which contradicts the expectations that the individuals seek shelter from hunting activity within these areas. Interestingly however, the use of game reserves shows a tendency towards increased during summer at day and decreased use at night as is the case for forests. This might indicate that animals make us of the game reserves to protect themselves from human disturbance during daytimes. Even though the relative resource analysis gives valuable insights into resource use patterns, it does not take relative abundance of each resource within the entire home range into account. The Jacobs Index (section 2.3.4) solves this problem by calculating the use of a certain resource in regad of its abundance. However, red deer might be located at different areas within the entire home range whereby some areas might be over- or underrepresentated as is the case for agricultural areas which are prominent in the southern region of the study area but not at all in northern regions such as Mesocco.

The analysis of the resource use by using the Jacobs index reveals a clear positive preference for forests during daytimes for all study years and regardless of the season and sex except for stags in the study period 2014 - 2015. Closer inspection of the individual Jacobs indices of the respective year of study (Figure A.10) reveals that especially individual h4 has a strong negative preference for forest areas. This negative values are partly a result of the response of h4 to the coarse regulation hunting season which lasted from the 01.09.2014 - 07.09.2914 to 15.09.2014 - 29.09.2014. During this time h4 was located above the timberline within the game reserve Trescolmen. In regard of the weak positive forest preferences of the other stags the aggregated mean values result in a negative overall preference of forests. At night the index values are negative, indicating a negative preference for most of the cases. What could not be seen in the relative resource analysis, is that there are stronger positive forest preferences at winter than during summer and the hunting seasons. This corresponds well with the findings of Beier & McCullough (1990) who found that the use of closed forests increases for white tailed deer (*Odocoileus virginianus*) at winter to seek shelter from cold winds. In addition, Arnold et al. (2004) observed a voluntary decrease of the metabolic rate and food intake during winter for red deer. This might partially explain, why the preference for grasslands is lowest during the period of 2014 - 2016 as well. In the other study periods no such distinctive difference between the Jacobs index values for grasslands between summer, winter and the hunting seasons occur. This might be due to the increased temperatures during the winters 2015/2016 and 2016/2017. Generally, the positive preference of forests during daytimes with corresponding decreased preference for grasslands can most probably be linked to the avoidance of anthropogenic disturbance.

In addition to the Jacobs indices for forests and grasslands the indices for urban areas, agricultural fields and vineyards were calculated as well. For all of these ground cover types negative preferences were detected for all seasons and years. This is surprising as problems with red deer damaging agricultural fields are a prominent issue for wild life management within the study area (Haller 2002, Jenny et al. 2011) and thus a positive preference of agricultural fields was expected. However, when examining the individual Jacobs index patterns, there are indeed only a few individuals who show positive preferences for agricultural fields. As can be seen in Figure A.10 only the individuals h9 and h12 reach positive index values during the hunting seasons and at winter of the study period 2014 - 2015. Both of these individuals were classified as migratory animals by the NSD migration pattern classification in section 4.1. During the hunting season h9 has its home range in the municipality Arbedo - Castione at the river Ticino. H12 also has its winter home range in Arbedo, south of Bellinzona where the river Moesa meets the river Ticino. On the other hand, there are five animals animals which do not access agricultural fields at all (h1, h5, h8, h13 and h18) during the studied periods. H1 is a resident animal which has its home range around Mesocco where no agricultural areas are located. The other animals migrate within the Calanca valley. Especially h5 and h8 can be found within agricultural areas if not only the defined months for summer, winter and hunting season are regarded. Interestingly h11 has its summer home range in a similar area as h9 and h12. However, h11 accesses agricultural areas less than the other individuals and stays within the alluvial forests which line the rivers Ticino and Moeasa. For the study period of 2016 - 2017 no positive Jacobs index values were reached by any individual during the study seasons. However, h25 has relatively high index values even though they remain negative. H25 is a resident individual which has its home range around Biasca where agriculture is prominent. Although it shows a negative preference for agricultural areas, it reaches the highest index values throughout the year. The animals which do not access agricultural areas at all during the analysed seasons are h20, h23, h24, h28, h29, h32 and h35. H20 has is a resident animal and has its home range around Mesocco. The other animals all have their seasonal home ranges around Bellinzona in the mountains and on the eastern valley flank. H32 and h33 access agricultural areas outside of the study seasons. During the study period of 2016 - 2017 h43 shows a positive preference of the agricultural areas at summer even though the overall index values remain negative. H43 is a resident animal which stays in the border region of Bellinzona between the rivers Ticino and Moesa all year round. In addition, h39 has positive preferences for agricultural areas during the hunting season. It also is a resident animal which has its home range around Grono. Those individuals which do not access agricultural areas at all during the three studied seasons are h38, h40, h41, h42, h47 and h48. Except for h38 and h47 all of those individuals have their home ranges around the San Bernardino Pass where no agricultural fields are located. H38 and h47 actually access agricultural areas but not within the the defined months of summer, winter and hunting seasons. Generally agricultural fields are accessed at night with lower index values during the day. The fact that some of the individuals which were found to not access agricultural areas in the predefined seasons actually use agricultural fields might lead to a general increase of the Jacobs index values and show more positive preferences, matching the long lasting experiences of local residents. The reason as for why agricultural areas are accessed only little during the study seasons could be that some of the cultivated crops do not ripe until August. For example Mais usually reaches its ripeness at the beginning of October. Harvest time then lasts from October until the beginning of November and for corn from June until August (Schweizer Bauernverband 2018). The same accounts for soy fields which reach their highest nutritional value in August and are usually preferred by red deer[7]. As a consequence, it might have been beneficial to chose the months of August until October as well to get a more encompassing impression of the resource use patterns. In addition, the values of September were merged with the values of November and December to derive information of the hunting periods. However, during November and December crops are already harvested which leaves the agricultural areas unattractive for red deer. This might blur potential positive resource selection during September.

Generally, negative preferences are shown for vineyards and urban areas as well during all study periods regardless of the migration type and sex. However, for urban areas u-shaped patterns for negative selections can be observed which sometimes nearly reach values for positive selection. When considering the individual animals positive selection of urban areas occurs mainly occur at winter and during the hunting seasons for all study periods. This supports the findings of Mysterud et al. (2011) that red deer shift their winter home range to urban areas in order to benefit from increased winter conditions (see section 2.1). In addition, Burcham et al. (1999) found that red deer avoid hunters by getting close to urban areas where hunting is prohibited. This behaviour might explain why positive Jacobs index values occur during the hunting seasons. Overall, vineyards are accessed more often than agricultural areas, resulting in higher index values which decreased at day, reaching minimum values around noon and maximum values at night. Reasons as for why vineyards were more often used than agricultural areas might be that vineyards are often located close to forest edges or even within forests. As a consequence, it might be easier for red deer individuals to access this resource.

The relative resource analysis reveals that game reserves are more often used at summer for non-resident animals and regardless of the sex. The increased values during the summer months suggest that red deer individuals mainly access game reserves during the day. However, during all seasons areas which do not belong to game reserves were used more often than game reserves. This is surprising as especially during the hunting season it was expected that game reserves were used more often in order to be save from hunters. The analysis of game reserve use with the Jacobs index surpisingly

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[7] Personal communication with Hannes Jenny AJFGR, 04.01.2018

shows a negative preference during the hunting seasons no matter of the migration type and sex for all the study periods. However when the individual values are analysed h1 shows a preferred use of game reserves during all seasons (see Figure A.13). However, negative selection occurs as well during the winter months. The generally high index values of the individual h1 are probably influenced by most parts of the location of the animal's home range which overlaps a game reserve to a large extend and not necessarily due to hunting pressure or other human disturbance as the index values during the hunting seasons then would presumably be higher than those of the summer month and the preference would remain positive at winter at least during the daytimes since that is the time when human activity is highest. In addition h5 and h13 have a positive preference toward game reserves as well but only during the summer months. The reason as for why such a high positive preference at summer occurs is not entirely clear since it is the intend of game reserves to mainly protect animals from human disturbance during the hunting seasons and at winter. During this study period h8, h9, h11, h14, h15 and h18 do not access game reserves at all all during the predefined seasons. However h8 accesses the game reserve Trescolmen at October but since the summer home range is located in that area and only a few points were recorded within the game reserves it can be assumed that the game reserve was not visited on purpose. The remaining animals which do not access the game reserve are located around Bellinzona close to urban areas where hunting is prohibited. This might be a reason as for why these animals do not seek protection from hunting within game reserves. During the time period of 2015 - 2016 only individuals h23 and h25 show a positive preference for game reserves. Generally the patterns look similar with high preference during summer and the hunting season and lower values at winter where h25 shows a negative preference for game reserves. For h25 the case is very similar as for h1 where the preference of game reserves is probably more based on the location of the home range than on anything else. On the other hand, h23 seems to make us of the function of the game reserves as it stays within the game reserve at winter as well which might be explained by the ski region which is close by. H19, h24, h28, h29, h32 and h35 do not use game reserves during the analysed seasons. H24 enters the game reserves during April. However since winter and hunting seasons are over by then, the game reserve has no particular purpose at that time. Hence it is assumed that the use of the game reserve is more a coincidence since the area is part of the animal's home range. The same accounts for h28 of which only 4 GPS fixes are located within the game reserve. In the following study period of 2016 - 2017 positive h41 shows a distinctive increase of positive game reserve preference compared to the other seasons where the preference is negative. This might indicate that h41 is seeking shelter from hunting pressure. The unimodal pattern with increased index values at daytimes supports this assumption as hunting mainly takes time during the day. H40 shows a positive preference for all three seasons. However, since the index values are relatively high during all periods it might as well be that the game reserves overlaps with the home range of the individual by coincidence. However, the negative preference of the game reserve at night for the winter and hunting season also hints to the fact that the red deer might actively seek protection during the day from human disturbance.

