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40 Years of Roe Deer Markings in Switzerland:

An Analysis of the Mobility Behavior

Master Thesis GEO 511

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Submission: January 15, 2015

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Abstract

Roe deer are the most frequent ungulates in Europe (Danilkin 1996: xii) and live in almost every biotope available in Central Europe (Grzimek 1988: 201). During the 1970s and 1980s, when most of the fundamental research on the species was conducted, several fawn marking projects were started to study roe deer further. In Switzerland, the project "Rehkitzmarkierung Schweiz" was initiated in 1971. During the last century the landscape fragmentation has increased drastically through the construction of transportation routes and settlement areas (Andrén 1994, Bender et al. 1998, Jaeger et al. 2007, Schwick et al. 2010). Such anthropogenic structures act as barriers dividing ecosystems into smaller areas (Schwick et al. 2010). For a frequent and widely distributed species the likelihood of being affected by landscape fragmentation is higher than for rare species. Belonging to the former, the roe deer is a suitable species for the study of the mobility behavior in a fragmented landscape.

This thesis analyzes the data from the project "Rehkitzmarkierung Schweiz" in the context of the mobility behavior of roe deer in Switzerland. Besides more general analyses about the distance covered and the distance covered in relation to sex, age, weight and cause of death, the data is also compared between regions and analyzed over time. Furthermore, it is investigated whether barriers such as motorways were crossed and what possible dispersion paths of the deer might have developed.

The general analyses corroborates several previously known facts, such as the site fidelity and the sex independence of the dispersion distance. In comparison with other marking projects the mean dispersion distance is higher here. The regional analysis showed that the mean dispersion distance is lowest in the Swiss Plateau and increases significantly in the Pre-Alps and the Alps, respectively. Even though only a small part of the marked animals have crossed barriers it could be concluded that even fenced motorways were overcome. Finally, further insights on possible paths chosen by individuals could be obtained through the calculation of the least cost paths from the marking to the finding location.

Overall, the data represents the species as a generally philopatric animal with some more adventurous individuals that are able to overcome major barriers and, thus, also live and survive in fragmented landscapes.

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1 Introduction

Roe deer (*Capreolus capreolus*) are the most frequent ungulates in Europe as well as an important game animal (Danilkin 1996: xii). While the species has been extinguished in parts of Europe in the 18th century, nowadays it is spread over almost all of Europe again (Danilkin 1996: 42ff). Roe deer live in almost all biotopes available in Central Europe ranging from coastal areas to alpine habitats within the forest boundary (Grzimek 1988: 201). Most of the fundamental research on the species was conducted in the 1970s and 1980s (Heurich 2013: 33), for instance by Ellenberg (1978), Strandgaard (1972), Hespeler (1988), Mertens and Turner (1983), Staines and Ratcliffe (1987), Stubbe (1990) in Germany, Reimoser (1986) in Austria or Kurt (1974) in Switzerland. To get to know the species better several roe deer fawn marking projects were started in this time, for example in Baden-Württemberg (Bauch et al. 2014: 1), Switzerland (Rehnus and Reimoser 2014: 1) as well as a project in Lower Austria in the 1980s (Reimoser et al. 1999: 10).

The "expansion and intensification of human land use" (Andrén 1994: 355) have lead to increasing landscape fragmentation (Andrén 1994, Bender et al. 1998). Anthropogenic structures such as motorways or settlements divide landscapes and ecosystems into smaller areas (Jaeger et al. 2007: 6, Schwick et al. 2010: 79). Besides the actual loss of habitat area, for flora and fauna such landscape fragmentation acts as a barrier restricting its movement and dispersion between patches and dividing subpopulations (Schwick et al. 2010: 79f). As every species requires a minimal habitat size to survive an important aspect is the spatial distribution of habitats (Schwick et al. 2010: 80). Nowadays, often suitable habitats for wildlife are distributed like isles over a heavily human-used landscape, but for the long-term survival of a subpopulation an exchange of individuals between subpopulations is essential (Senn and Kuehn 2014: 13f). The fragmentation of habitats entails a decrease of the subpopulation size, which in turn is more prone to extinction by, for example, demographic randomness and environmental variations (Senn and Kuehn 2014: 23f). Thus, in addition to the size and quality the connectivity of habitats, i.e. sufficient mobility, is essential for survival (Schwick et al. 2010: 80).

In Switzerland the landscape fragmentation has steadily increased since 1885 (Jaeger et al. 2007: 54). The Swiss Plateau and the Jura are more heavily fragmented than the alpine regions (Jaeger et al. 2007: 48). Historically, between 1960 and 1980 the landscape fragmentation increased the most due to the construction of motorways (Schwick et al. 2010: 81, Jaeger et al. 2007: 55).

For a frequent and widely distributed species the likelihood of being affected by landscape fragmentation is higher than for rare species. Belonging to the former, the roe deer is a suitable species for the study of the mobility behavior in a fragmented landscape. The migration and dispersion of wild animals requires requires that there are no unconquerable barriers present. The studies of Hepenstrick et al. (2012) and Coulon et al. (2006) investigated whether and to what extent motorways, railways and rivers act as barriers for roe deer. Coulon et al. (2006) concluded that none of the considered barriers are impermeable for the roe deer. Note, however, that in the region several wildlife passages and bridges exist. In the study of Hepenstrick et al. (2012) it is concluded that motorways act as barriers due to their fencing whereas even highly frequented railway tracks and rivers are not impermeable. Kuehn et al. (2007) and Senn and Kuehn (2014) investigated the influence of motorways on the genetic divergence and diversity and found that motorways act as a barrier having an impact on the genetic divergence but not on the genetic diversity.

Until present time, the data set of the project "Rehkitzmarkierung Schweiz" has been evaluated mostly descriptively in 1984 by Stocker (1984). In 1999 Müri evaluated the data omitting the Canton of Grisons, and consequently the data of the Canton of Grisons was evaluated by Signer and Jenny in 2006. This partial evaluation of the data motivates further analysis. Moreover, being a long-term project it provides the possibility to investigate changes over time in the mobility behavior of the roe deer.

The goals of this thesis are the description and analysis of the data from the project "Rehkitzmarkierung Schweiz" in the context of the mobility behavior of roe deer in Switzerland. Besides more general analyses about the distance covered and the distance covered in relation to sex, age, weight and cause of death, the data is also compared between regions and analyzed over time. Furthermore, it is investigated whether barriers such as motorways were crossed and what possible dispersion paths of the deer might have been. The following research questions will be investigated:

1. What is the dispersion behavior of the roe deer? Are there individual-specific (age, sex, condition, cause of death) differences?
2. Does the dispersion behavior differ between regions?
3. Does the increasing landscape fragmentation over time have an impact on the dispersion behavior and dispersion distances?
4. Are barriers crossed?
5. What are possible dispersion routes of roe deer that crossed a barrier? Can corridors be identified?

2 Materials and Methods

2.1 Study Species: the Roe Deer

Roe deer are a widely distributed (Figure 2.1), frequent and well researched animal species in Europe (Danilkin 1996: xii).

Figure 2.1: Distribution of the Roe Deer (extract from Kurt 1974: 19)

In Switzerland, roe deer were eradicated prior to the nineteenth century due to deforestation, cattle breeding and hunting (Danilkin 1996: 42). In the twentieth century, however, roe deer immigrated again from the surrounding countries into Switzerland (Imesch-Bebié et al. 2010: 358f). It is the smallest native deer species in Europe (Mosler-Berger 1998: 1). Typically, a grown roe deer measures around 70 cm shoulder height, has a length of 95-135 cm and weighs 15-27 kg (Kurt 1974: 16).

The spatial and social organisation of roe deer is described sex dependent and seasonally. Adult bucks start their territorial behavior in spring, immediately after snow melt. They then establish their territories, typically the same every year, by marking them through visual means and scents and defending them against other bucks (Danilkin 1996: 93). The territory size is inversely proportional to population density, ranging from 2 to 200 ha and territories only start overlapping at high population densities (Danilkin 1996: 95ff). Furthermore, the territory size depends on the season, climate, food availability, as well as the animal's age and sex (Kurt

1974: 75). In Switzerland the territory size measures $60 - 80$ ha from spring to autumn (Kurt 1974: 75). Adult does separate from their groups by the end of April and the beginning of May, approximately three to four weeks prior to giving birth, and occupy kidding ranges which remain the same from year to year measuring several hectares (Danilkin 1996: 100). When the fawns are one to two weeks old the doe starts expanding their home ranges that may overlap with territories of other does, though the main areas are separate (Danilkin 1996: 100f). In winter the bucks are no longer territorial allowing the formation of small groups (Danilkin 1996: 104), typically consisting of a doe with her fawns, a young female and a buck (Kurt 1974: 84). Varying between populations and typically depending on the snow depth, there are some that settle on a particular range, while others migrate seasonally to winter ranges. Home ranges of individuals and groups may overlap (Danilkin 1996: 103ff).

Generally, the roe deer is philopatric and does not move farther away from the birth place than about one to three kilometers (Danilkin 1996: 100f; Müri 1999: 42; Signer and Jenny 2006: 52). Nevertheless, there are individuals that move much greater distances (Danilkin 1996: 100f). Already before the separation from the mother at the age of almost one year (Grzimek 1988: 204ff) the young roe deer explore the surrounding area (Wahlström and Liberg 1995: 460). During the separation, the young males, especially if well built, are often chased away by the territorial male and, hence, look for their own territory (Heurich 2013: 40). The females typically occupy an uninhabited area close to their birth place and the habitat of their mother (Danilkin 1996: 102). With higher population density also young females emigrate (Danilkin 1996: 102).

If roe deer disperse they are typically in the age of one to two years taking place after the separation from the mother (Wahlström and Liberg 1995: 460). Generally, roe deer disperse if the population density is low to medium. A high population density leads to an average loss of body weight and, thus, prevents migration due to the poor body condition (Wahlström and Liberg 1995: 461f). Debeffe et al. (2012), Müri (1999: 44), and Signer and Jenny (2006: 52) found that dispersion is not sex dependent and heavier individuals are more likely to disperse, earlier and further away. Moreover, subadults of less than 14 kg did not disperse (Debeffe et al. 2012: 1327).

Besides the dispersion of subadults, there exists also seasonal migration in roe deer. Cagnacci et al. (2011: 1797) investigated the reasons for seasonal migrations and found that it depends on the hill slope combined with snow and forest cover. Moreover, they observed four different migration patterns. Firstly, the "classical migration" that describes the movement between a summer and a winter habitat. The deer stayed as long as possible in one habitat, then "shifted a few times between ranges, before finally stabilizing again" (Cagnacci et al. 2011: 1796). Secondly, there were deer that stayed most of the time in a summer range and only for a short period moved to a winter refuge (Cagnacci et al. 2011: 1796). The third pattern describes deer that stay predominantly in a summer habitat with short interruptions in a secondary range (Cagnacci et al. 2011: 1796; Robin 1974). Lastly, there were animals that commuted between several home ranges without following a temporal pattern (Cagnacci et al. 2011: 1796).

2.2 Study Area

The data has mainly been collected in three of six biogeographical regions of Switzerland. The biogeographical regions provide regions within which the fauna and flora show the best resem-

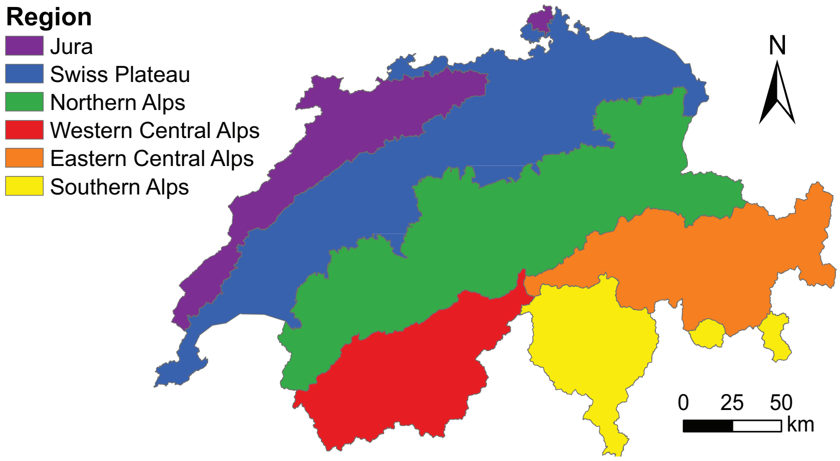


Figure 2.2: Biogeographical Regions of Switzerland (Gonseth et al. 2001, data source: BAFU)

blance (Gonseth et al. 2001: 11). In the coarsest resolution six main biogeographical regions were defined: the Jura, the Swiss plateau (Mittelland), Northern Alps (Alpennordflanke), the Western Central Alps (Westliche Zentralalpen), the Eastern Central Alps (Östliche Zentralalpen) and the Southern Alps (Alpensüdflanke) (Gonseth et al. 2001: 17ff) (Figure 2.2).

Due to the great range in the height above sea-level (193 - 4634 m) and the geographical latitude the climate in Switzerland varies significantly, ranging from maritime climate in the Northern Alps to continental climate in the Central Alps and submediterran climate in the Southern Alps (Ott et al. 1997: 116f). The mean annual temperature varies from -8.5 degrees Celcius on the Jungfrau Joch (3572 m), to 2.5 degrees Celsius in Davos (1590 m), 7.8 degrees Celsius in Zurich (556 m) located in the Swiss Plateau, 8.5 degrees Celcius in Sion (482 m) in the valley of Valais, and 10.6 degrees Celcius in Locarno (197 m) in the Canton of Ticino. Similarly, the annual precipitation is highest in the Jura and the Northern Alps where the humid maritime air from the Atlantic ocean is forced to rise to higher altitudes and thus rains out. This leads to a maximum of 411 cm annual precipitation on the Jungfrau Joch, and much lower values in Zurich (107 cm) and in the protected Alp valleys (Davos, 97.9 cm and Sion, 51.1 cm). In Locarno the value of 186.6 cm of annual precipitation is quite high, though this is concentrated in fewer precipitation days, usually during a foehn situation, with intensive rains (Wachter et al. 1995: 48ff).