All in all, game reserves were accessed less often than expected especially during the hunting seasons. A part of this might account to the urban areas in the valley bottoms where hunting is restricted anyway. On the other hand it might also be the case that the home ranges of h1, h24 as well as h40 are not overlapping game reserves by accident but that the animals set up their home ranges in those regions purposely out of a feeling of safety. This assumption is supported by Burcham et al. (1999) who illustrated that red deer know about the value of such areas as game reserves where hunting is banned. In addition game reserves are usually created in areas which seem to be favourable for red deer. As a consequence it is not surprising when animals set their home range around those areas [8]. If this is truly the case for the animals whose home ranges overlap with the game reserves, the game reserves are of great value since they prevent that more deer are seeking refugee within urban areas during the hunting seasons.

The results of James Patrick (2017) concerning forest use differ in that the Jacobs index shows a bimodal pattern in positive forest preference. Such a bimodal pattern could not be observed in this study. However, the underlying cause of this might be the coarse sampling rate which could blur such short term changes in resource use. On the other hand the results are similar in regard to the general negative preference at night. In addition, Patrick (2017) was able to illustrate the importance of game reserves within his study area. In both theses there were animals which showed an increased preference for game reserves during summer, indicating overlapping home ranges. However, since the character of the study area of this thesis is more heterogeneous it is difficult to draw concluding remarks especially since deer seem to abuse rural areas as game reserves during the hunting seasons.

### 5.5. Resource Use and Activity

Figure 33 shows the proportion of used resources in combination with the behaviour types fast locomotion, slow locomotion / feeding and resting in order to illustrate where certain behaviour types occur most often. All three behavioural types mainly happen within forest areas. In times were a resident and non-resident individual moved fast during summer months there is a tendency that the probability of it standing in grasslands is lower than when exhibiting the other behavioural types. In addition, for both non-resident and resident animals the share of grasslands on the total resource use is during slow locomotion / feeding higher for all seasons than when deer were resting except for the hunting season in non-resident animals were the use of grassland was highest for fast locomotion. Complementary to that, forest use is higher during times of rest compared to times when other activities prevail. During winter forest use increases for all activity types but the biggest change can be seen for fast locomotion in resident animals which barely show fast locomotion activity in urban areas anymore. During the hunting seasons, fast locomotion within urban areas increases again. For non-resident animals on the other hand resting activity as well as slow locomotion are shown less often in grasslands as is the case at summer and during the hunting seasons. The use of agricultural fields emerges at winter months for non-resident animals and increases during the hunting season with fast and slow locomotion / feeding behaviour being exhibited more often in agricultural land than resting. Resident animals already used agricultural areas at summer but only to a very small extent where slow locomotion and resting behaviour was shown as during the hunting season. Stags and hinds performed all activity types mainly within forest areas which is logical since forests are the resource which were most often accessed according to the resource utilization study (see Figure 33). During the summer months the share of forest areas was highest for stags during times when they were resting and for hinds when they were moving fast. In contrast, the probability of a stag being within a forest was lowest when it performed fast locomotion. This pattern occurs during all seasons stags. However, at winter all activity types occur of stags occur less often in grasslands but also in urban areas. Fast and slow locomotion / feeding are also performed in agricultural areas. During the hunting seasons the use of grasslands for all activity types is higher than at winter. Moreoever all activity types occurred less often within forests. For hinds the share of forests at summer was lowest when slow locomotion was performed. Resting behaviour

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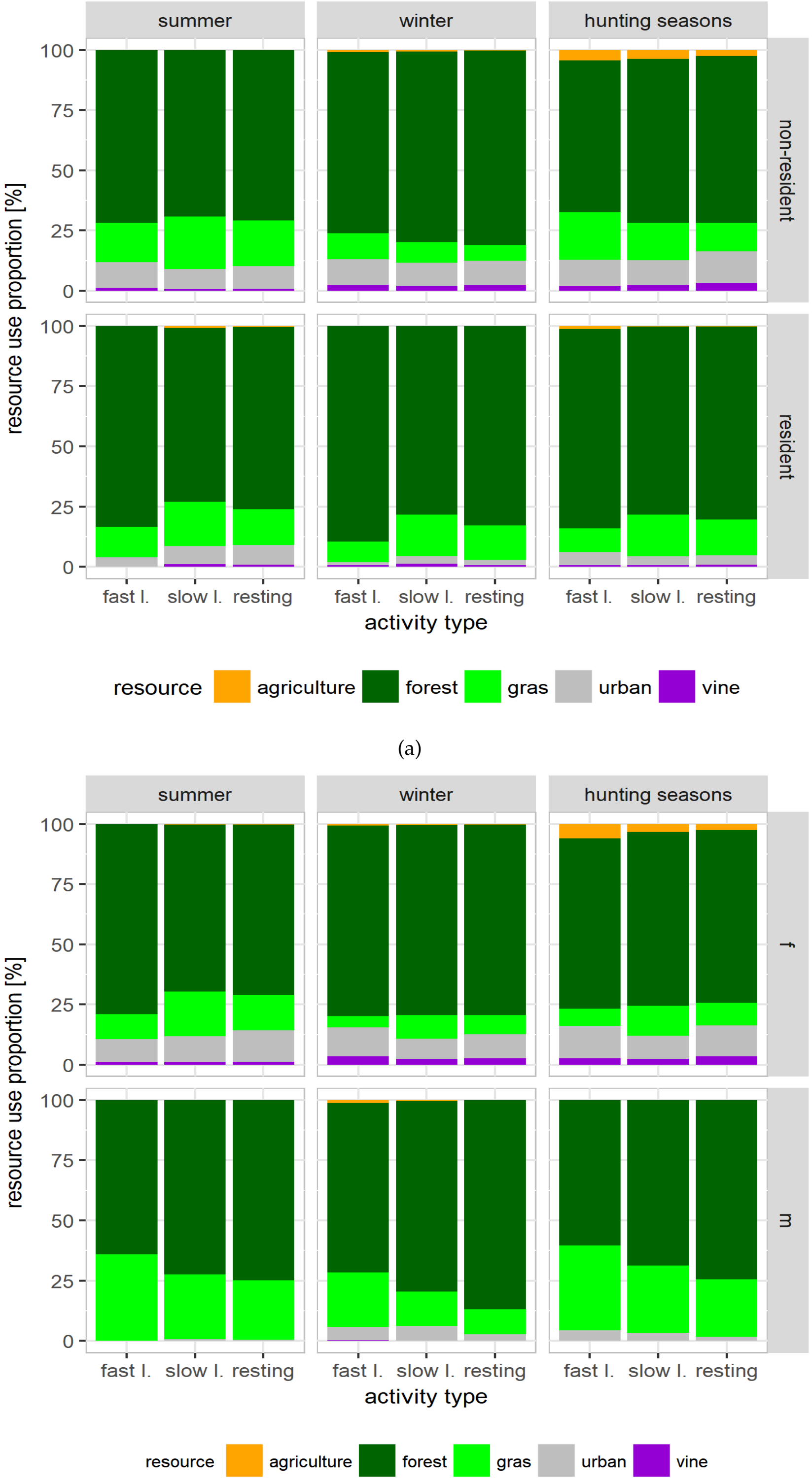
[8] Personal communication with Flurin Filli (Swiss National Park) and Hannes Jenny (AJFGR), 04.01.2017

was also observed in urban areas. The share of urban areas for resting behaviour is even higher than for fast and slow locomotion / feeding. In addition, hinds performed fast locomotion less often within grasslands during winter months but the share of fast locomotion which was performed in urban areas increased. During the hunting season, agricultural fields were used more commonly with fast locomotion being the most often performed activity within such fields. In comparison to the summer months all types of activites are shown less in grasslands but more often in urban areas or agricultural fields during the hunting season.

### 5.5.1. Discussion

Generally, the results of the resource analysis in connection with activity types confirm the findings of Mysterud et al. (1999) that resting behaviour is most often carried out in covered habitats while slow locomotion and feeding behaviour are more common in open areas such as grasslands compared to resting behaviour. Moreover, it is reasonable that the share of grasslands where all three behaviour types are performed is higher at summer than during the winter period since the use of forest areas is generally lower during the summer month (see section 5.4). It is a bit of a surprise that the share of agricultural areas is highest for the activity of fast locomotion during the hunting seasons, followed by slow locomotion / feeding because it was assumed that agricultural fields are mainly accessed for feeding. However, it might be that the animals are especially vigilant in agricultural areas since usually human settlements are close by. The vigilant behaviour might result in higher activity values due to increased head movement activity.



(a)

(b)

Figure 33: Occurrence of the behaviour types fast locomotion, slow locomotion / feeding and resting during the time periods 2014 - 2015 and 2015 - 2016 within the resources agriculturally used fileds, forest, grasslands, urban areas and vineyards. Aggregated per migration pattern (resident and non-resident) (a) and sex (b).

# 6. Conclusion

Patrick (2017) mentions the difficulties of correctly interpreting results from computational movement analysis (CMA) when data such as accelerometer data or data of the studied animal's physiology is missing. Laube (2014) refers to this issue with the term of a semantic gap, which is described as follows:

*"A recurrent theme in recent deliberations concerning Geographic Information Science is the perceived gulf between, on the one hand, the low-level observational data that constitutes the 'raw material' of our science, and on the other hand, the high-level conceptual schemes through which we as humans interpret, understand, and use that data. A priority for Geographic Information Science is to find appropriate ways and means of bridging that gulf."*(Galton 2005, 300)

Extracting information out of the red deer data was approached with different methods and contextual information in this thesis and in the work of Patrick (2017). While for example the data of this thesis only had a low temporal resolution which hindered the analysis of small scale movement patterns Patrick (2017) could rely on the high temporal resolution of his dataset to derive information of daily activity patterns which could only be done in this work with the use of accelerometer data. However, apart from additional contextual and ecological information about the study subject the value of expert knowledge is still high for CMA.

### 6.1. Insights and Major Findings

The **migration pattern classification** (Research Question 1) illustrated that red deer should not just be classified into resident and migratory animals since a lot of individuals do not perform full migration but only perform partial migration as was illustrated by Cagnacci et al. (2016). The migration classification resulted in patterns of migratory, mixed-migratory, dispersal, nomadic and resident animals. However, high differences in elevation for resident animals indicated that the mere euclidean distance between points does not suffice in an alpine environment to correctly describe migration patterns. In addition it could be shown that migration patterns cannot be solely explained by temperature but that multiple criteria have to be taken into account, such as the start of the hunting season. I conclude that migration patterns cannot simply be categorized by the MCP, KDE and NSD methods alone but that especially in an alpine environment external factors such as elevation differences have to be considered as well.

In regard of the **home range size analysis** (Research Question 2) it was found that home ranges which were calculated with the MCP methods were overestimated significantly. More accurate results were found with the KDE and the dBBMM methods. The differences between the summer and the winter home range size were also higher for the MCP calculations with winter home ranges being larger than summer home ranges which was not reasonable according to findings in previous studies. As a consequence it is concluded that the MCP is not suitable for the estimation of home range sizes. In addition, it was observed that snow cover might indeed play a role for decreased winter home range sizes as was found by Georgii & Schröder (1983) since the difference of summer and winter home range size decreased with lower elevation and when the winter home ranges were located further south in the study area. The home range sizes were generally smaller in comparison to the home ranges in the Swiss National Park.

The analysis of the **temporal activity pattern** (Research Question 3) revealed a bimodal activity pattern throughout the study period with peaks of activity occurring during the twilight hours. In addition, the activity values showed an increase of activity starting from March until August for both sexes as well as decreased activity during the winter months. Moreover, the diurnality index illustrated that red deer prefer nocturnal activity throughout most of the year while diurnal activity is preferred during the months May and June. The nocturnal and crepuscular activity patterns are believed to be caused by a high amount of human disturbance which is typical for the study area. Yet, the behaviour type fast locomotion occurred very rarely, indicating a high quality of the habitat with enough possibilities to seek cover. Moreover, closer inspection of the daily activity pattern revealed that the increased activity during the twilight hours was related to feeding / slow locomotion behaviour which constitutes the main activity throughout the day.

Including contextual information for the analysis of the **resource use** (Research Question 4) patterns revealed the high use of forests compared to other areas with increased positive preferences during the day and mostly negative preferences at night. Contrary to this pattern grasslands were more often accessed during the night revealing once more the nocturnal activity behaviour. The annual pattern of forest and grassland use consisted of an increased use of forests at winter with a corresponding decreased use of grasslands. The alternating use of forests and grasslands show that there is a constant trade-off between the requirements of feeding and shelter which can be used for red deer management systems. The u-shaped daily pattern could also be observed for man made structures such as agricultural fields, vineyards and urban areas with an increased use of urban areas during winter and the hunting seasons. This increased used during the winter and hunting seasons indicates that red deer shirt their home ranges to urban areas during harsh times in order to profit from increased circumstances during winter and hunting restrictions, confirming the high adaptability of red deer. Surprisingly a mainly negative preference for agricultural areas could be detected. This is believed to be mainly the case due to the unlucky definition of summer, winter and hunting seasons which exclude the times were crops are ripe and the inclusion of months (November and December) where the crops are already harvested. It is assumed, that the preference for agricultural areas would be more positive if the seasons were chosen differently. Furthermore, the results indicate that the game reserves help to provide a good dispersion of red deer in space since they prevent that all animals move into urban areas to seek protection from hunting activity. The overall high variability in the individual resource use patterns show that it is not an easy task to derive information which are valid across the whole population and emphasize the high individuality within red deer populations.

Finally, the analysis of **resource use in context of activity** (Research Question 5) showed that resting behaviour is indeed carried out most often within forests and less in grasslands while for slow locomotion and feeding behaviour the share of grasslands increases at expense of the forests. In addition it can be observe that all activity types are more often performed in forests at winter than in summer, hinting again at the generally increased use of forests during the winter months. These findings underline the importance of the resources forest and grasslands during the daily life of red deer.

### 6.2. Limitations

The results and conclusions of this thesis are limited to the study area at the border region of the cantons Ticino, Grisons and the Lombardy and the individuals which were analysed. Since the study area has a very unique characteristic with high variations of human influence, climatic conditions and unusual topography makes inferences to other areas and populations not viable. Moreover, the coarse sampling interval of the GPS location fixes made it difficult to extract short term changes and patterns.

While the ground cover data of agricultural fields, vineyards, urban areas and forests were provided by official agencies, information about grasslands was derived by using remotely sensed data to calculate the NDVI. The thus derived grassland data set was not controlled with ground truth information.

In light of the home range estimations and resource use analysis it has to be mentioned that the results are highly dependant of the parameters which were chosen for the KDE and dBBMM analysis. The viability of these parameters can only be judged with expert knowledge and are susceptible to subjective decisions. This results in another limitation limitation of this work. The interpretation and validation of the results which were computed from the GPS derived data sets often rely on the findings of previous studies of red deer which were conducted in similar circumstances, ground observations and expert knowledge. Hence, the correct interpretation of the derived results, or as Laube (2014, 83) calls it "bridging the semantic gap", is a task that should not be underestimated in its complexity.

### 6.3. Future Work

In the classification of migration patterns it was shown that the classification with only the use of methods which rely on horizontal distances does not do justice to the complex topographic environment of an alpine area. In future work the NSD classification could be supplemented with a second step where changes in elevation are included as well for example by replacing the euclidean distance in the NSD computation with differences in elevation to reclassify animals which were wrongly classified as resident animals by the standard NSD calculations.

Moreover, environmental factors such as precipitation and snow cover could be included in the analysis of migration patterns in order to be able to derive information about the reasons for the onset of migration.

In addition the approach of Patrick (2017) to gain information about activity levels by calculating the speed between two consecutive fixes might be combined with the activity data in order to reach a higher accuracy in the evaluation of activity.

Generally, a shorter temporal resolution of the sampling interval of the GPS fixes might reveal finer behaviour patterns in regard to resource selection. More information about this topic may be generated as well with the inclusion of information about the weekly growth of crops on agricultural fields as well as ground cover vegatation such as grass.

# 7. References

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# A. Appendix

## A.1. Migration Pattern Classification

### A.1.1. GPS Data Overview

The following maps show overviews of the red deer individuals during their respective year of study, including the game reserves of the canton of Grisons and Ticino.