Like the climate also the flora is very diverse. The lower regions up to 600 m belong to the colline zone where central European and, in the Canton of Ticino, mediterranean plant species are found. Historically, the colline zone was covered with deciduous forest that today still is a characteristic for the montane zone up to 1200 m. In the subalpine zone up to 1900 m the coniferous forest is predominant. Above the forest boundary that lies between 1800 m in the Northern Alps and 2400 m in some parts of the Central Alps the alpine zone begins with its typical alpine pastures. Above 2500 - 2700 m the nival zone begins (Wachter et al. 1995: 51f).

2.3 Data Collection

In 1971 the monitoring project "Rehkitzmarkierung Schweiz" has been initiated by the "Arbeitsgruppe Wildforschung" of the Department "Ethologie und Wildforschung" at the University of

Figure 2.3: A fawn being marked (Picture: Maik Rehnus, 2014)

Zurich with the goal to gain better knowledge about the roe deer in Switzerland. It started off with the participation of 13 cantons of Switzerland. Ever since, each year various cantons participate with the support of volunteers such as gamekeepers, hunters and fawn rescuing projects.

The data collection of the project occurs by two 'Meldekarten' (report cards, Appendix A). The first one, 'Meldekarte 1', is filled out by the person marking the fawn. It gives information about the date the marking occured, the mark used, the sex, the approximate age, siblings, the vegetation around the marking place, and the coordinates.

Similarly, 'Meldekarte 2' informs about a previously marked individual when found dead. Again the date of the finding is recorded along with information on the mark used, the sex, the weight, the nearby vegetation, the cause of death, and the coordinates.

Essentially there are two main methods available to study the mobility of the roe deer: ear marks and telemetry. Ear marks are small plastic marks that are applied to the fawns ears shortly after birth during the first 2-3 weeks when they typically lie hidden (Kurt 1991: 76). Since at this age fawns do not try to escape but instead freeze (Danilkin 1996: 190ff) the application of the ear marks is simple once a fawn is found (Kurt 1974: 148f) (Figure 2.3). The marks used by "Rehkitzmarkierung Schweiz" are colored and have a number imprinted. Each year a distinct number range is used and the side of the ear used is alternated such that the individual can be identified if found. Data collection by ear marks allows collecting data in the form of a starting point and, if the animal is found upon its death, an endpoint. Due to its simplicity and low costs this method is attractive for monitoring purposes as is the longterm project "Rehkitzmarkierung Schweiz". One disadvantage of the method is the overall low feedback ratio around 11-18 % due to the fact that the ear marks can easily fall out, especially when not applied to the base of the ear, and due to fawn mortality as well as emigration (Kurt 1991: 23).

A more sophisticated method to track animals is telemetry where transmitters are attached to the animals (Boldt and Willisch 2011: 1). This allows collecting data with a high temporal resolution in the range of hours or even higher (Millspaugh et al. 2012: 262). While having the advantage of high temporal and spatial resolution data, telemetry has several disadvantages compared to the ear marks. Namely, having to capture the animal to attach the receiver (Boldt and Willisch 2011: 5), the limited data collection period due to battery run time (Millspaugh et al. 2012: 263) and the relatively high costs (Hebblewhite and Haydon 2010: 2304).

2.4 Statistics

2.4.1 Individual-specific Variables

After a first description of the data set, the mobility analysis will look at the subset consisting of animals that have been reported back and include all the coordinates (from the marking and the finding location). Henceforth, distance is defined to be the beeline distance from the marking location to the finding location.

Sex

The roe deer dispersal behavior is not sex biased (Linnell et al. 1998: 272). To confirm this fact for our data a Welch Two Sample t-test (Hatzinger et al. 2011: 338f) was used.

Age

As mentioned in Section 2.1 the mobility of the animals is age dependent. Before giving birth to the new fawns the mother and offspring separate. Danilkin (1996: 100) speaks of a time period of 3-4 weeks prior to giving birth, Kurt (1991: 103) defines the "separation time" (German "Auflösungszeit") from the middle of March until the middle of May, while Linnell et al. (1998: 267) names April. From this the age group of the 'fawns' was defined to be all the individuals that were found in their first year until 1st of April of the year following their birth year and, accordingly, 'subadults' are the animals that have been found in the year following the 1st of April of the year following their birth year. All older animals are categorized as 'adult'. The distance classes were chosen as 'less than 1 km', 'between 1 and 3 km' and 'greater than 3 km' according to Danilkin (1996: 100f). To investigate the dependence of the walking distance and the age group, a Chi-Square Test of Independence was conducted.

Condition

In the second report card (Meldekarte 2) there are three possible ways of weighing distinguished: "eviscerated with head" ("aufgebrochen mit Haupt"), "eviscerated without head" ("aufgebrochen ohne Haupt"), "not eviscerated" ("nicht aufgebrochen"). This makes it somewhat hard to analyze the data. However, Krämer (in Stocker 1984) presented formulas to calculate the eviscerated weight (with head) from the weight of an eviscerated animal without head:

$$\text{males: } y = 0.591 + 1.046 * x$$

$$\text{females: } y = 0.451 + 1.043 * x$$

where x is the weight of the eviscerated animal without head. The formula has been tested for animals older than 14 months. Thus, in the following analysis only subadult and adult animals from the age of 14 months were considered. To study the weight difference between the sexes a Welch Two Sample t-test was used. As mentioned in Section 2.1, the likelihood of roe deer dispersing increases linearly depending on the subadult weight. To examine the dependence of the weight and the covered distance in our data, a linear regression was performed.

Cause of Death

The site fidelity of the roe deer may suggest that the animals that walk further are more likely to die in traffic accidents than the philopatric ones. The second report card (Meldekarte 2) asks for the cause of death, suggesting the following categories: shot (erlegt), traffic accident (Verkehrsverlust), disease (Krankheit), mown (vermäht), prey (gerissen), other/unknown (andere/unbekannt). To investigate the relationship between the walking distance and the cause of death, a Chi-Square Test of Independence was conducted.

2.4.2 Regional-specific Analysis

As seen in Section 2.2 Switzerland provides several distinct habitats for wildlife, making a stratified regional comparison interesting. The analysis of the data only looks at data of subadult and adult animals.

In the project "Rehkitzmarkierung Schweiz" some animals were marked in Liechtenstein while there are some marked just outside the Swiss border in the region of the Canton of Schaffhausen. Since the GIS (Geographical Information System) data record of the biogeographical regions do not include these entries, they were assigned the biogeographical region that is located closest to the specific coordinates. That is, the ones in Liechtenstein were assigned to the Northern Alps and the ones just across the border of the Canton of Schaffhausen were assigned the biogeographical Region of Jura.

Due to the low counts of records (Figure 3.5) an analysis of the regions Jura, Western Central Alps, and Southern Alps does not seem sensible. Thus, the Swiss Plateau, the Pre-Alps (Alpennordflanke), and the Alps being the Eastern Central Alps aggregated with the Southern Alps were investigated. The Southern Alps were counted to the Alps due to the few markings in this region that are located in the Canton of Grisons and, thus, are (bio)geographically closest to the Eastern Central Alps.

Dispersion Distance

To examine the mean dispersion distances in the different regions an Analysis of Variance (ANOVA) and a subsequent Games-Howell Post-Hoc (IBM 2012a; IBM 2012b) Test were used.

Cause of Death

Different habitats might influence the cause of death. To investigate the relation between the cause of death and the regions, a Chi-Square Test of Independence was performed.

2.4.3 Changes over Time

Having collected data since 1971 the data set of “Rehkitzmarkierung Schweiz” has the potential to show changes over time in the behavior of the roe deer in Switzerland. Transportation routes, settlement areas and industrial areas fragment landscapes and ecosystems (Jaeger et al. 2007: 11). Jaeger et al. (2007) computed the “effective mesh size” for Switzerland from 1885 to 2002. The “effective mesh size” is an indicator for the fragmentation of landscapes that describes the probability that two points in an area are connected, i.e. not separated by a barrier (Jaeger et al. 2007: 38). Thus, low values signify a high fragmentation of the area. One important result is that over time the “effective mesh size” has decreased, and thus the fragmentation of the landscape has increased (Jaeger et al. 2007: 60ff). The “effective mesh size” in the Swiss Plateau decreased 29.5 % from 41.54 km^2 in 1935 to 29.22 km^2 in 2002 (1960: 36.70 km^2, 1980: 30.30 km^2) (Jaeger et al. 2007: 205). In the Central Alps the “effective mesh size” decreased with 41.1 % even more from 2222.86 km^2 to 1310.24 km^2 (1960: 1995.32 km^2, 1980: 1350.92 km^2), but the fragmentation is much less severe than in the Swiss Plateau (Jaeger et al. 2007: 205). Due to the regional differences in the change of the “effective mesh size” as well as the regional differences of the average distance walked by roe deer, the Swiss Plateau, the Pre-Alps, and the Alps will be investigated in detail. As before the analyzed data includes only the subadult and the adult individuals.

To analyze the relation between the dispersion distance categories and pentades, a Chi-Square Test of Independence was done.

Time Series per Region

To investigate the dispersion distance per region in more detail a linear regression of the mean dispersion distance per marking year as well as a linear regression of the walking distances per marking year were performed.

2.4.4 Barriers

Barriers are defined as “something (such as a fence or natural obstacle) that prevents or blocks movement from one place to another” (Merriam Webster 2014). In the case of the roe deer these are typically fenced linear landscape elements (Hepenstrick et al. 2012, Coulon et al. 2006: 636). To prevent roe deer from overcoming fences they need to be at least 1.50 m high (Nemestothy 2010). Furthermore, roads only start to act as barriers if the daily traffic amount exceeds 2000 - 2500 per day (Krisp 2006: 57, Iuell et al. 2003: 5f, Berthoud 1987) and railways should only be considered if highly frequented (Krisp 2006: 57). These facts led to the definition of barriers being: motorways, railway lines and waterbodies. Swiss motorways (‘Autobahn’ and ‘Autostrasse’) are equipped with game fences (Bundesamt für Strassen ASTRA 2013: 4) and, thus, act as barriers. For the railway network only railway lines with multiple tracks were considered as it would be expected that they are the most frequented lines. Due to the structure of the VECTOR25 dataset that has an own category for railway stations, such line segments within a distance of 500 m from the considered railway lines were included. Theoretically, the threshold could include some line segments that do not connect railway lines with multiple tracks but since all the segments are less than 3 km long it will not impose a problem for the method. Furthermore, the motorways and railway lines were considered as continuous lines (i.e. tunnels,

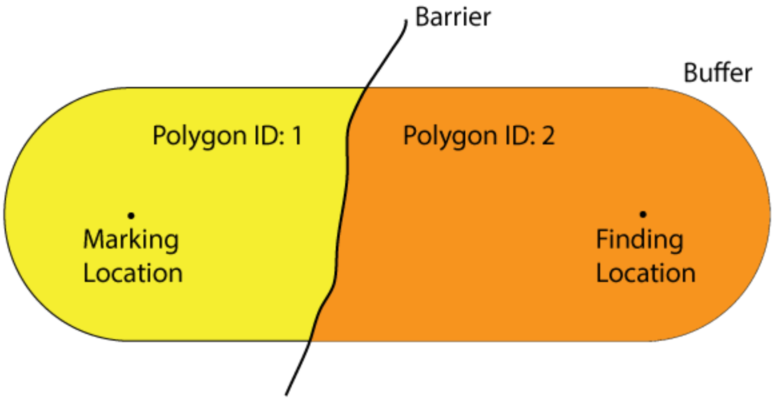


Figure 2.4: Schematic diagram of a possible outcome when testing whether a barrier was crossed or not. Here the barrier was crossed.

bridges and wildlife crossings are not excluded) that split up the landscape of Switzerland into several polygons. As roe deer are good swimmers (Burton and Burton 2002: 2201) only lakes and rivers were considered to act as barriers. All the barriers were extracted from the vector dataset VECTOR25 by the Federal Office of Topography swisstopo. For specific details see Table 2.1.

Layer	Feature Type	Selected Categories
Strassennetz (road network)	line	Autobahn, Autob_Ri, Autostr
Eisenbahnnetz (railway network)	line	NS_Bahn2, Str_Bhof within 500 m of NS_Bahn2
Gewässernetz (drainage network)	line	See, Fluss

Table 2.1: Layers of VECTOR25 used for definition of barriers

To test whether an individual roe deer has crossed a barrier or not the following basic idea was used. As mentioned before, typically roe deer do not move farther away from their birth place than about 1 to 3 km. Following the idea of Horne and Garton (2006), who use an information-theoretic approach to compute home range models, one can assume it is likely that an individual moved within a radius of 3 km around the marking and the finding place. Thus, a polygon was created for each individual consisting of a 3 km radius around the beeline distance from the marking to the finding location. The polygons were then cut by the barriers and each resulting polygon was numbered with a unique identification number (Polygon ID). After a spatial join (which combines two data sets based on the location of the topologically contained features (ESRI 2013)) of the polygons with the marking and finding locations the Polygon ID of the marking location was compared with the Polygon ID of the finding location. If the Polygon ID is the same the individual has not crossed a barrier, otherwise a barrier was overcome (Figure 2.4). This approach ensured that, in the special case where the barrier follows a curve and the beeline distance is crossed twice by the same barrier, the result is that the animal has not crossed the barrier but rather walked alongside the barrier (Figure 2.5).

For the reason that the analysis over time showed no significant results as well as the fact that the swisstopo data set VECTOR25 only exists since 2000 (Dominik Käuferle, personal

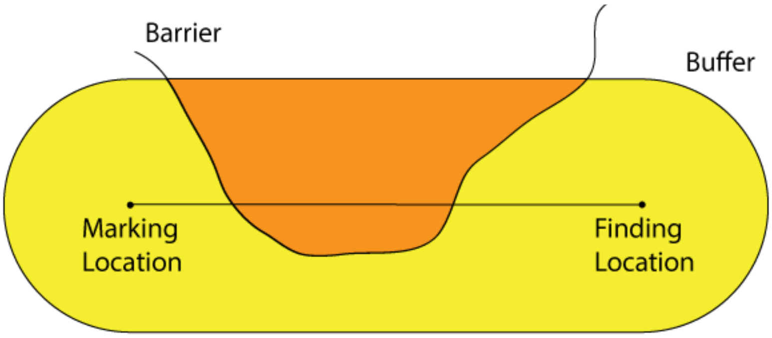


Figure 2.5: Schematic diagram of the situation that the beeline distance is crossed twice while the animal moved alongside the barrier.

communication, March 2014) changes over time of the infrastructure were neglected. Due to the increasing fragmentation one can expect that in the case of change over time barriers were mostly added (not removed). This means, if this influences the result it will likely be towards a higher number of animals that crossed a barrier. Also, the guidelines for including wildlife crossings in road construction projects have increased the number of wildlife crossings since 1990 (Bundesamt für Strassen ASTRA 2013: 6) and, thus, a tendency towards a higher number of animals that overcame a barrier is expected.