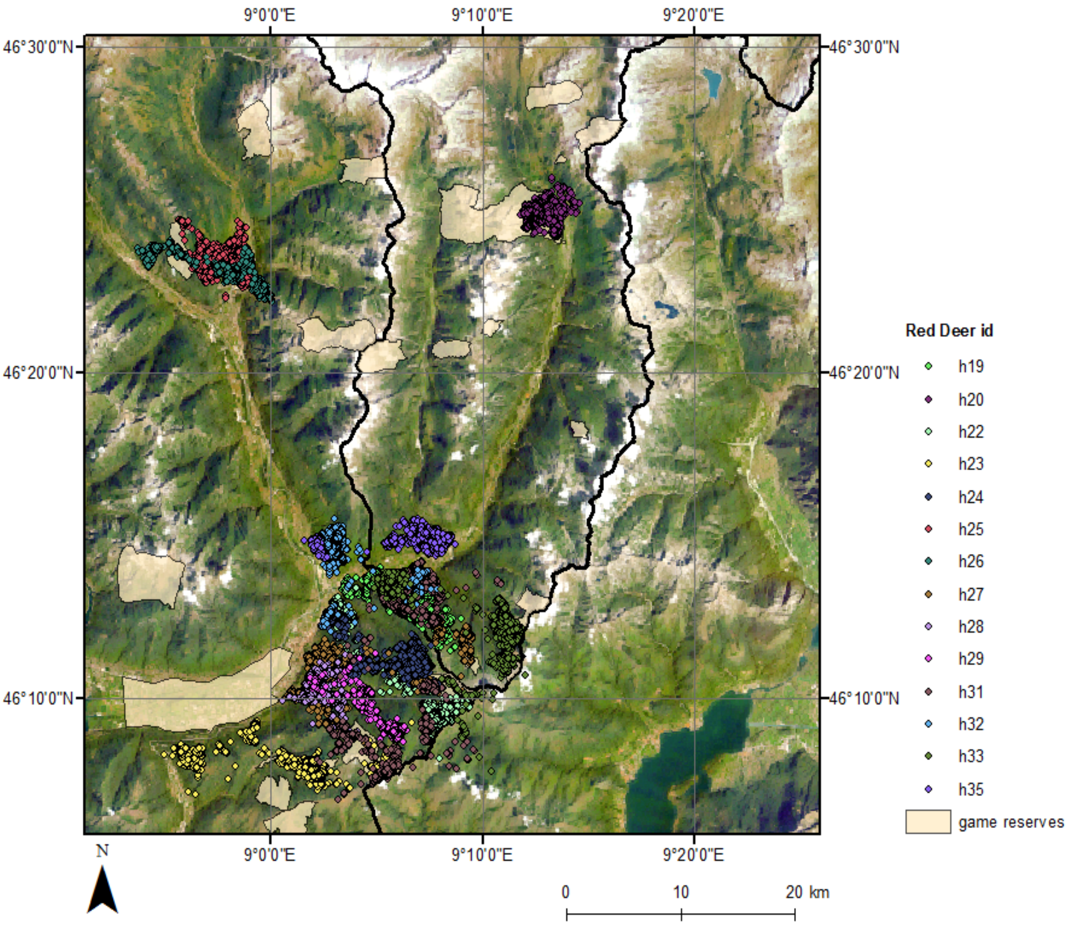

Figure A.1: Overview of the red deer individuals during the study periods 2015 - 2016.

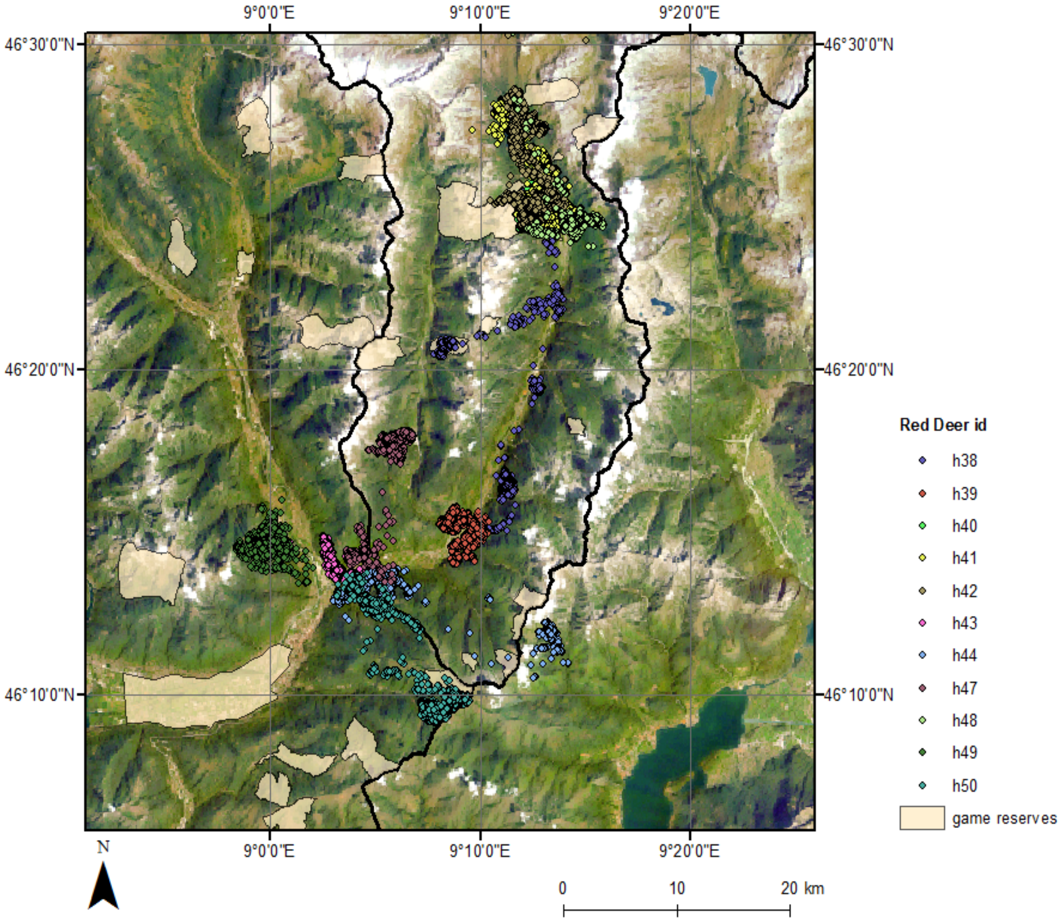

Figure A.2: Overview of the red deer individuals during the study periods 2016 - 2017.

### A.1.2. Influence of Temperature on Migration Behaviour

The following graphs represent the daily travelled distance in metres as well as the daily mean elevation [m.a.s.l.] of each red deer individual in the course of its study year. In all graphs the dark green curve shows the mean daily temperature within the area where an individual was present during the first three days of the analysis period (see section 3.2.1). The light green curve, on the other hand, depicts the temperature which was measured by the GPS collar. The red curves represent the travelled distance in km as was described in section 2.2. Blue curves depict the daily mean elevation [m.a.s.l.]. The yellow beams indicate the coarse regulation ((*Hochjagd*), followed by the orange beam which shows the time of the fine regulation period.

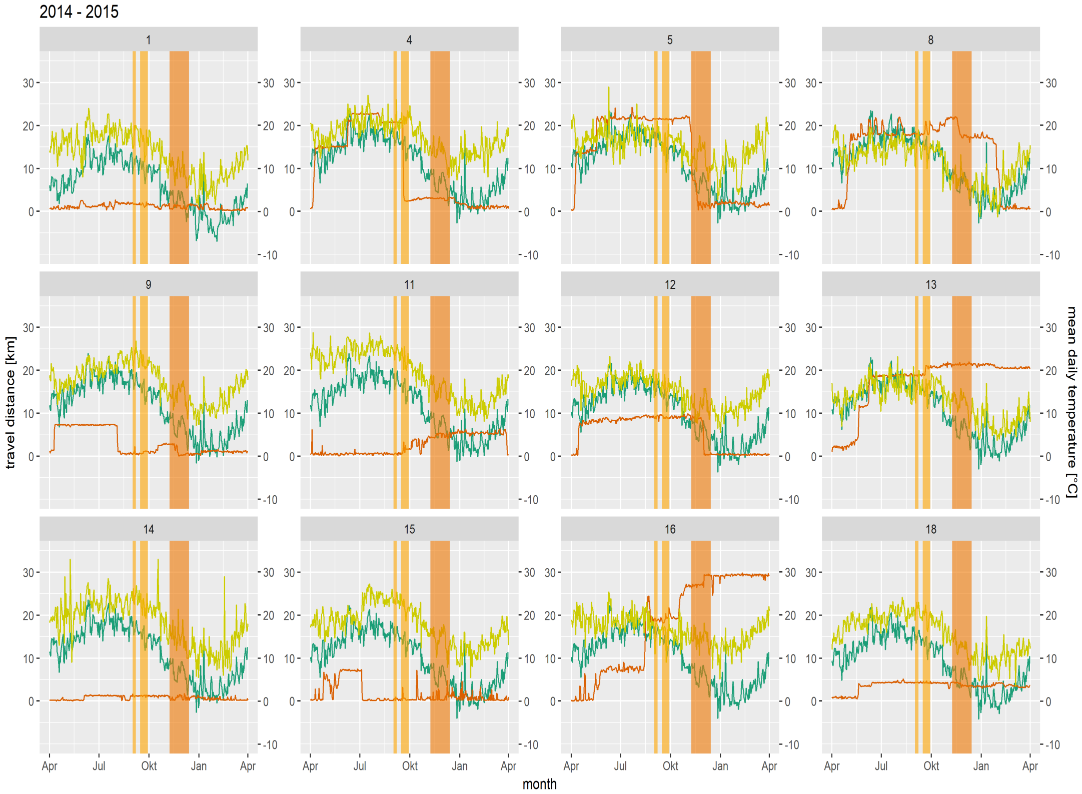

Figure A.3: Daily mean travelled distance of each individual of the study period 2014 - 2015.

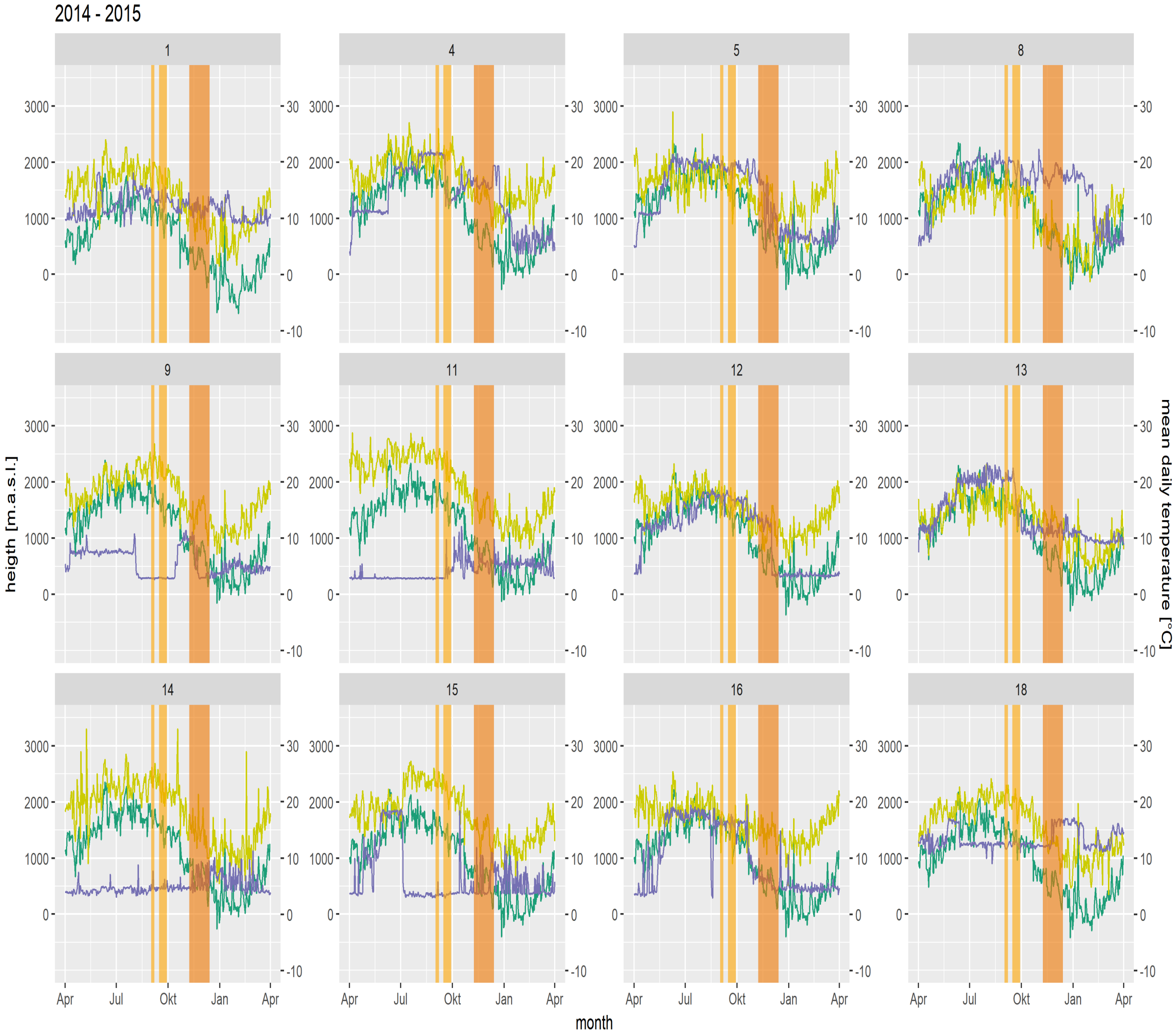

Figure A.4: Daily mean elevation of each individual of the study period 2014 - 2015.

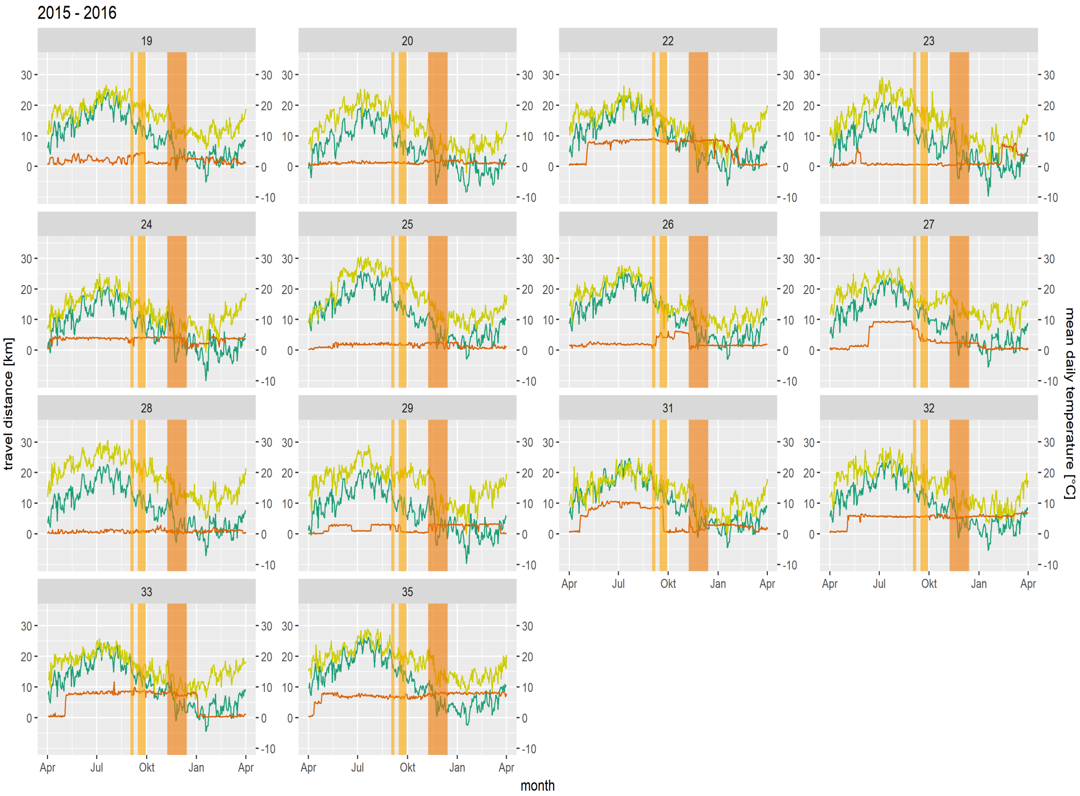

Figure A.5: Daily mean travelled distance of each individual of the study period 2015 - 2016.

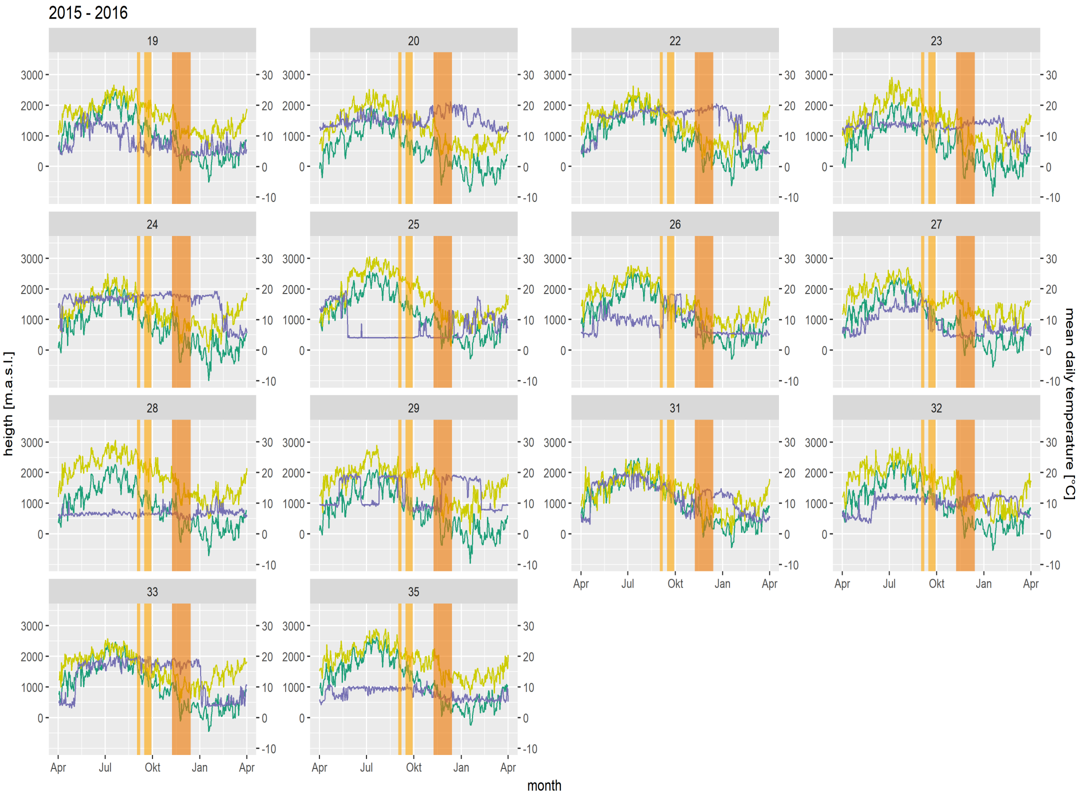

Figure A.6: Daily mean elevation of each individual of the study period 2015 - 2016.