The calculations were done using ArcGIS 10.1. The project data had to be prepared for testing whether a barrier was crossed or not. The first step was to merge the markings and findings into one data set. This then allowed creating a line data set that connects the marking with the finding location that was used to calculate a 3 km buffer area around the connecting lines. Upon that, the procedure for the test consisted of the following steps. First the polygon of Switzerland was cut with the barrier dataset. After that, an additional field 'PolyID' was added and numbered increasingly. The next step was to carry out a 'Spatial Join' of the polygons with the marking and finding locations dataset. These two datasets were then joined and a field 'hasCrossedBarrier' was added. This made the last step of the testing possible which compared the 'PolyID' of the marking and finding location with each other and determined whether those were equal or not. For further use, the result was written into the 'hasCrossedBarrier' field. To analyze whether a bridge or a tunnel lies within the 3 km buffer zone of the connection line the spatial selection tool was used.

Finally, to account for differences of the occurrence of motorways and railway lines, respectively, the 'Line density' within a radius of 3 km for each raster cell was calculated. The 'Line Density' is calculated by summing the lengths ($L1$, $L2$ in Figure 2.6) of each line feature within the defined radius and dividing the total by the circle's area (ESRI 2012d).

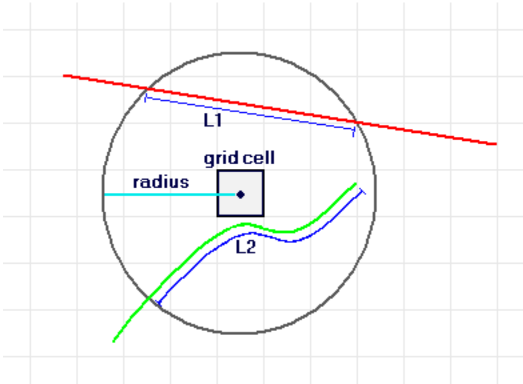


Figure 2.6: Illustration of the calculation of 'Line Density' (Source: ESRI 2012d)

2.4.5 Least Cost Path

The main goal of the analysis is to find the least cost path (LCP) from marking to finding location. The least cost path describes the least costly path from a source location to a destination by means of a cost surface (Chang 2014: 368, ESRI 2012b). The LCP will give a better impression of the dispersion path that the individual animals chose. Also, it will allow to compare the bee line distance with the length of the LCP.

To calculate the LCP, the first step is to create a cost surface in ArcGIS. The cost surface or raster "identifies the cost of travel[l]ing through each cell" (ESRI 2012c). For this the data set "Primärflächen" (primary areas) of swisstopo's VECTOR25 was used as a basis. The many classes were reclassified into the broader classes "settlement area", "water bodies", "forest", "stony grounds", "remaining area". After that, the vector data set was rasterized using the "Feature to raster" method of ArcGIS. Since roads and railway lines are not included in the primary areas they were converted into a raster dataset and afterwards included into the cost surface. These datasets also made it necessary to use a 25 m resolution because a coarser resolution would have resulted in problems with the bridges and tunnels – they would have appeared in most cases in the rasterized dataset but often would have been enclosed by raster cells classified as road. Thus, this would have given a cost surface with enclosed bridges, i.e. not passable for roe deer in the cost distance calculation. For this reason, a sensitivity analysis was performed for chosen individuals at a coarser raster resolution of 50 m which will be reported later. As the waterbodies of the primary areas are not necessarily connected, the rasterized water bodies data set was combined with the primary areas such that, if in either data set the pixel was classified as a water body, it would be classified as a water body in the combined raster. Lastly, since in our data the highest recorded altitude that a roe deer was shot is 2450 m, areas above 2500 m above sea level were excluded.

The weighting of the different classes was chosen after Krisp (2006: 92). He did an expert survey on barrier values during summertime in Finland in which several landscape objects had to be described with a value from 1, meaning 'no barrier, crossing possible' to 100, signifying an 'absolute barrier, no crossing possible' (Krisp 2006: 90). The survey resulted in mean barrier values of about 80 for 'fenced major highways', less than 10 for various forest types, 60 for 'settlements', 75 for 'industrial areas' and between 50 and 70 for waterbodies (Krisp 2006: 92). These values were used as a guideline as they describe a rather general situation of area types that are comparable to the ones in Switzerland. Roe deer "retain a strong link to woodland structures while avoiding areas of high human activity" (Hewison et al. 2001: 688). Also, roe deer dispersal is connected to woodland structures (Coulon et al. 2004). This coincides with Krisp's expert survey and, thus, the suggested value of 5 was assigned to forest areas and 70 to settlement areas. Fences from a height of 1.5 m inhibit the movement of roe deer (Nemestothy 2010). Since 1968 Swiss motorways are fenced to prevent collisions (Bundesamt für Strassen ASTRA 2013: 4). Thus, motorways were defined to be unconquerable, i.e. assigned a value of 100, but since motorways are conquerable when there exists a tunnel or bridge (Kuehn et al. 2007: 8) the tunnels and bridges were assigned the value 70 in the cost surface. The values for the railway network, areas higher than 2500 m above see level and unclassified areas had to be defined reasonably for they were not evaluated in Krisp's survey. In the study of Hepenstrick et al. (2012) unfenced railway tracks showed close to no barrier effect. Nevertheless, highly frequented railway tracks should be considered (Krisp 2006: 57). Therefore, a value of 80 was chosen for the tracks and 50 for tunnels and bridges. The areas over 2500 m altitude were assigned a value of 100 such that they are excluded. For the definition of the unclassified areas they were visually compared with satellite imagery which showed that a big part consists of agriculturally used land. As roe deer are known to live in agricultural areas (Mosler-Berger 1998: 2) (but prefer woodland) a value of 20 was chosen. Since it should not be possible to cross a motorway or areas above 2500 m and the algorithm does not understand the value of 100 as impermeable, it was set to 10000 instead. To assess the influence of cost choices the sensitivity analysis will also cover different values for railway lines, tunnels and bridges of railway lines and motorways, waterbodies and settlement areas.

After the definition of the cost surface the cost distance, "the least accumulative cost distance for each cell to the nearest source over a cost surface" (ESRI 2012a), is calculated with the 'Cost Distance' tool. Finally, the LCP is computed with the 'Cost Path' tool. In GIS two basic data models, vector and raster, are known. The vector model consists of point, line and polygon entities. Every entity represents an object and is described by XY coordinates and attributes (Burrough and McDonnel 1998: 22f). An example could be a point entity representing a house at coordinates (10,25) that has a height '5 m', was built in the year '1999' and is of color 'red'. The attributes would be 'height', 'construction year' and 'color'. Raster data models are typically used to describe continuous phenomena such as temperature or elevation (Burrough and McDonnel 1998: 22). A raster is a grid built through square cells, each having a different value, that describes the attribute (e.g. temperature) at the coordinate of the cell (Burrough and McDonnel 1998: 24). All the mentioned calculations were done using the raster format resulting in one raster file per LCP. A collection of raster files, however, is impractical to handle the further analysis. Therefore, the LCPs were converted into line features with the tool 'Raster to Polyline'. This also allows, for example, the easy calculation of the LCPs lengths. Like in the case of the barriers, changes of the land cover over time were not considered. To compare the bee line distance with the LCPs an Analysis of Variance (ANOVA) was conducted.

In order to answer the last research question whether corridors can be identified the 'Intersect' tool was used to find the intersecting parts of the previously calculated LCPs. Again by using the 'Intersect' tool, the result was associated with the national wildlife network system and the wildlife corridors (Bundesamt für Umwelt BAFU 2013). Since the latter is a line data set and it does not seem reasonable to only consider the given lines a buffer of 500 m was created before conducting the intersection.

3 Results

3.1 Individual-specific Variables

3.1.1 Marking and Finding Rate

From 1971-2013 a total of 14987 roe deer have been marked. The mean of the number of marked roe deer per year is 348.5 with a range of 127 - 597 marked animals per year. Before 1990 around 150, after 1990 around 400 roe deer were marked per year. Of all the marked roe deer 2619, i.e. 17.48 %, were reported back. The mean is 59 with a range of 1 - 109 findings per year. Figure 3.1 shows the markings and findings per year.

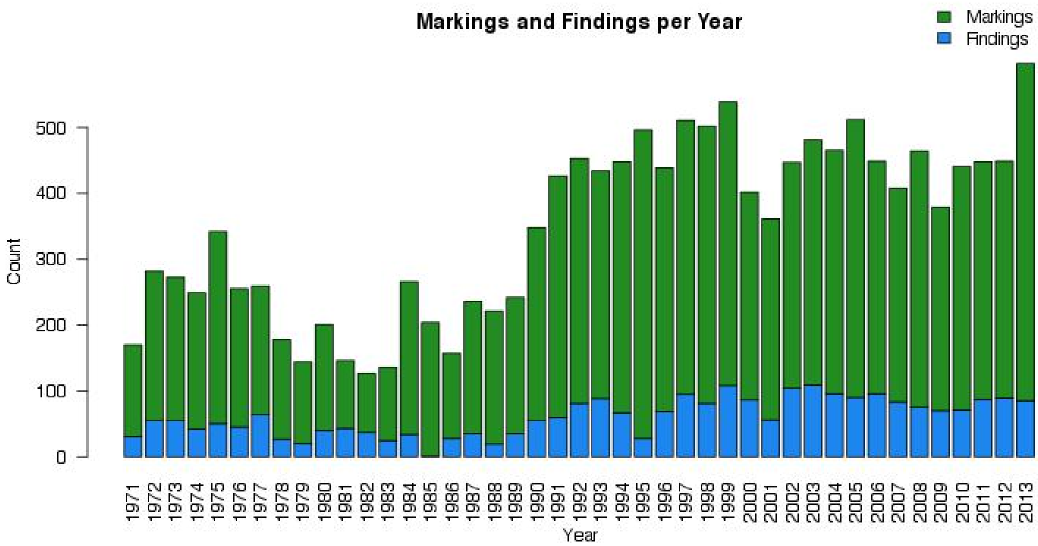


Figure 3.1: Number of marked and found roe deer per year

3.1.2 Dispersion Distance

Of all the findings, 2537 data sets contain the complete coordinates of both the marking and the finding location. The mean of the covered distance lies at 2399 m with standard error 108 m, the median at 700 m and the third quartile at 1968 m, i.e. 75 % of all marked roe deer covered a distance up to 1968 m. This leaves 633 individuals that covered a distance of more than 1968 m (Figure 3.2).

The maximum distance, 109.2 km, was covered by a 4.9 year old male roe deer that was marked in the Canton of Grisons close to the village of Mulegns and found in the Canton of Zurich close to the village of Mönchaltorf.

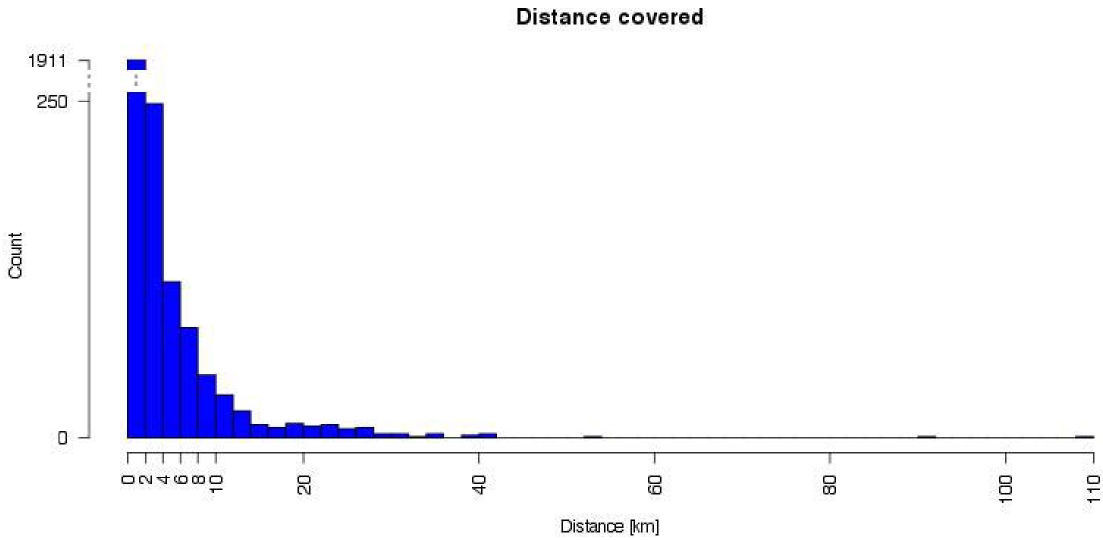


Figure 3.2: Distribution of the distance covered of all animals

3.1.3 Sex

The males (n = 1441) covered a mean distance of 2378 m with standard error 139 m. The maximum distance was 109.2 km. The does (n = 1026) covered a mean distance of 2500 m with standard error 179 m and a maximum distance of 91.0 km. Statistically there is no significant difference in the mean covered distance between sexes (p-value = 0.562).

3.1.4 Age

The mean distance covered per age group is 965 m (standard error 71 m) for the fawns, 3504 m (standard error 240 m) for the subadults and 3384 m (standard error 250 m) for the adults. More than 80 % of the fawns were found within 1 km of their marking location (Figure **??**). Of the older ones (both subadults and adults) about half of the marked roe deer covered a distance greater than 1 km. Statistics shows that the walking distance is related to the age group ($\chi^2 = 371.759$, df = 4, p-value < 0.001).

3.1.5 Condition

The does (n = 547) weigh less in average (mean 16.58 kg, standard error 0.13) than the bucks (n = 819, mean 17.58 kg, standard error 0.14) (Figure 3.4). This hypothesis is also statistically significant (p-value < 0.001).The according linear regressions between weight and distance covered do not show a significant correlation for either sex (male: p-value = 0.876, female: p-value = 0.523).

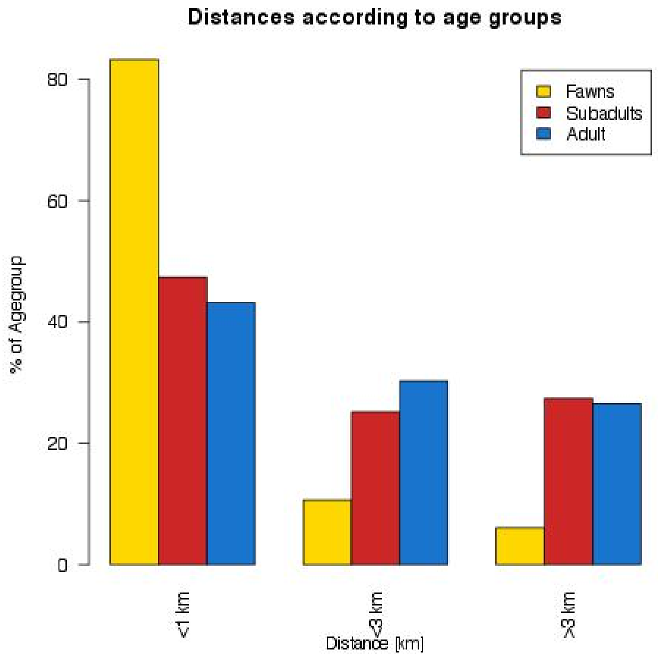


Figure 3.3: Distances in Agegroups

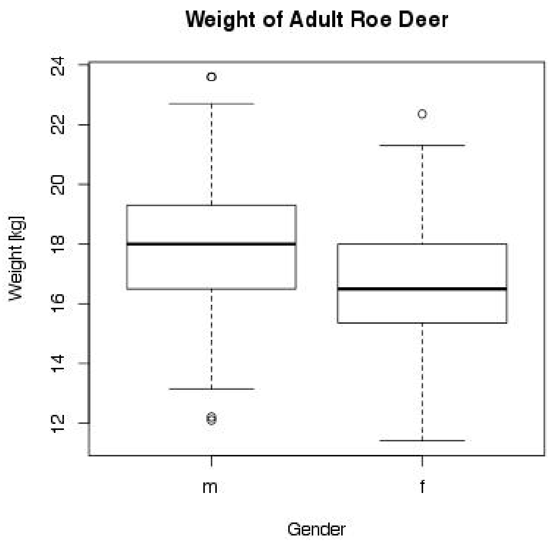


Figure 3.4: Boxplot of the weight of the adult roe deer

3.1.6 Cause of Death

Overall most of the animals were shot. As typically fawns are prone to die in mowing accidents, the percentages for the subadult and adult animals (n = 1541) move even more towards being shot (Table 3.1). Moreover, the cause of death is independent of the distance being either below or above 3 km ($\chi^2 = 7.641$, df = 5, p-value = 0.177).

	Shot	Traffic	Mowed	Disease	Unknown	Prey
All ages	63.04	13.90	7.98	2.49	9.52	3.12
Fawns	43.82	14.48	19.56	3.16	13.33	5.66
Subadults	75.72	13.78	0.27	1.50	6.96	1.77
Adults	76.36	13.24	0.25	2.35	6.93	0.87

Table 3.1: Cause of death of animals by agegroup in percentage

3.2 Regional-specific Analysis

3.2.1 Dispersion Distance

The absolute number of findings per distance class varies between regions (Figure 3.5). Remarkable are the many findings in the distance class "≥ 3 km" in the Eastern Central Alps.

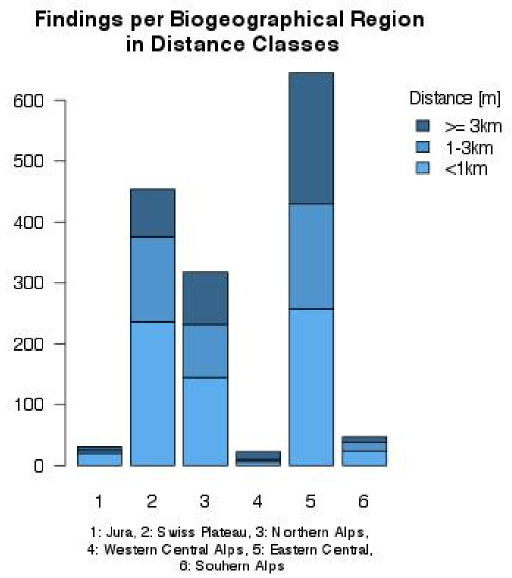


Figure 3.5: Findings per biogeographical region in distance classes in absolute counts

An analysis of the distance per region reveals that the mean distance covered between all groups varies significantly. The mean distance covered in the Alps (mean 4323 m, standard error 321 m) is significantly higher than in the Swiss Plateau (mean 1998 m, standard error 149 m, p-value < 0.001) and the Pre-Alps (mean 3107 m, standard error 281 m, p-value < 0.001). Also the mean distance covered of the animals from the Pre-Alps is significantly higher than the ones from the Swiss Plateau (p-value < 0.001).

3.2.2 Cause of Death

Figure 3.6 shows the proportion of death causes per region. As expected in all regions the most common cause of death is "shot". Nevertheless, some regional differences are noticeable. In the Pre-Alps and Alps the proportion of the "shot" roe deer decreases and, for the animals that came to death in traffic accidents, there is a higher proportion in the Alps. Statistically the cause of death depends on the region ($\chi^2 = 93.782$, df $= 10$, p-value < 0.001).

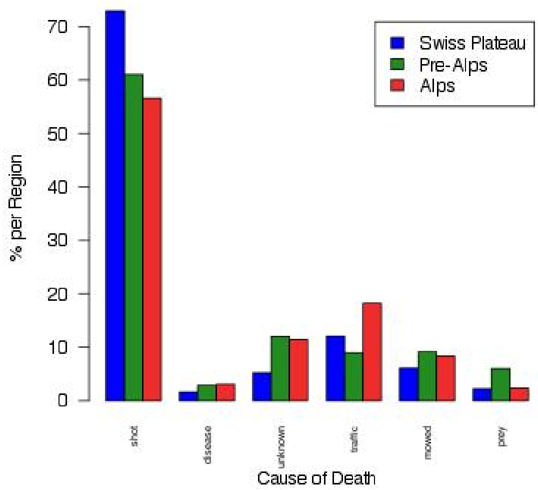


Figure 3.6: Cause of Death by Region in Percentages of the Region Total

3.3 Changes over Time

The following plots will give an overview of the findings in distance classes over time.

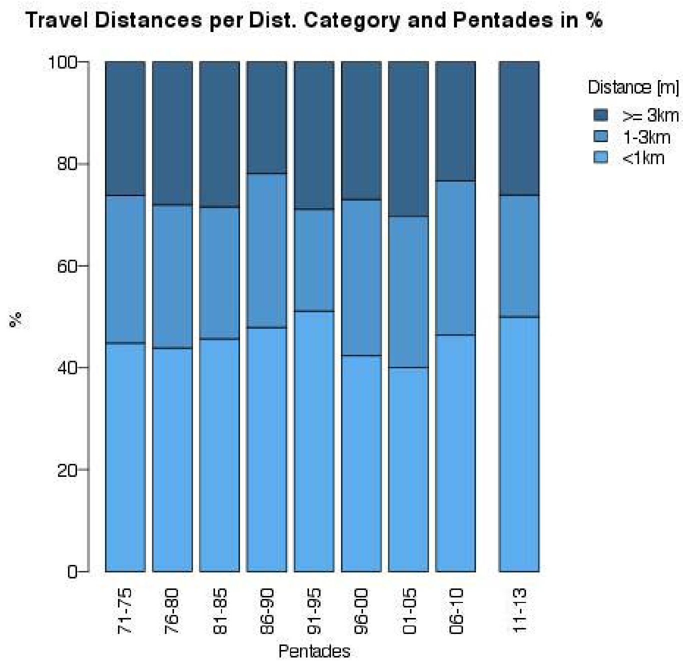
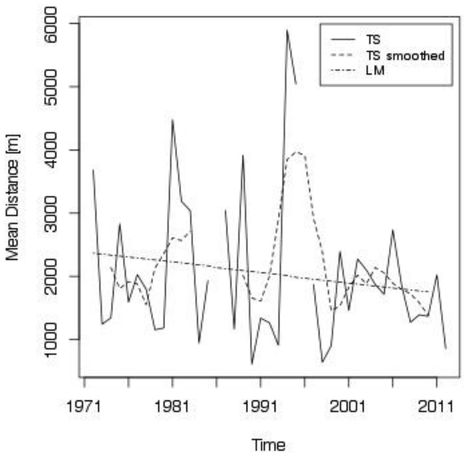


Figure 3.7: Distance Classes per Pentade in Percentage

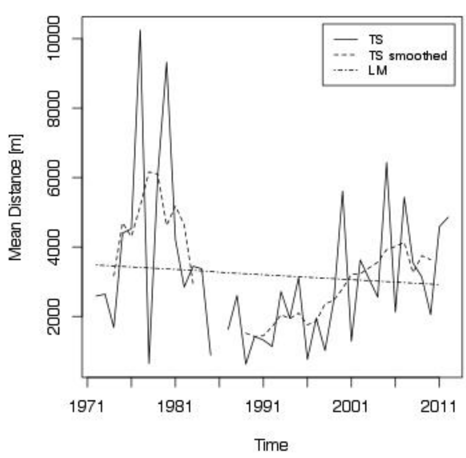
Statistically there exists no dependence between the distance categories and the pentades ($\chi^2 = 8.069$, df = 16, p-value = 0.947) (Figure 3.7).

3.3.1 Time Series per Region

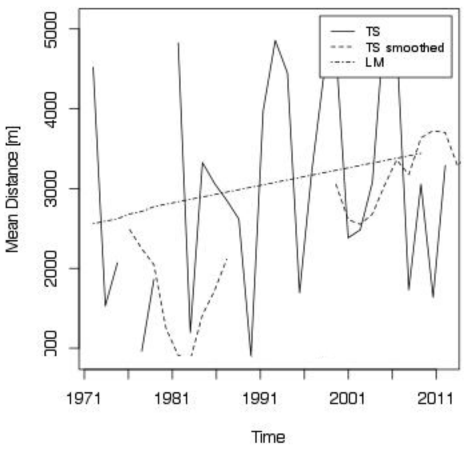
For each region the plot of the mean annual distance covered as a time series (TS) is shown together with the smoothed time series of the annual distance covered (by averaging over 5 year periods; TS smoothed) and the linear regression (LM) (Figure 3.8).



(a) Swiss Plateau



(b) Pre-Alps



(c) Alps

Figure 3.8: Time series (TS) and linear regression (LM) of mean distance over the years 1971 - 2011

Figure 3.8a shows that the mean annual walking distance in the Swiss Plateau ranges from less than 1000 m up to 6000 m, with several peaks and low points. Similarly the smoothed curve shows high and low points. The linear regression reveals a slight decrease in the annual walking distance but this result is statistically not significant (p-value = 0.496). Also, the according linear regression of the walking distance and year is not significant (p-value = 0.161).

In the Pre-Alps (Figure 3.8b) the mean annual distance covered ranges from about 1000 − 10000 m and shows two peaks between 1971 and 1985 that are interrupted by a low point.

From 1985 until 1998, the mean annual walking distance is around 1800 m and after that it increases again. Note that there are several years in the 1970's throughout the 1990's in which less than five animals were reported back for this region. The linear regression of the mean annual walking distance again decreases slightly but not significantly (p-value = 0.629) while the linear regression of the walking distances increases by 2.7 m per year (p-value = 0.914). Thus, in this case, one cannot speak of a tendency either.

In the Alps (Figure 3.8c) the mean annual walking distance ranges from 1000 to 7000 m, with several peaks. Here, until about 1980, there were very little individuals reported back such that the data from before 1980 is of little relevance and, thus, were excluded. The linear regression of the mean annual walking distances increases by 30 m per year with no statistical significance (p-value = 0.310) and the linear regression of the distances covered and years increases slightly by 17 m but not statistically significant (p-value = 0.503).

3.4 Barriers

Of 1570 roe deer (subadults and adults) 40 crossed a motorway (2.55 %), 27 (1.72 %) crossed a railway track and 112 (7.13 %) crossed a river or lake. For all the individuals that crossed a motorway or a railway line, the motorway or railway passes through a tunnel, goes over a bridge or both (Figure 3.9) within a 3 km buffer zone of the bee line distance between the marking and finding location.

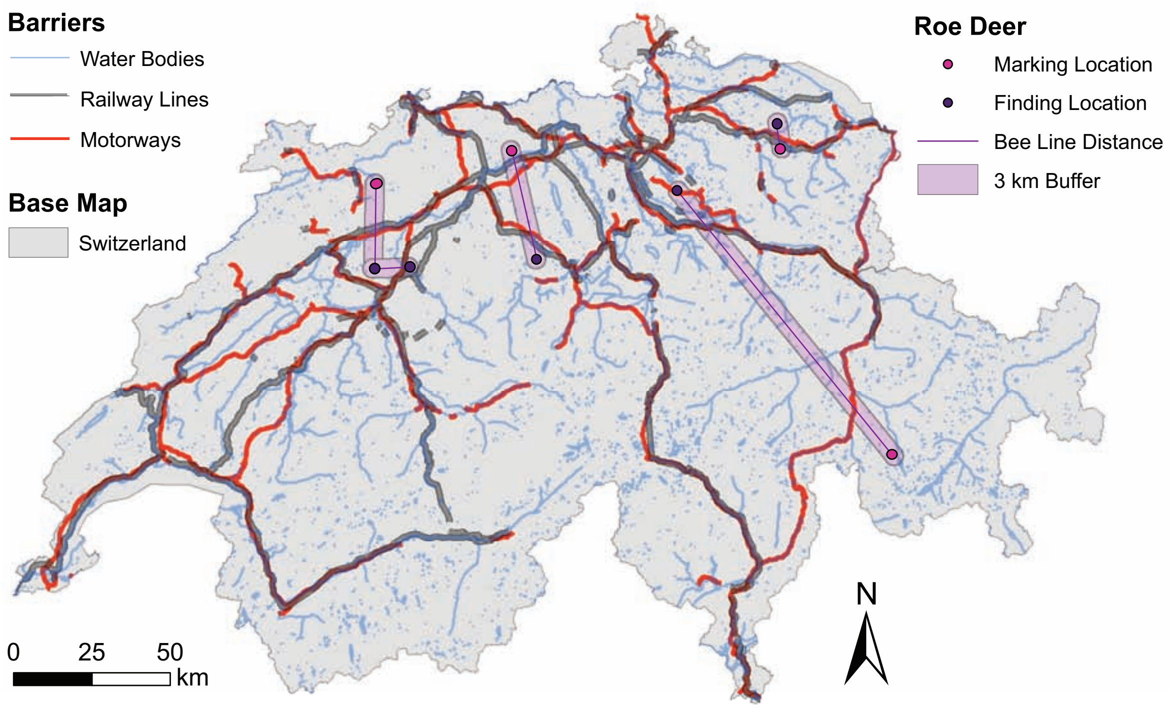


Figure 3.9: The barriers and the marking and finding locations with the beeline distance and the 3 km radius buffer of the five individuals that crossed a motorway, railway line and a waterbody (data sources: Federal Office of Topography swisstopo and Rehkitzmarkierung Schweiz)

All barriers combined gives a number of 148 individuals (9.43 %) that crossed a motorway, railway track or a water body or some combination of these (Table 3.2).