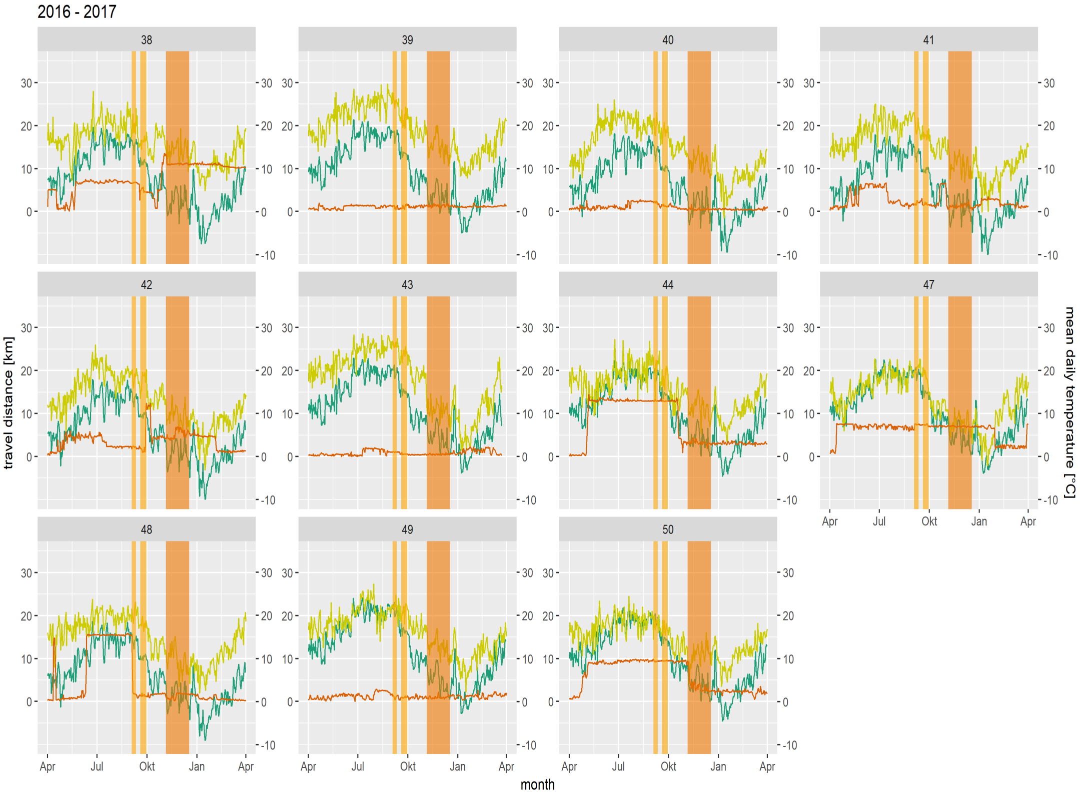

Figure A.7: Daily mean travelled distance of each individual of the study period 2016 - 2017.

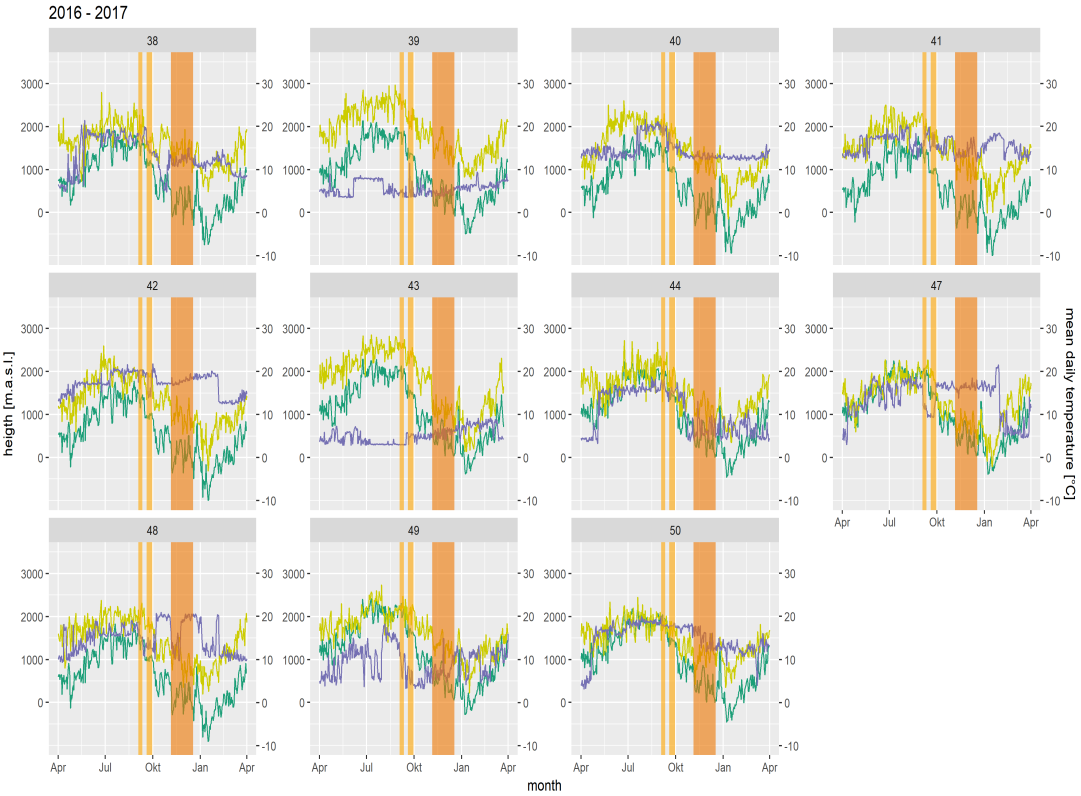

Figure A.8: Daily mean elevation of each individual of the study period 2016 - 2017.

## A.2. Temporal Activity Pattern

### A.2.1. Monthly Activity Pattern

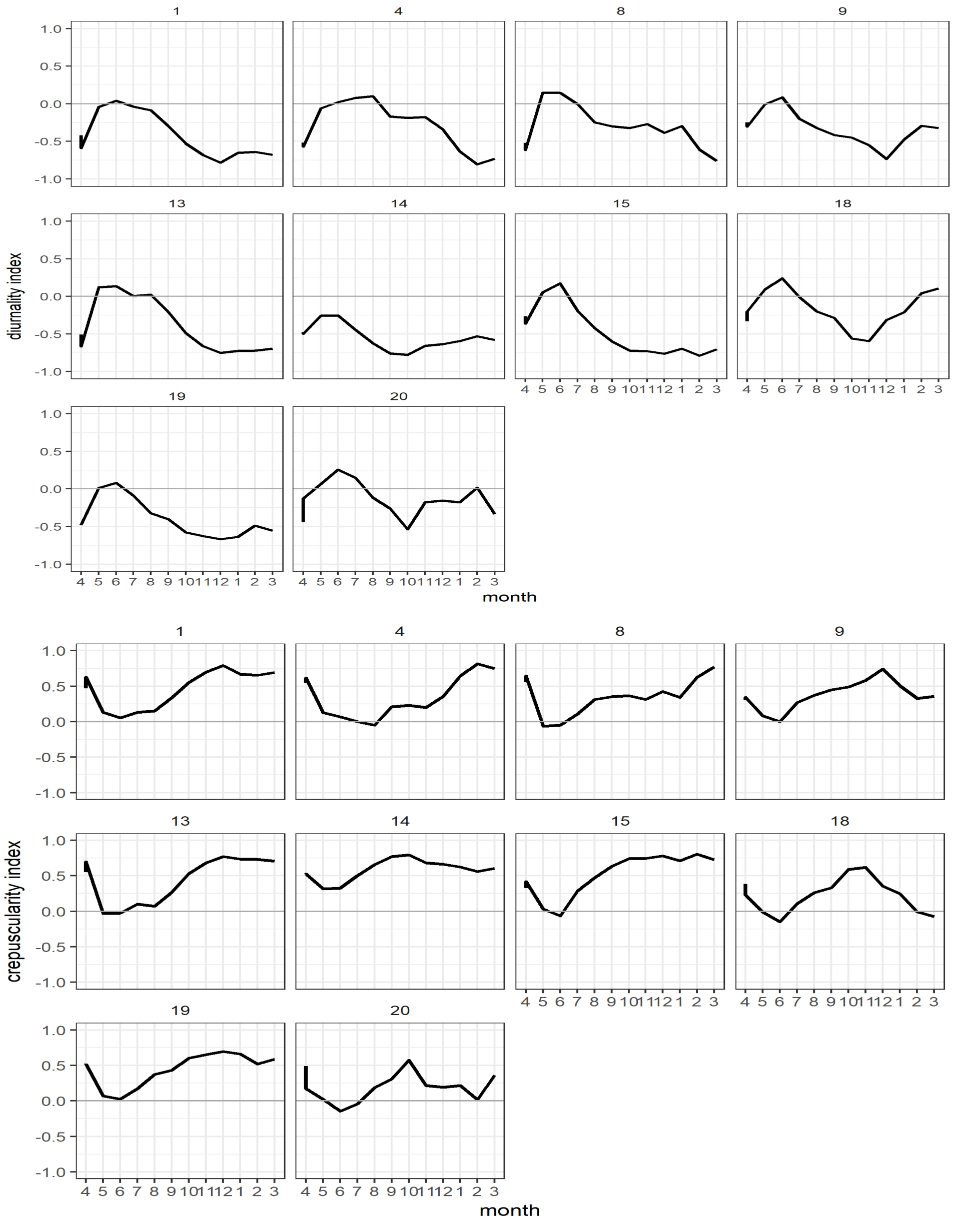

Figure A.9: Diurnality and crepuscularity index for the periods 2014 - 2015 and 2015 - 2016.