M	R	W	M+R	M+W	R+W	M+R+W
17	9	96	10	8	3	5

Table 3.2: Number of animals that crossed a motorway (M), a railway line (R), a waterbody (W) or a combination

Of all the 1570 considered individuals almost all animals were marked within 3 km of a waterbody. Within a 3 km radius of motorways and railway lines less animals were marked. However, of these numbers most animals crossed a railway line, followed by the individuals that overcame a motorway or waterbody (Table 3.3).

The individuals that crossed a barrier covered distances ranging from 451 m to 109.2 km, with a mean distance 11.3 km. Most animals that overcame a barrier covered more than 3 km

	M	R	W
number of marked animals within 3 km	350	206	1559
percentage of animals that crossed barrier	11.43	13.04	7.18

Table 3.3: Number of animals marked within a 3 km radius of a barrier and the percentage of animals that crossed a barrier

	< 1 km	$1 < 3$ km	> 3 km
number of animals that crossed a barrier	13	23	112
percentage of all animals that crossed a barrier	1.83 %	5.25 %	26.48%

Table 3.4: Number of animals per distance class that crossed a barrier and percentage of animals of a distance class that crossed a barrier

(Table 3.4).

The mean of the line density for all considered roe deer is $0.058\,\mathrm{m}^{-1}$ for the motorways (standard deviation $0.133\,\mathrm{m}^{-1}$) while for the railway lines it is $0.021\,\mathrm{m}^{-1}$ (standard deviation $0.060\,\mathrm{m}^{-1}$).

3.5 Least Cost Path

The LCP was calculated for 147 of the 148 animals that crossed a barrier - one was not computed since it was found in Austria where the cost surface could not be calculated (and therefore neither the LCP). In beeline distance the animals covered a mean distance of 11.21 km (standard deviation 14.8 km). The distances covered in the LCP calculations increased between 5.7 and 326.6 %. When looking at the different distance classes, the class '$<$ 1 km' increased more than the other two, however, an Analysis of Variance yields no significant result (p-value = 0.172) (Table 3.5).

	Bee line distance [m]	LCP [m]	Increase [%]	N
$<$ 1 km	623	913	48.9	13
1 - 3 km	1699	2211	29.5	23
$>$ 3 km	14417	18570	29.9	111

Table 3.5: Mean bee line distance, LCP length and increase per distance class

The map of the LCPs is shown in Figure B.1, Appendix B.

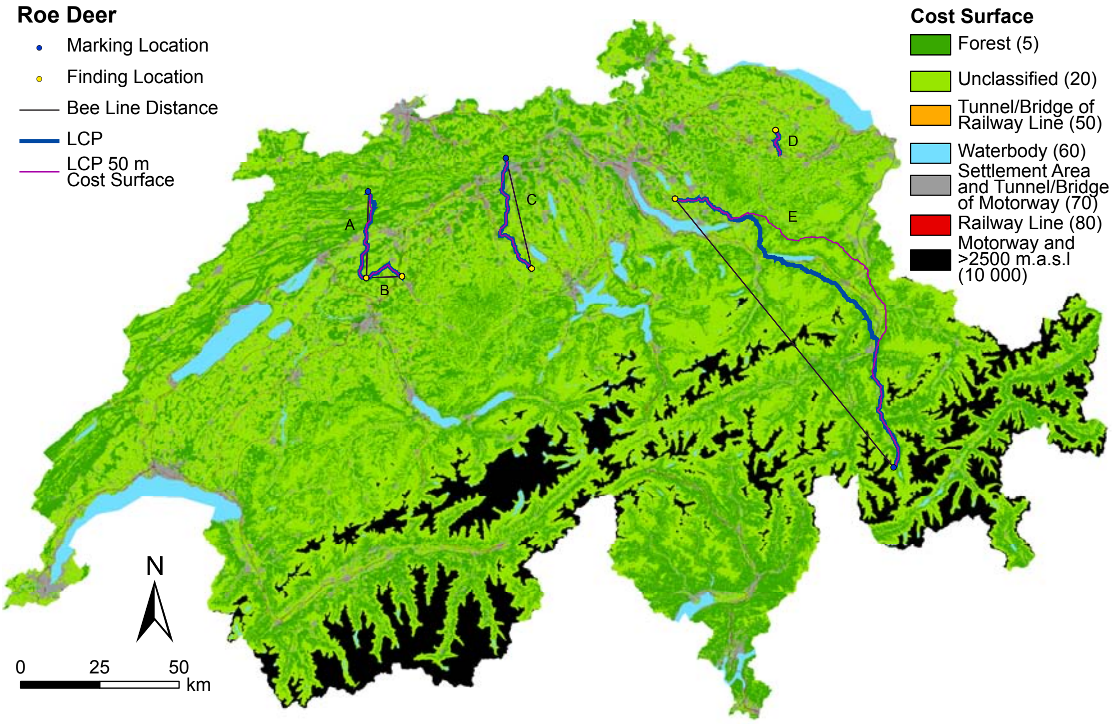


Figure 3.10: LCPs of the animals that crossed all barrier types and the corresponding LCPs of the sensitivity analysis (data sources: Federal Office of Topography swisstopo and Rehkitzmarkierung Schweiz, see Appendix B for detailed maps)

Sensitivity Analysis

Due to the time consuming calculations the sensitivity analysis was performed only for the five animals that crossed all barrier types. The values of the cost surface were varied ±20 separately for railway lines, tunnels/bridges of railway lines, tunnels/bridges of motorways, waterbodies and settlement areas. The resulting LCPs remained the same as the one calculated with the original cost surface. With a lower resolution of 50 m minor variations in the LCPs occur for animals A - D. These LCPs are maximally 1.5 km apart from the original one. For animal E, which travelled the longest distance of 109.2 km, the LCPs' deviation amounts to 11.5 km (Figure 3.10 and Figures B.2 to B.5 in Appendix B).

Corridors

To identify potential corridors the LCPs were intersected with each other. 9.74 % (206.940 km) of the overall LCPs' length (2123.971 km) coincide with each other and are potential corridors. Further, the LCPs were compared to the wildlife network system, a dataset that describes the wildlife movement axes in Switzerland (Bundesamt für Umwelt BAFU 2013). 41.01 % of the LCPs lie within 500 m of the wildlife network system (Figure 3.11). 52 of the 147 LCPs pass through a wildlife corridor.

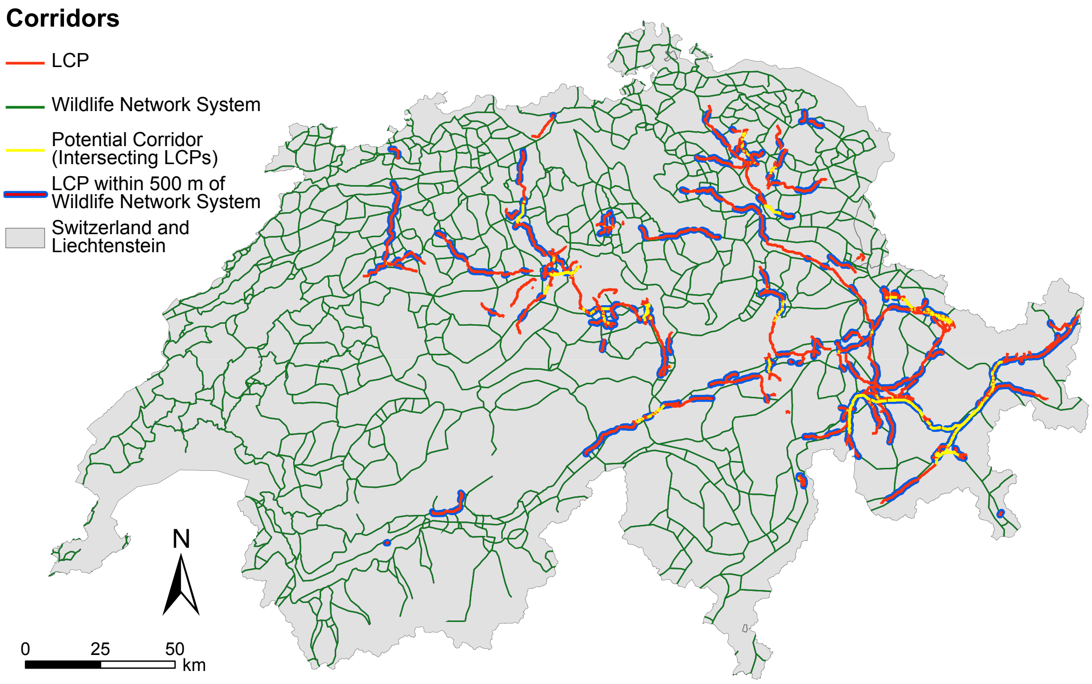


Figure 3.11: LCPs with potential corridors (intersecting LCPs) and the wildlife network system (data sources: Federal Office of Topography swisstopo, BAFU and Rehkitzmarkierung Schweiz)

4 Discussion

4.1 Individual-specific Variables

4.1.1 Finding Rate

17.48 % of the marked animals were reported back. This is close to the average response rate of 21 % of the marking projects in Baden-Württemberg (Bauch et al. 2014: 3) and 15.7 % in Lower Austria (Reimoser et al. 1999: 10), respectively. Reasons for the low rate of findings are the high fawn mortality, the high probability of up to 24 percent that ear marks fall out as well as lacking knowledge about the project such that people do not know where to report a finding (Rehnus and Reimoser 2014: 7). For the analysis of the data further sources of error are the incomplete or incorrect finding reports. In case of the coordinates there were several finding reports with the right coordinates but with confused easting and northing. Luckily such errors could be corrected easily in the database as the coordinate range in the Swiss national reference system is unambiguously identifiable.

The sudden increase from about 200 markings to about 400 in 1990 is due to a decision in the Canton of Grisons to yearly mark at least 10 % of the number of shot animals (Signer and Jenny 2006: 2).

4.1.2 Dispersion Distance

The median of 700 m and the third quartile at 1968 m indicate that the marked animals are no exception to the fact that the roe deer is a philopatric animal (Danilkin 1996: 100f). The mean of 2399 m is higher compared with other marking projects: in Lower Austria the mean walking distance was 1310 m (Reimoser and Zandl 1993: 28), and the one of the marking project in Upper Austria is 1761 m (Waldhäusl 2011). The project from Baden-Würtemberg does not give a precise number but a sex separated graphic shows that for the fawns the mean lies around 500 m while for subadults, 2-4 year olds and 5-14 year old it is between 1200 - 2200 m (Bauch et al. 2014). Thus, the mean also lies below 2399 m. The reason for this partly big difference are most likely the different topographic situations of the study sites. While Switzerland is mountainous all other marking sites are not. Furthermore, it is known that roe deer seasonally migrate to lower altitudes in winter depending on snow depth and follow the growth of fresh shoots in spring that gradually rises in altitude (Danilkin 1996: 111ff, Heurich 2013: 39f). Therefore, animals marked in the mountains are likely to walk greater distances than animals from lowlands.

The maximum distance covered of 109.2 km is the furthest of all the marking projects. In the German project, a fawn was marked that walked 50 km – presumably with its mother. Among the adults, the record of 44 km is held by a subadult buck (Bauch et al. 2014: 6). In the project of Lower Austria the record of 64 km is held by a doe (Reimoser et al. 1999: 11) and in Upper Austria a record distance of 83 km was covered by an adult buck (Waldhäusl 2011). Linnell et al. 1998: 110f conclude that the longest movements were recorded of 90 and 205 km towards the northern European countries, Norway and Sweden. This shows that roe deer are able to cover distances of more than 100 km, and thus, our record lies within a reasonable range.

4.1.3 Sex

The non-significant difference of the mean covered distance shows that the marked animals behave as known from other European studies (see Heurich 2013: 40, Gaillard et al. 2008, Linnell et al. 1998). Gaillard et al. (2008: 2028) note that "the absence of a between-sex difference in dispersal behaviour [...] is thus consistent with the low sexual size dimorphism, the mating tactic of resource defence and the low level of polygyny exhibited by roe deer". Also Müri (1999: 44) and Signer and Jenny (2006: 51) found no significant difference between sexes.

4.1.4 Age

The dependency of the walking distance on the age group shows the known behavior patterns of the roe deer. In the first year. the fawns stay with their mothers and move within the mother's home range (Linnell et al. 1998: 266). With the separation, they need to look for their own territory (Heurich 2013: 38f). This pattern manifests itself in our data: more than 80% of the fawns were found within 1 km of their marking location while only about 50% of the subaldults and the adults were found within 1 km of their marking location. A similar result was obtained in the marking project of Upper Austria (Waldhäusl 2011). The project of Baden-Württemberg only published some age dependent results about the mean walking distance. Both sexes of the fawns walked around 500 m in Baden-Württemberg, the male subadults about 1400 m, the females about 2300 m, 2-4 year old males around 1500 m, females 2400 m, and the 5-14 year old males around 1200 m, females 2200 m (Bauch et al. 2014: 6). Compared to the means of the Swiss project (fawns: 965 m, subadults: 3504 m, adults: 3384 m) the mean walking distances are much lower in the project of Baden-Württemberg, but the fawns show the same tendency of staying much closer to the birth place than the subadults and the adults (Bauch et al. 2014: 6).

4.1.5 Condition

Adult does are known to be smaller and weigh less than the bucks (Burton and Burton 2002: 2201). This is also reflected in our data. Similarly, the adult male marked roe deer of the marking project in Baden-Württemberg weigh on average more than the females (Bauch et al. 2014: 7). Debeffe et al. (2012) showed that the probability of dispersing earlier and further increases with higher weight. Moreover, in their study, no animal below a weight of 14 kg dispersed (Debeffe et al. 2012: 1334). As we do not have data about the individuals' weight as a subadult this result cannot be compared with our data. The lack of correlation in our data between the weight and the covered distance can be explained by the fact that even though heavier animals have the potential of covering greater distances than lighter ones, the weight as such does not imply that they do. Moreover, it is possible that the presence of barriers hinder roe deer with good condition to disperse over further distances. Müri (1999: 44) found that the distances covered of the adult does are correlated with the weight, i.e. well conditioned does dispersed further. An explanation for these different results is most likely that in the time between Müri's (1999) and this analysis much more data has been collected. Furthermore, Müri (1999) did not investigate the data from the Canton of Grisons. Signer and Jenny (2006: 59f) analyzed the data of the Canton of Grisons sex-specifically. For both sexes only very weak correlations were found (Signer and Jenny 2006: 59f).

4.1.6 Cause of Death

The cause of death has been collected also in the marking projects of Baden-Württemberg, Lower and Upper Austria (Table 4.1). As the categories of 'prey' and 'disease' were not collected in the projects of Baden-Württemberg and Lower Austria, they will be counted towards the category 'unknown' for the comparison. This amounts to 15.09 % in Switzerland and 4 % in Upper Austria.

Project	Shot	Traffic	Mowed	Disease	Prey	Unknown
Switzerland	63.0	13.9	8.0	2.5	3.1	9.5
Baden-Württemberg	66.0	14.0	9.0			11.0
Lower Austria	51.1	20.3	9.3			19.3
Upper Austria	86.0	4.0	6		1.1	2.9

Table 4.1: Percentage of reported causes of death in different marking projects

The values of the Swiss and the German marking projects show very similar numbers, while the ones of Lower Austria show over 10 % less shot animals and, thus, more traffic accidents and unknown causes of death. Nevertheless, the tendency that most of the animals were shot remains the same. Also the percentages of Upper Austria show a similar tendency that most of the animals were shot. but here it is 20 % more than in our data, leaving less to the other causes of death. These different rates of shot animals can either be explained by better and worse reports by the hunters or by different hunting concepts. Also a combination of these two could be possible. However, these numbers should be interpreted with caution, as the finding rate of shot animals and animals that came to death in traffic accidents is close to a hundred percent, while it is unlikely that animals which were taken prey or died of disease are found (Signer and Jenny 2006: 29).

More interesting is the fact that the distribution of the cause of death does not depend on the distance category (below or above 3 km). This suggests that dispersing animals do not have a higher risk of dying in traffic accidents than the philopatric animals.

4.2 Regional-specific Analysis

4.2.1 Dispersion Distances

The mean dispersion distance increases significantly from the Swiss Plateau to the Alps. Therefore, we can conclude that the roe deer from the Swiss Plateau have a stronger site fidelity than the ones from the Pre-Alps and the Alps. One possible explanation is the seasonal migration due to snow cover in the Alps. It would be expected that the same can happen in the Pre-Alps but to a lesser extent, thus, the roe would have to travel less than the ones in the Alps to find a range that suits them better during the winter. Another possible explanation is that the landscape fragmentation in the Swiss Plateau is much higher than in the Pre-Alps and the Alps such that roe deer in the Swiss Plateau encounter a hindering barrier earlier than the ones in the Pre-Alps and the Alps.

4.2.2 Cause of Death

The cause of death depends on the region. In all the regions most animals were shot but compared to the Pre-Alps and the Alps where around 60 % were shot more than 70 % were shot in the Swiss Plateau. This can be explained by different hunting regulations or the report probability. However, as already mentioned in Section 4.1.6, these numbers need to be interpreted cautiously. Generally, one expects that it is much more likely that animals that were shot or killed in a traffic accident are reported back as these are the cases where the animal is not found by stumbling upon it. Animals from the Alps are more likely killed in a traffic accident than the ones from the Swiss Plateau and the Pre-Alps. As the fragmentation is much higher in the Swiss Plateau than in the Pre-Alps and the Alps, it cannot be explained by the presence of (more) roads. A reason for this could be the seasonal migrations from places at higher altitudes towards the valley where most of the main roads are located. In the Pre-Alps, individuals that were taken prey were reported much more often than in the other regions. It seems unlikely that roe deer are taken prey more in just one region, thus, one could explain this difference by the low report probability for this category – especially since only between 18 and 34 animals per region were reported. A last difference can be observed in the percentage of animals that were reported with an unknown cause of death which is about half as high in the Swiss Plateau than in the Pre-Alps and the Alps. This is probably an artefact of the finding reports. Only minor differences are found in the number of animals that came to death by a mowing machine or a disease.

4.3 Changes over Time

The goal of the analysis of the walking distances over time was to investigate whether the increasing landscape fragmentation in Switzerland (Jaeger et al. 2007: 54) had an influence since the beginning of the project. If so, it would have been expected to show the most effect in the region of the Swiss Plateau as the "effective mesh size" of 29.22 km^2 (in 2002) is much lower than in the Pre-Alps (883.73 km^2 in 2002) and the Alps (1310.24 km^2 in 2002) (Jaeger et al. 2007: 50, 205). The increasing landscape fragmentation impacts all wildlife by reducing the size of connected habitat patches as well as isolating populations (Hewison et al. 2001: 679). Two scenarios in relation to the walking distance of the roe deer come to mind: due to the smaller habitat patches the walking distance decreases, or conversely, the walking distance increases because high quality patches might lie further apart. Note that the data collected from the last couple years only present the findings up to 2013 and thus have a bias towards the younger population (Figure 3.7).

The analysis investigating the dependence between the distance categories and pentades yielded no statistically significant results. Thus, when looking at all data there is no trend of the walking distance over time present.

4.3.1 Time Series per Region

As in the overall analysis of the walking distances in pentades, for none of the three regions a statistically significant result was obtained. This implies that the increasing landscape fragmentation does not correlate with the walking distance in our data. However, due to the low sample size (< 5) for several marking years, particularly in the Alps and the Pre-Alps, and the high data range, conclusive results are not to be expected.

Interestingly, Müri's (1999) result of a decreasing dispersion distance over time in the Swiss Plateau could not be confirmed. Müri (1999: 46) investigated the dispersion distance over time and found a significant negative correlation between distance category and birth year. Note that she analyzed the data of animals marked from 1971 until 1995 in the Cantons of Aargau, Berne, Lucerne, Nidwalden, St. Gallen, Schaffhausen, Solothurn, Thurgovia, Uri, and Zug (Müri 1999: 42), which includes different biogeographical regions. As only some cantons have taken part regularly, it is possible that her results are influenced by the ratio of animals from different regions. For instance the Cantons of Berne, Lucerne and Nidwalden do not (entirely) belong to the Swiss Plateau. Therefore, data from the same region was used to minimize the risk of such influences.

Furthermore, it seems that Müri considered all animals, i.e. including fawns, in the analysis of the dispersion distance over time (Müri 1999: 46) while here only subadult and adult animals were used. As seen in Section 3.1.4 most fawns cover distances below 1 km and thus a higher ratio of fawns can decrease the dispersion distance of a year (Elliger 1999: 1). This is especially critical if the number of fawns included is not constant over time (yielding lower mean distances covered for those years with a higher rate of fawns). Müri (1999: 46) further investigated the dispersion distance of the adult does and bucks. While there was no significant correlation for the bucks, the does' distance covered decreased significantly over time. The analysis was done using six distance classes and year classes of two to three years combined which shows methodical differences to the analyses presented here. Here, linear models which are recommended for analyses over time were used (Falk et al. 2012: 2ff). To account for extreme values, the present time series analysis was done for the absolute values as well as the mean values per year. However, for both approaches no significant changes over time were found. Since there are no known differences between sexes (Sections 3.1.3 and 4.1.3) and due to the already low sample size (< 5) for several years, a sex specific analysis does not seem sensible.

Müri (1999) presented three more results which were not investigated here. Firstly, she showed a significant decrease of the mean dispersion distance when comparing the two time periods 1971 - 1975 and 1989 - 1993 (Müri 1999: 46). Such an analysis is sensitive to extreme values if one is contained in one time period but not in the other. For this reason, a similar analysis comparing different periods was omitted here. The second result investigated the ratio of emigrants in the two time periods of 1971-1983 and 1984 - 1993. In the second period, significantly less adult animals as well as adult does emigrated. Nevertheless, Müri (1999: 42) herself considered this approach a "construct", therefore, such an analysis was also not considered here. Signer and Jenny (2006: 51ff) did the same analysis with the two thresholds of 1.5 km and 2 km where the latter was chosen because the animals' mean dispersion distance in the Canton of Grisons (3478 m) is higher than in the data investigated by Müri (1999) (2950 m). The ratio of emigrants decreases from 50 % when using 1.5 km as threshold to 42 % when using 2 km, respectively (Signer and Jenny 2006: 52). Müri (1999: 47) furthermore investigated whether the population density has an influence on the dispersion distance. This, however, correlated only for the female fawns. The analysis was done by using the official Swiss hunting statistics (Müri 1999: 42). Again, Müri (1999: 44) noted that this estimates the actual population density inexactly. With roe deer such estimations are almost impossible (see Kurt 1991: 12ff for several examples). So, again such an analysis was not considered here.

4.4 Barriers

Having the marking and finding locations of 1570 subadult and adult roe deer allowed investigating whether and to what extent individual animals have overcome a motorway, railway line or water body lying between their birth and death place. To test this, a 3 km buffer polygon around the beeline distance of the marking and finding location was created and cut with potential barriers. An animal has crossed a barrier if the buffer polygon was cut between the marking location and finding location, i.e. the two points lie in different polygons. Altogether 148 (9.43 %) animals crossed a barrier. 96 individuals (7.13 %) or 64.86 % of the roe deer that have overcome a barrier crossed a water body solely, and another 16 crossed a water body in combination with a railway line and/or a motorway, resulting in a total of 75.68 % that crossed a water body. Compared to the 40 roe deer (2.55 %) that crossed a motorway or the 27 (1.72 %) that traversed a railway line, considerably more animals crossed a water body, implying that rivers and lakes are more permeable barriers than railway lines or fenced motorways. However, when investigating the numbers that crossed a barrier with the presence of possible barriers within a 3 km radius it shows that only 7.18 % crossed a waterbody while 13.04 % traversed a railway line and 11.43 % a motorway. This suggests that waterbodies are not impermeable barriers but at the same time roe deer seem not to cross them readily. This coincides with Hepenstrick et al. (2012: 637) who also found that the river Aare acted as a moderate barrier in their study.

Of all of the individuals that crossed a motorway or a railway line, a bridge was present or the motorway or the railway line passed through a tunnel within an area of 3 km around the beeline distance, providing at least one possibility to cross. Similarly, Hepenstrick et al. (2012: 636) find that “traffic infrastructure effectively impairs movement of large wildlife”. Kuehn et al. (2007) and Senn and Kuehn (2014) too find that motorways represent barriers but Kuehn et al. (2007: 8) observe that already small over- and underpasses are used by roe deer to cross motorways. Coulon et al. (2006: 1677) found that fenced motorways do “not constitute an impermeable barrier” but note that three wildlife passages are present in the study area. For railway tracks Hepenstrick et al. (2012: 637) conclude that they do not necessarily act as barriers, especially if they are not fenced. Here, only 27 animals in total have crossed a railway track. This would imply that railway lines may act as greater barriers than motorways. But considering that 206 of the 1570 animals (13.04 %) were marked within 3 km of a railway line and 350 within 3 km of a motorway (11.45 %) railway lines can nevertheless be considered a barrier that is easier to overcome than a fenced motorway. Moreover, the mean line density of the railway lines is less than half as high as the mean line density of the motorways within a 3 km radius of all the 1570 considered animals. Therefore, it is much more likely that an individual encounters a motorway than a railway line. Also, it should be considered that occasionally roe deer are fatally hit by trains (Hepenstrick et al. 2012: 637). A marked animal will probably not be reported back – as it seems unlikely that the mark is found – and, thus, will not show up in the data. The increasing percentages of animals within the distance classes ('< 1 km', '$1-3$ km', and '> 3 km') show, as expected, that the further an animal walks the more likely it needs to overcome a barrier. However, the project data only provides the birth place and the location the animal died and thus needs to be interpreted carefully.

Müri (1999: 47) also investigated whether there exists a correlation between distance categories and weighted barrier density and found that adult animals born in areas with low barrier densities dispersed significantly more often further than animals from areas with high barrier densities. Barriers were distinguished in two classes: first order barriers consisted of motorways, multi-track railway lines and settlement areas of more than 2 km length, and second order barriers were defined to be smaller settlements, roads of width at least 6 m and agricultural areas with little structure (Müri 1999: 42f). The barriers were recorded within four corridors of 1 km width and 2 km length, each starting at the marking location and running in the dispersion direction of the animal as well as the opposite direction and $\pm 90°$ (Müri 1999: 43). From this, a weighted barrier density was calculated by summing the barriers weighing the first order barriers with a factor of 3 and the second order barriers with a factor of 2, respectively (Müri 1999: 43). Furthermore, Müri (1999: 47) investigated how many animals overcame a first order barrier. Therefore, she defined areas that are surrounded by at least 80 % of first order barriers as 'population areas' and investigated whether animals reached another population area (Müri 1999: 47). Of the 152 considered animals only one overcame a barrier and in this case there existed a tunnel close to the bee line (Müri 1999: 47). So, the pattern that only a small part of the marked roe deer cross barriers shows in the present analysis as well as in Müri's (1999) investigation of the data. In our study, settlement areas were not considered directly as their permeability is hard to assess and typically there is a railway track or motorway present in all major settlement areas such that – indirectly – major settlement areas are represented. Moreover, they will be considered in the Least Cost Path analysis.