## A.3. Resource Use

### A.3.1. Jacobs Index

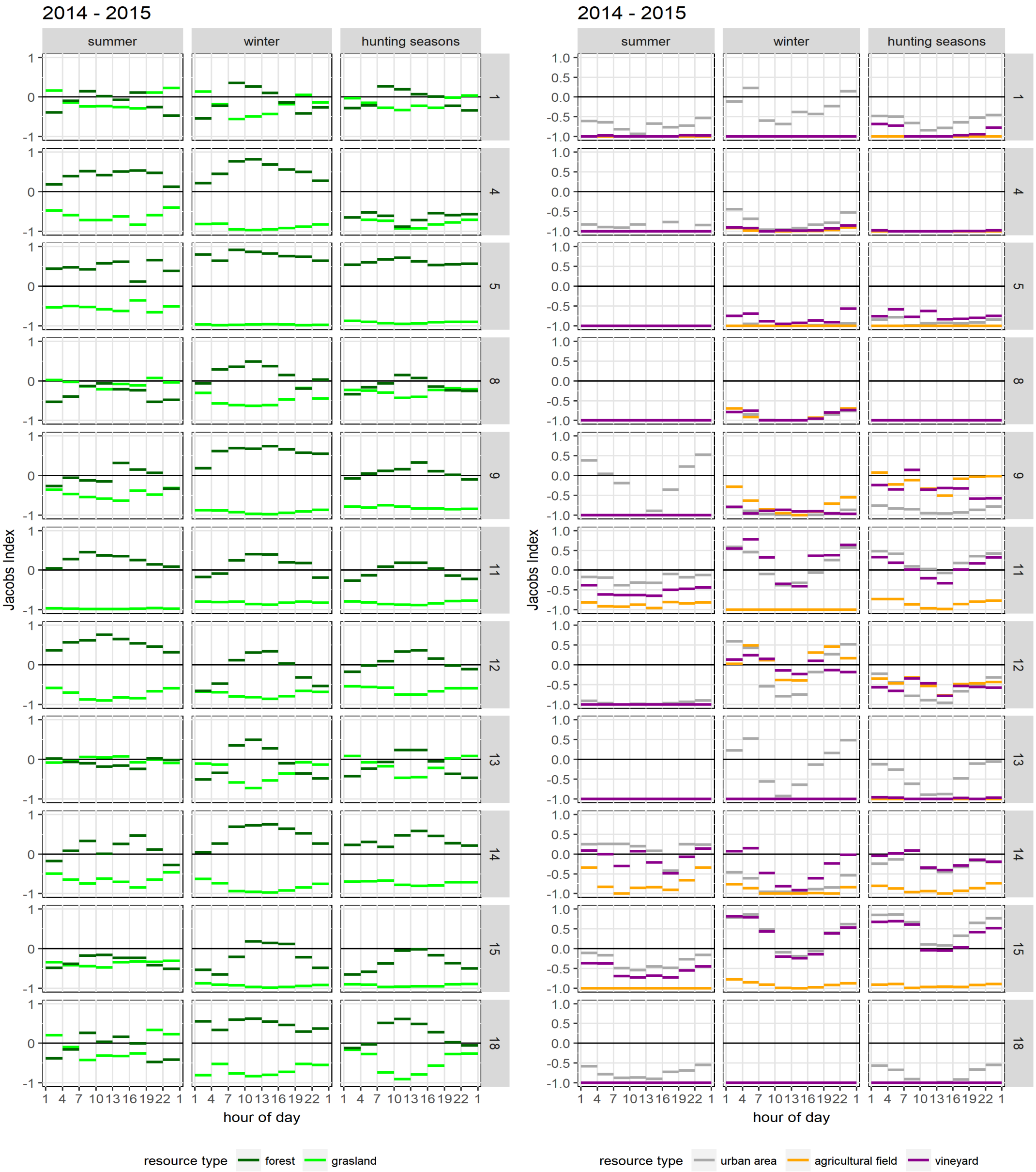

Figure A.10: Jacobs Index (1973). Temporal preference during 2014 - 2015 of the resources forest, grassland, agricultural land, urban area and vineyards for all individuals. Beams indicate time intervals of 3 hours.

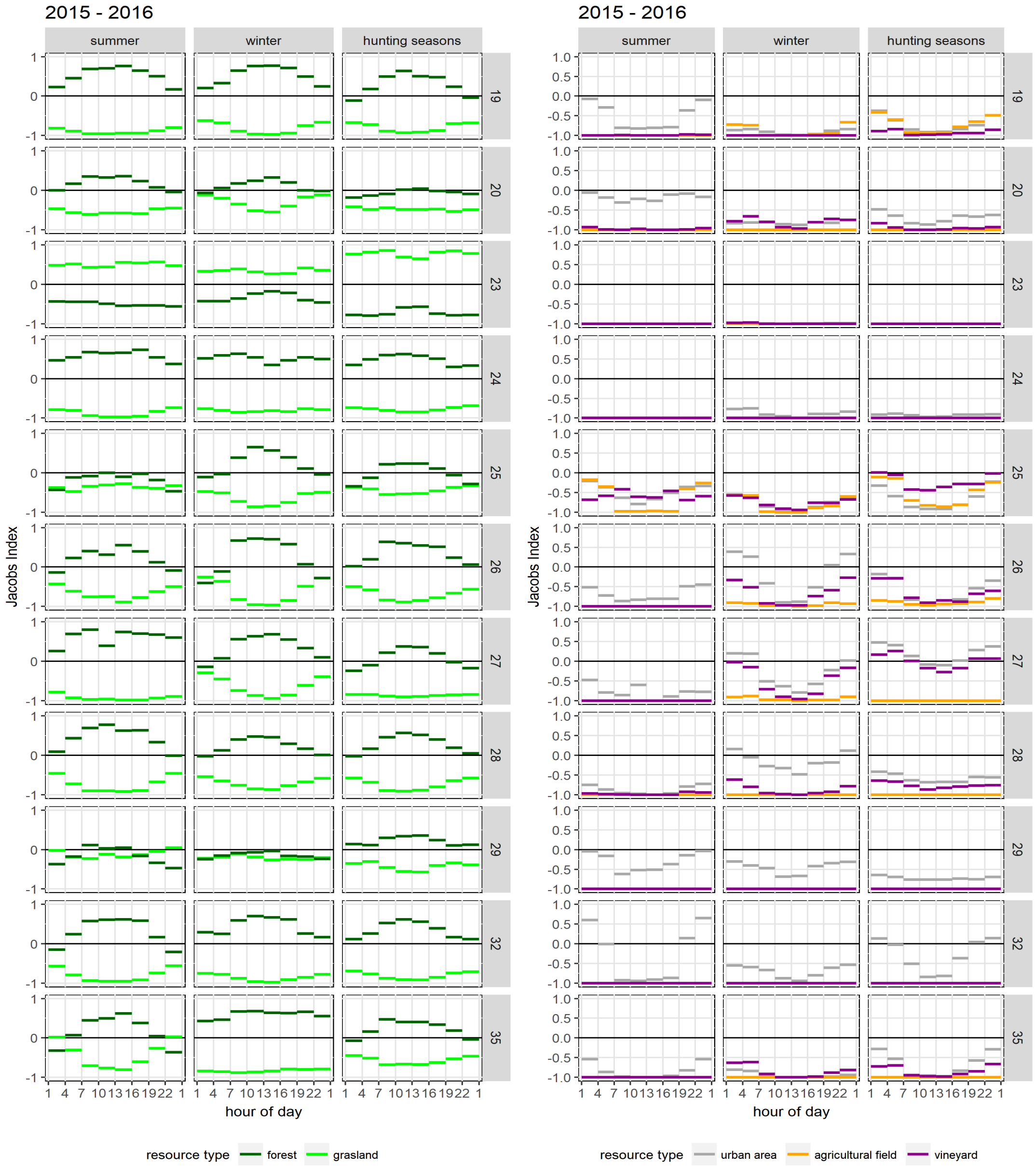

Figure A.11: Jacobs Index (1973). Temporal preference during 2014 - 2015 of the resources forest, grassland, agricultural land, urban area and vineyards for all individuals. Beams indicate time intervals of 3 hours.

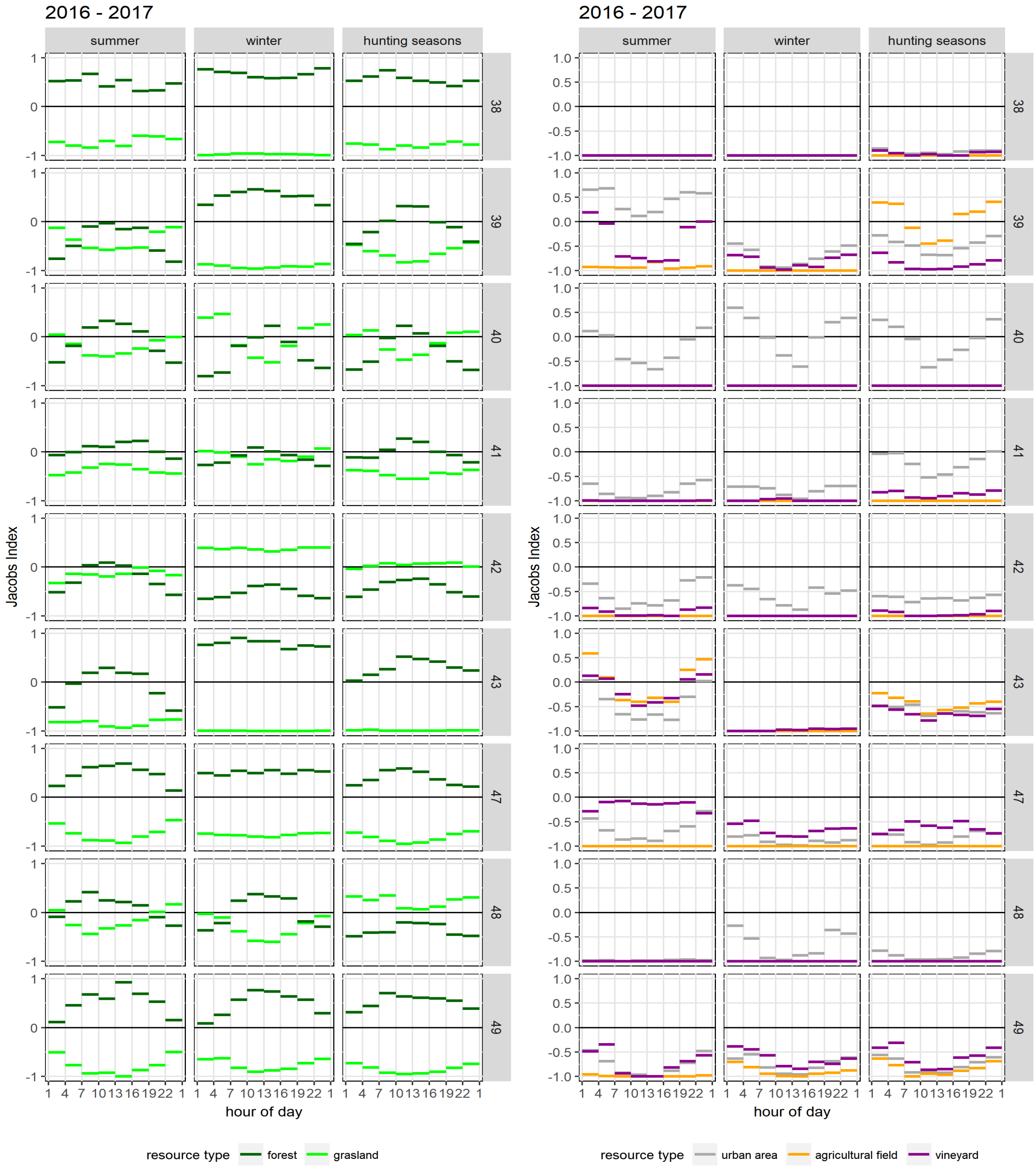

Figure A.12: Jacobs Index (1973). Temporal preference during 2014 - 2015 of the resources forest, grassland, agricultural land, urban area and vineyards for all individuals. Beams indicate time intervals of 3 hours.

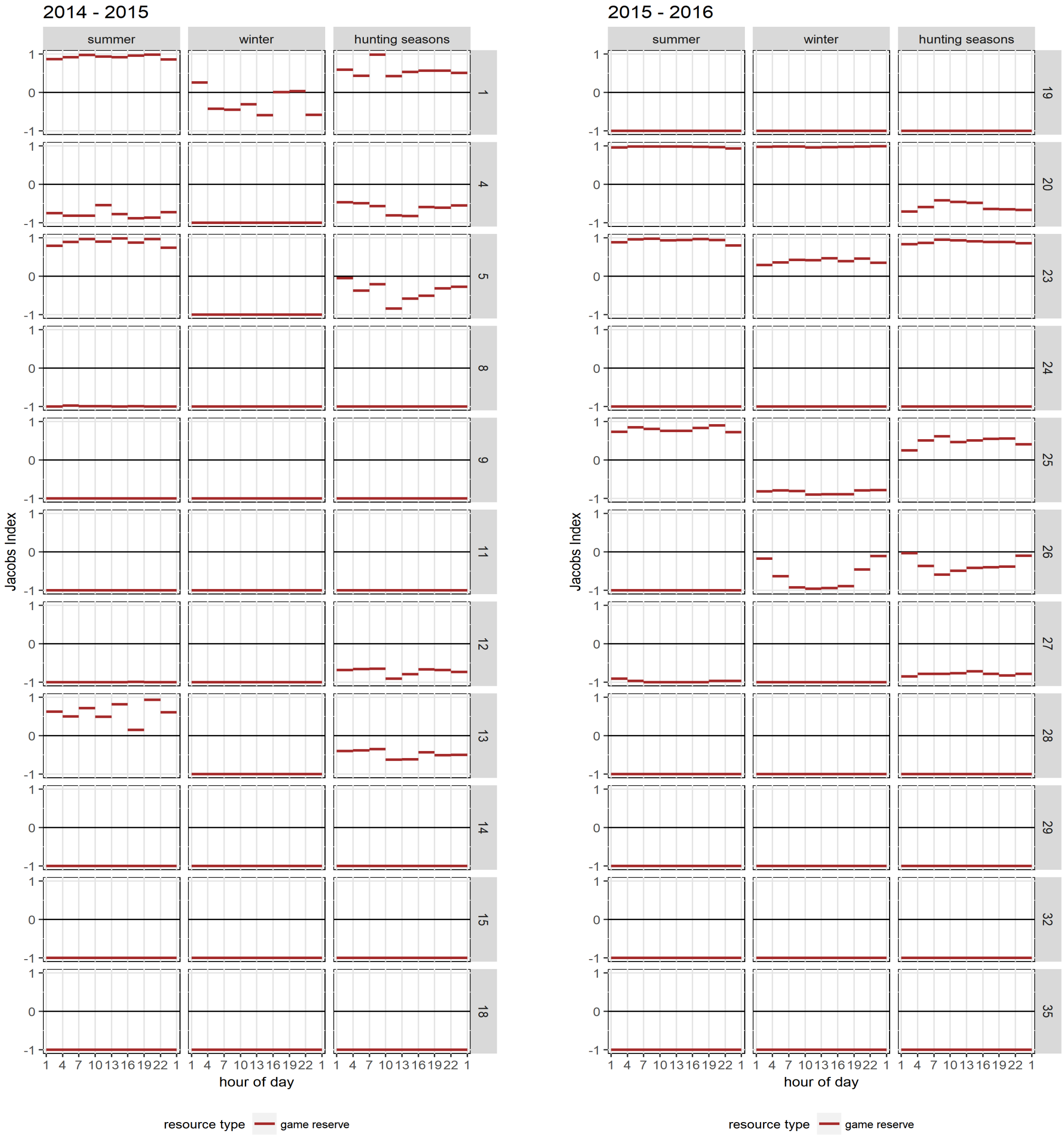

Figure A.13: Jacobs Index (1973). Temporal preference during 2014 - 2015 and 2015 - 2016 of the game reserves for all individuals of the respective study year. Beams indicate time intervals of 3 hours.

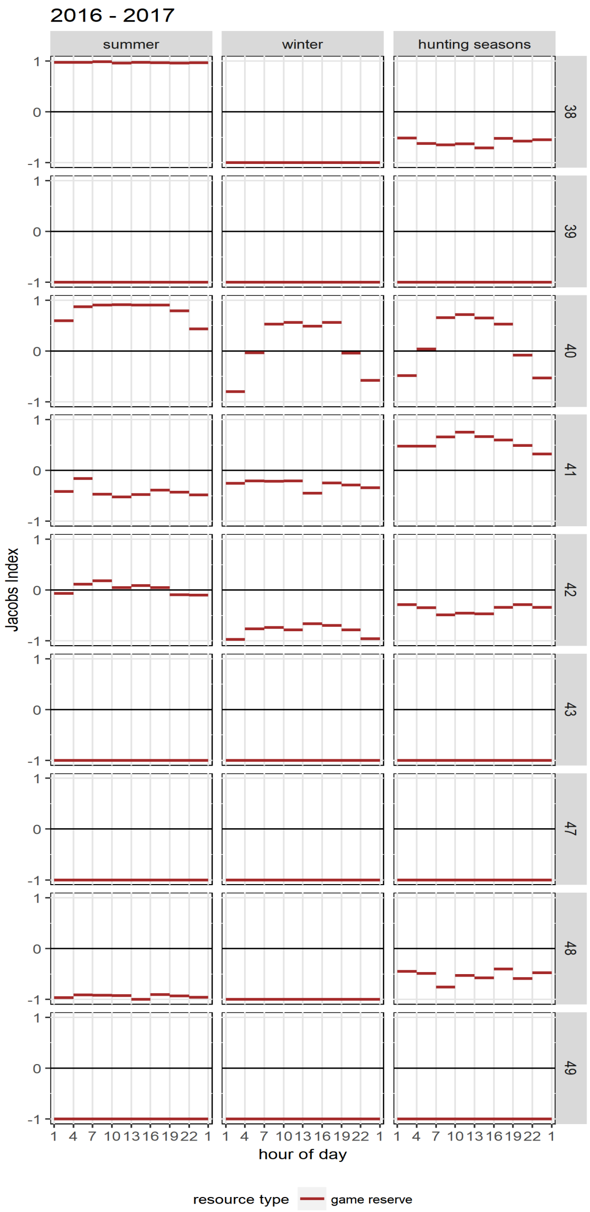

Figure A.14: Jacobs Index (1973). Temporal preference during 2016 - 2017 of the game reserves for all individuals. Beams indicate time intervals of 3 hours.