4.5 Least Cost Path

Having only the birth and the death location of individual roe deer makes one wonder how their dispersion route might have looked like. The calculation of the LCP for various individuals was an attempt at answering this question. Furthermore, it is clear that the actual distance covered typically is considerably longer than the bee line distance (Jerina et al. 2014). One example is a doe that, before settling about 5 km from her birth place, covered a distance of more than 100 km (Heurich 2013: 39). The LCP, being the closest and least costly path from one point to another, gives an impression of the lower bound of the dispersion distance that incorporates movement through an anisotropic environment (as opposed to the beeline distance which assumes an isotropic environment).

Generally, the calculated LCPs all run through forested areas where possible, i.e. the LCPs represent nicely that the dispersion routes of roe deer are connected to woodland structures (Coulon et al. 2004). Also, settlement areas are avoided where possible.

It could be hypothesized that the increase from the bee line distance to the LCP could be different for different distance classes. For example, it might be that animals which covered a long distance and crossed a barrier did not have the same local knowledge as animals that were born close to a barrier. This would suggest that the LCP of animals in lower distance classes increases less compared to animals of further distance classes. However, this does not seem to be the case here. The tendency is opposite: the increase of animals in distance class '< 1 km' is 20 % higher than for the distance classes '1-3 km' and '> 3 km'. Also, due to the uneven sample sizes this result is difficult to interpret.

To assess whether small changes to input parameters have an impact on the results a sensitivity analysis was conducted. As mentioned, due to the time consumption of the cost distance calculation this was only done for five animals. The values of railway lines, tunnels/bridges of railway lines, tunnels/bridges of motorways, waterbodies and settlement areas were changed +20 and -20 individually. Especially changing the values of the tunnels and bridges as well as the railway tracks are interesting since these had to be chosen with little background information. The resulting LCPs remained the same as the original one which implies a robust choice of the costs and, thus, reasonable dispersion routes. The LCPs calculated with the raster at 50 m resolution also are mostly close to the original LCPs. In the case of animal E (Figure 3.10) it becomes obvious that the LCPs can vary depending on the cost surface properties (once it differs enough, the chance that it grows further apart can increase greatly, e.g. if barriers are present).

In the literature the application of LCP calculations to model wildlife corridors is criticized (Fahrig 2007, Leoniak et al. 2012). Cost surfaces typically do not consider the animal's behavior – animals do not make optimal choices (Fahrig 2007: 1010) and tend to react to human disturbances (Sawyer et al. 2011: 675). This also applies for our study. Furthermore, there is no additional information about the type and structure of bridges, thus, in the definition of the cost surface this information could not be factored in. Also, due to the lack of earlier versions of VECTOR25 changes in time in the cost surface were disregarded. Nevertheless, with appropriate assumptions LCP modelling can also be successful. Leoniak et al. (2012) showed that their predicted roadside wildlife corridors for Fishers and Bobcats were identified correctly. Since in our case we do not predict but reconstruct a path, the calculated LCPs give an idea of possible routes of roe deer that crossed a barrier.

Given the scarce data that, in addition, is distributed over Switzerland an identification of corridors seems unreasonable. However, the fact that more than 40 % of the LCPs' length lies within 500 m of the Wildlife Network System indicates further that the resulting LCPs represent reasonable dispersion routes.

5 Conclusion

The analysis of individual-specific variables confirmed several previously known facts about the roe deer: it is a philopatric animal (Danilkin 1996: 100f) that stays with its mother close to its birth site until the age of about one year (Grzimek 1988: 204ff) when subadult roe deer part from their mother to find their own territory (Heurich 2013: 40, Danilkin 1996: 102). This is also the time when young roe deer disperse (Wahlström and Liberg 1995: 460). In Switzerland the average dispersion distance has shown to be further than in other marking projects. The reason for this is probably the mountainous topography of the country – all other marking projects took place in flatland or Pre-Alpine areas at most. Furthermore, in alpine regions a typical behavior of roe deer is the seasonal migration from summer habitats at higher altitudes to winter home ranges in the valley. Moreover, in the Pre-Alps and the Alps the barrier density is much lower than in the Swiss Plateau (Jaeger et al. 2007). Both facts probably contribute to further dispersion distances than in other marking projects. As seen previously (Heurich 2010, Gaillard et al. 2008, Linnell et al. 1998), the dispersion behavior also proved to be sex independent in the presented data.

While in other works the animals' condition increased the likelihood of far dispersion distances (Debeffe et al. 2012, Müri 1999), in this study the weight does not correlate with the dispersion distance. An explanation could be that. even though heavier animals have the potential to disperse further than lighter ones, this does not imply that they actually do.

The analysis of the regions showed that the mean dispersion distance is lowest in the Swiss Plateau and increases significantly in the Pre-Alps and the Alps. Possible explanations are again the lower degree of fragmentation in the Pre-Alps and the Alps as well as the seasonal migrations that typically take place in mountainous areas due to the snow cover.

It was expected that over time the dispersion distance decreases due to the increasing landscape fragmentation. However, in no region the data showed any trends in the dispersion distance, i.e. there seems to be no apparent influence of the increasing fragmentation on roe deer in Switzerland. Due to the partially low sample sizes these results have to be interpreted with care however. Nevertheless, possible explanations are that either roe deer are not influenced by the barrier density, i.e. are spatially small-scaled, or they find a sufficient number passages over significant barriers such that they do not present major constraints to the population. The fact that already small passageways are used to cross motorways was also shown by Senn and Kuehn (2014).

Of the marked animals about 10 % of the subadult and the adult animals crossed a barrier. In this study, motorways, railway lines and water bodies (rivers and lakes) were considered as barriers. As expected, it showed that the further the animals dispersed the more likely they overcame a barrier. Overall, only a small part of the marked animals overcame a barrier and it seems that fenced motorways are the hardest to overcome. Nevertheless, there appear to be some animals that found a way to cross motorways, probably by using either a tunnel, bridge or wildlife passage. Furthermore, it is difficult to assess to what extent the considered elements impose barriers to roe deer because, by the data's nature, it can only by hypothesized which path individual animals actually chose between the marking and finding location. This black box was the incentive for the calculation of the least cost paths (LCP) of the individuals that crossed a motorway or a railway line. The least cost path is based on a previously defined cost surface and describes the least costly path from a source location to a destination. The comparison of the beeline distance and the LCPs in distance classes indicates that there is no difference between the distance classes, so the local knowledge of the roe deer probably does not have an influence on the chosen path.

Altogether, the LCPs clearly can only give an idea of possible dispersion routes. For more conclusive results the LCPs need to be calculated for all the subadult and adult animals that were reported back. In terms of further research, also the definition of the cost surface needs some adaptions – for instance, the inclusion of roe deer specific behavior as well as time specific cost surfaces would be desirable.

Apart from a better knowledge about the species' state, interesting results concerning regional differences could be obtained. The data also shows that roe deer are able to overcome barriers until today – even in fragmented landscapes. So, even though the data has its limitations – one can only make educated guesses about how and where the animals lived between the marking and their death – for general investigations and monitoring of the species the data is evidently well suitable. Also, due to the irregularity and the voluntariness of the data collection longitudinal analyses are difficult, but not impossible and will gain importance if the marking numbers stay constant or even increase in the future.

6 Acknowledgements

First of all, I would like to thank my advisors, Prof. Robert Weibel and Maik Rehnus, for their great support and supervision in realizing this thesis. Also, I would like to thank everyone at Wildtier Schweiz for sharing their critique, knowledge and motivation. Many thanks also go to my friends Marc and Sabine, who supported me in statistics questions, and everyone else with whom I could discuss the issues appearing in the course of the project.

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A Report Cards

Meldekarte 1 **Angaben über markiertes Rehkitz**

Markierdatum: Tag ______ Monat ______ Jahr ______

links  rechts

Ohrmarke: Nummer ____________ ____________

Farbe ____________ ____________

Geschlecht: ☐ männlich ☐ weiblich ☐ unbekannt

Alter geschätzt: ______ Tage **Satzgrösse:** ______ (Anz. Kitze total)

Ohrmarken-Nummern der Geschwister:

links ________________ rechts ________________

Liegeplatz: ☐ Wald ☐ Wiese ☐ Feld

Distanz vom Liegeplatz zum Waldrand: __________ m

Vegetationshöhe (im Wald Krautschichthöhe) :

☐ bis 20 cm ☐ 20-50 cm ☐ über 50 cm

Vegetationstypen im Umkreis von 100 m (mehrere möglich):

☐ Wald ☐ Acker ☐ Weide ☐ andere

☐ Wiese ☐ Hecke, bestocktes Ufer, Obstgarten

Koordinaten: ________________ / ________________

Landeskarte 1:25'000 / Blatt Nr. ______ Höhe über Meer: ______

nächste Ortschaft, mit PLZ ______ ________________

Name, Adresse, Tel-Nr. von MarkiererIn:

Meldekarte 2 **Angaben über totes markiertes Rehwild**

Funddatum: Tag ______ Monat ______ Jahr ______

links  rechts

Ohrmarke: Nummer ____________ ____________

Farbe ____________ ____________

Geschlecht: ☐ männlich ☐ weiblich ☐ unbekannt

Gewicht: geschätzt ________ kg gewogen ________ kg

Wenn gewogen, wie: ☐ aufgebrochen mit Haupt

☐ aufgebrochen ohne Haupt

☐ nicht aufgebrochen

Vegetationstypen im Umkreis von 100 m (mehrere möglich):

☐ Wald ☐ Acker ☐ Weide ☐ andere

☐ Wiese ☐ Hecke, bestocktes Ufer, Obstgarten

Todesursache: ☐ erlegt ☐ vermäht

☐ Verkehrsverlust ☐ gerissen (von ________)

☐ Krankheit ☐ andere / unbekannt

Koordinaten: ________________ / ________________

Landeskarte 1:25'000 / Blatt Nr. ______ Höhe ü.M.: ______

nächste Ortschaft, mit PLZ ______ ________________

Name, Adresse, Tel-Nr. von Finder:

Figure A.1: Report Cards 1 and 2

B Least Cost Paths

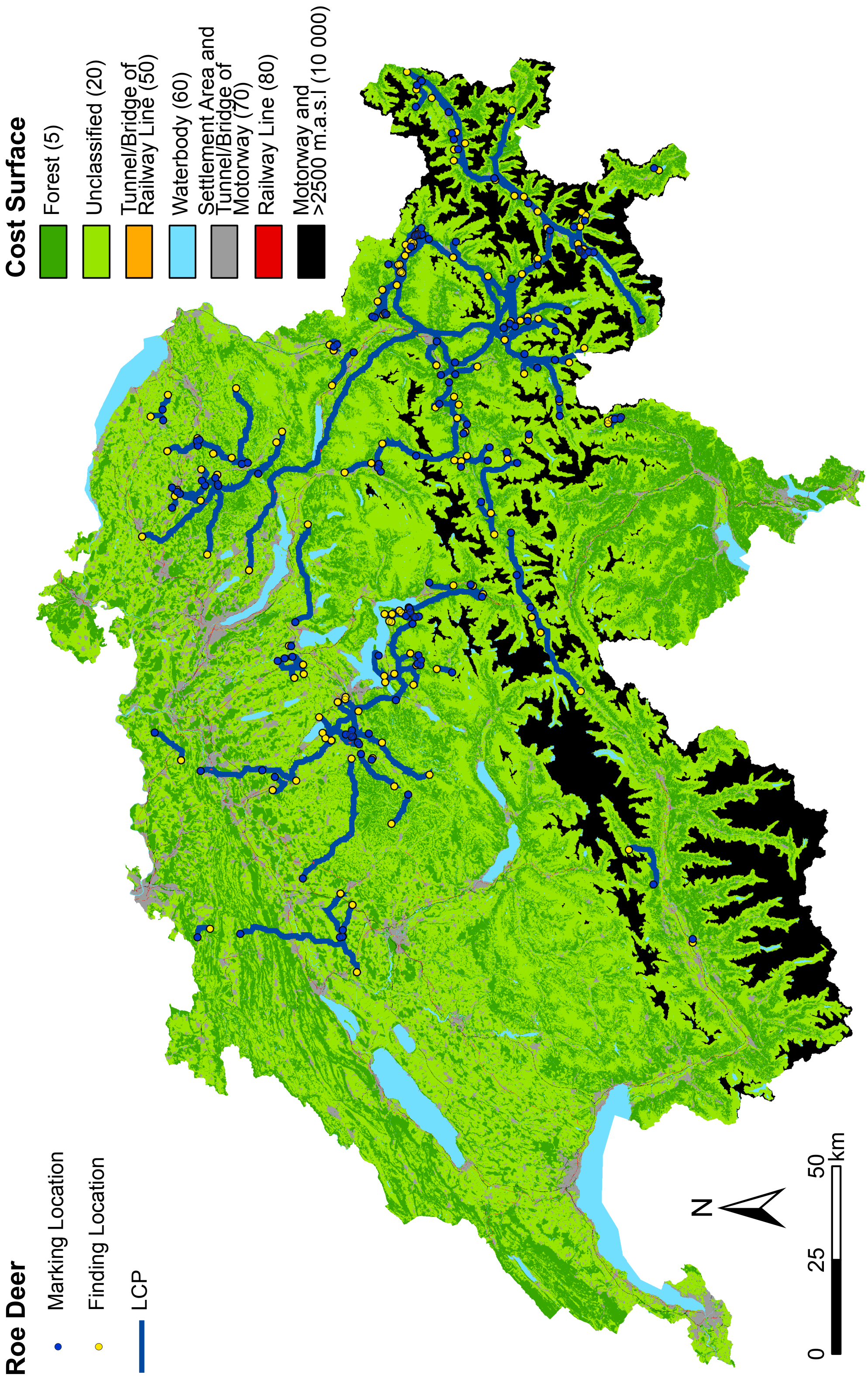

Figure B.1: All computed LCPs

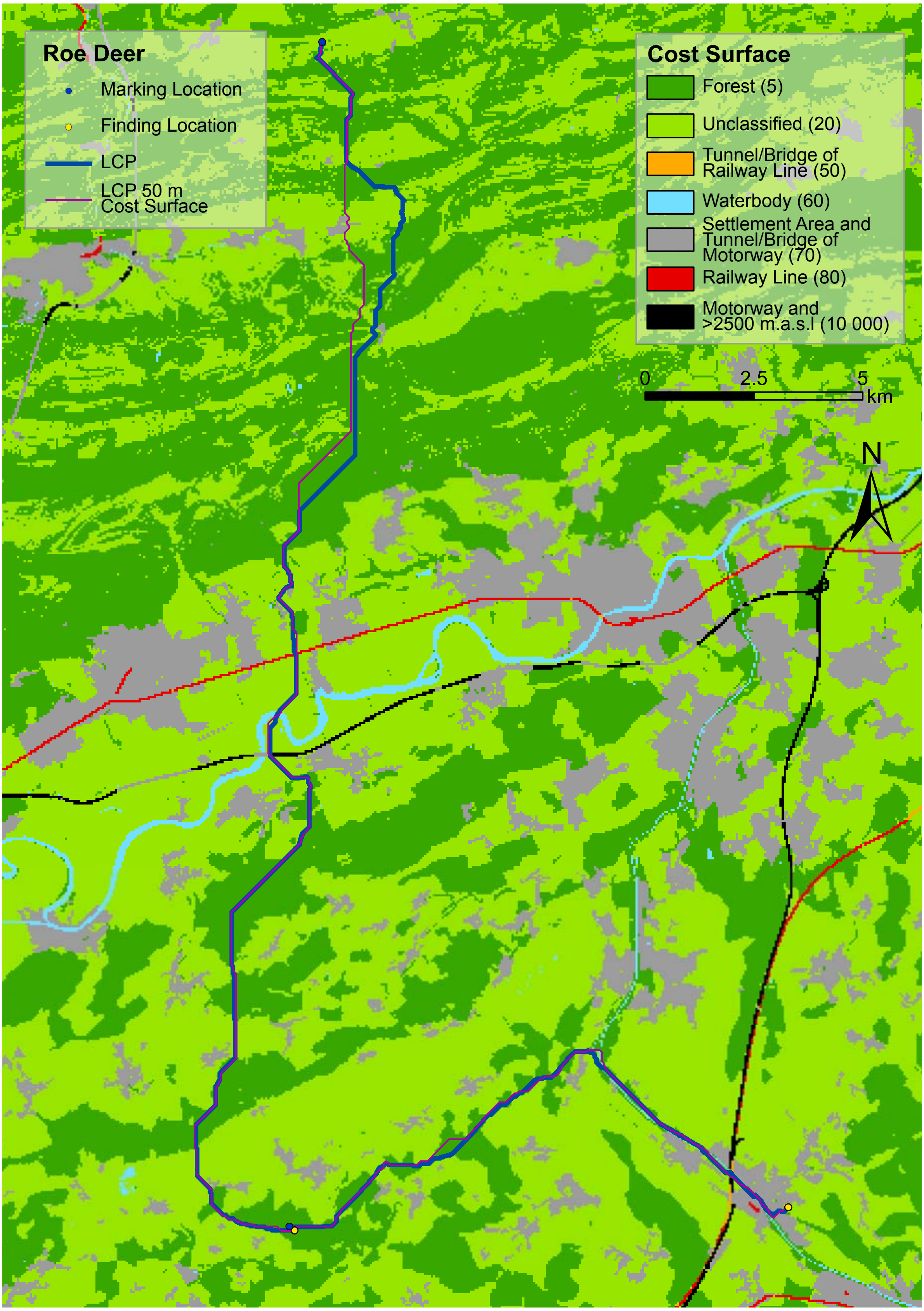

Figure B.2: LCPs A and B including LCPs of sensitivity analysis at 50 m raster resolution

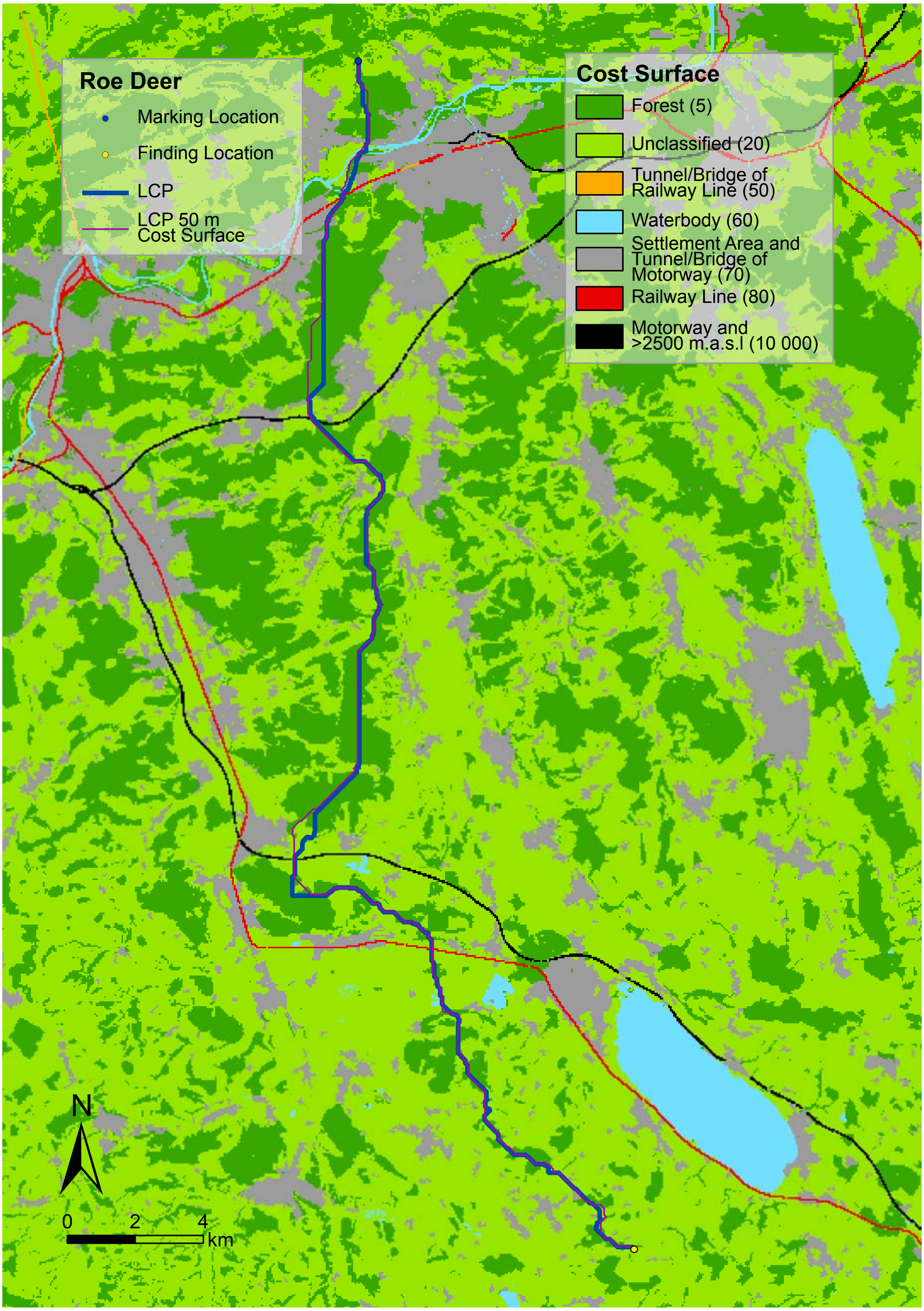

Figure B.3: LCP C including LCP of sensitivity analysis at 50 m raster resolution

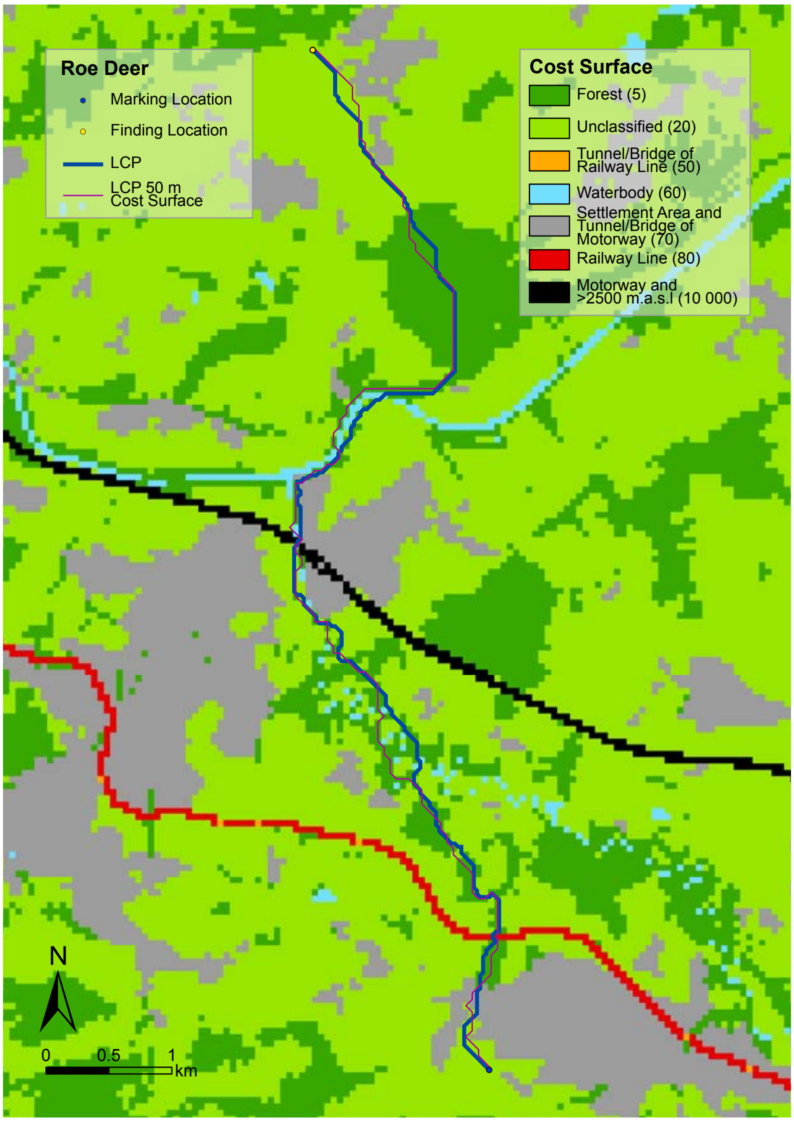

Figure B.4: LCP D including LCP of sensitivity analysis at 50 m raster resolution

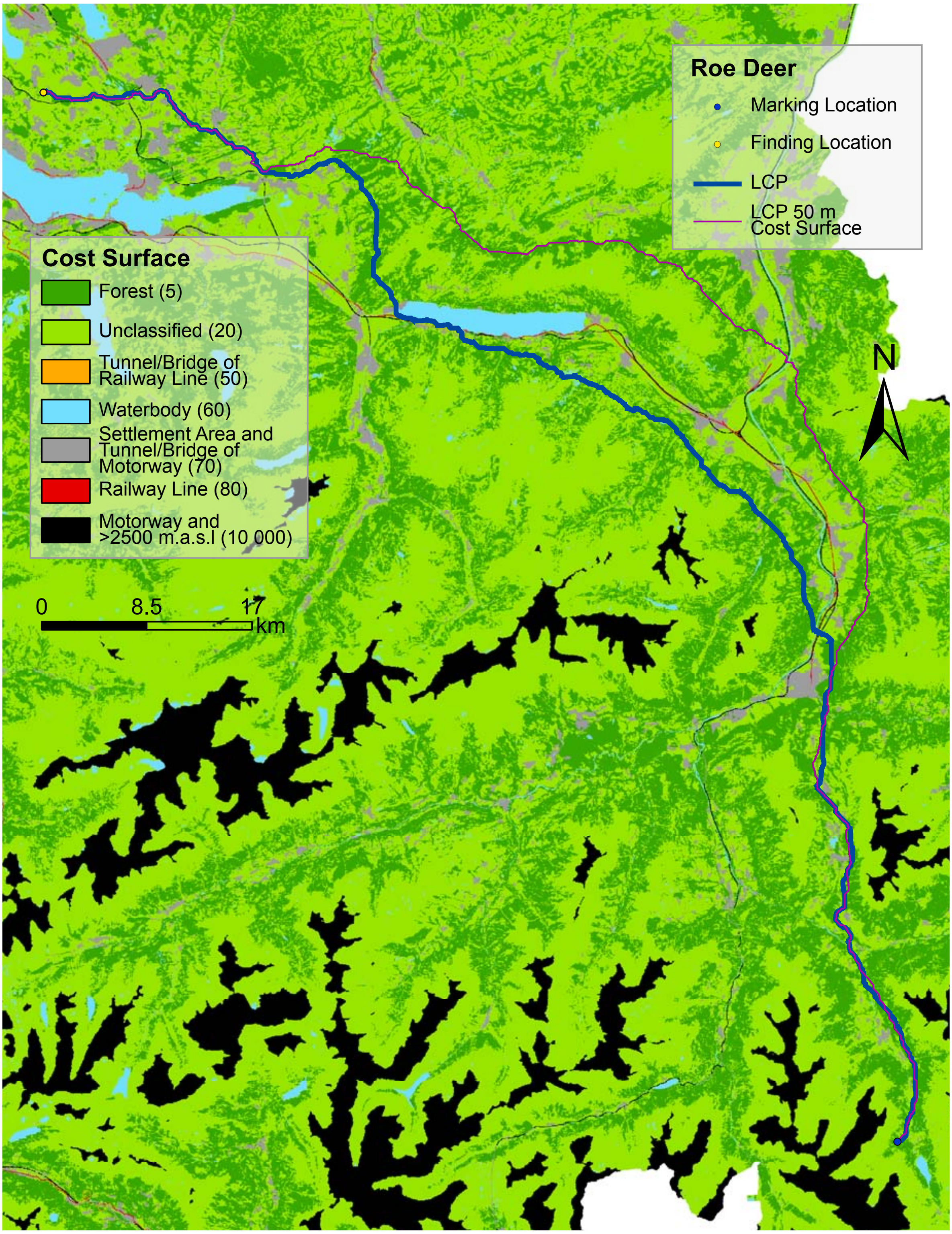

Figure B.5: LCP E including LCP of sensitivity analysis at 50 m raster resolution

Declaration

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