



**University of  
Zurich**<sup>UZH</sup>

# Determinants of stopover sites of migrating Swiss red kites (*Milvus milvus*)

GEO 511 Master's Thesis

**Author**

Philipp Schwitter

13-759-238

**Supervised by**

Prof. Dr. Robert Weibel

Martin Gruebler (martin.gruebler@vogelwarte.ch)

Stephanie Witczak (stephanie.witczak@vogelwarte.ch)

**Faculty representative**

Prof. Dr. Robert Weibel

30.04.2020

Department of Geography, University of Zurich



**University of  
Zurich** <sup>UZH</sup>



vogelwarte.ch

**Department of Geography**

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## **Author**

Philipp Schwitter  
13-759-238

## **Supervisor and faculty member**

Prof. Dr. Robert Weibel

## **External supervisors**

Dr. Martin Gruebler  
Stephanie Witczak

## **Submission date**

30 April 2020

## Contact

Prof. Dr. Robert Weibel  
University of Zurich  
Department of Geography  
Winterthurerstrasse 190  
CH - 8057 Zürich

Dr. Martin Gruebler  
Swiss Ornithological Institute  
Seerose 1  
CH - 6204 Sempach

Stephanie Witczak  
Swiss Ornithological Institute  
Seerose 1  
CH - 6204 Sempach

Philipp Schwitter  
philipp.schwitter@uzh.ch

## Abstract

Stopover sites are important places along the migration route of birds to rest, sleep and search for food before they move on, and can therefore be crucial for conservation measures. The aim of this thesis was the identification of regions with high densities of stopover sites of migrating Swiss red kites (*Milvus milvus*) along their migration path to Spain.

Based on the movement data of 400 red kites equipped with GPS transmitters from the Sense district (Switzerland), 271 autumn migration trajectories were identified, which were subsequently examined for stops, using a time- and distance-based clustering algorithm. In total, 792 stops of 202 individual birds were found, for which the 95% kernel density estimation polygon was generated in order to subsequently investigate characteristics of stopover site areas. French stopover sites and randomly placed sites of equal size within France were compared using a generalised linear model. A total of nine stopover site determinants were investigated. Five of them were related to the question of which areas are preferably selected as stopover sites in terms of habitat or resource variables, namely the proportion of forest and pastures, elevation and the occurrence of conservation areas, landfills or composting sites within the stopover site. The other four determinants, shortest distance to roads, railway lines, wind turbines and the occurrence of power lines within the stopover site, were related to the question of whether red kites are exposed to greater mortality threats at stopover sites than at random sites.

The results indicate that there are mainly three hotspot regions with high densities of stopover sites: (1) at the northwestern edge of the Alps 20 km west of Chambéry, south of the narrows between the Alps and the Jura, (2) in the Massif Central with especially high densities north of the Cévennes and south of the Aubrac high plateau and (3) at the northern foot of the Pyrenees, mainly in the southwest of Toulouse. Furthermore, stopover habitat was similar to the typical breeding area in Switzerland and includes pastures, highly structured arable land, minor settlements and small forest patches used for the overnight stays. The mortality threats at stopover sites were not larger than elsewhere. Only the higher presence of power lines indicated a slightly higher risk in the area of stopover sites than at random sites, while the threat from wind turbines was even significantly lower at stopover sites.

At stopover sites, red kites seem to prefer heterogeneous landscape compositions with high proportions of pastures, similar to the landscapes in the breeding areas. These preferred landscapes can be located at different elevations, but seem to be higher than other agricultural landscapes in France. Finally, the clear identification of high or low densities of stopover sites within France allows an efficient implementation of conservation measures and should therefore be taken into account in future action plans and conservation decisions.

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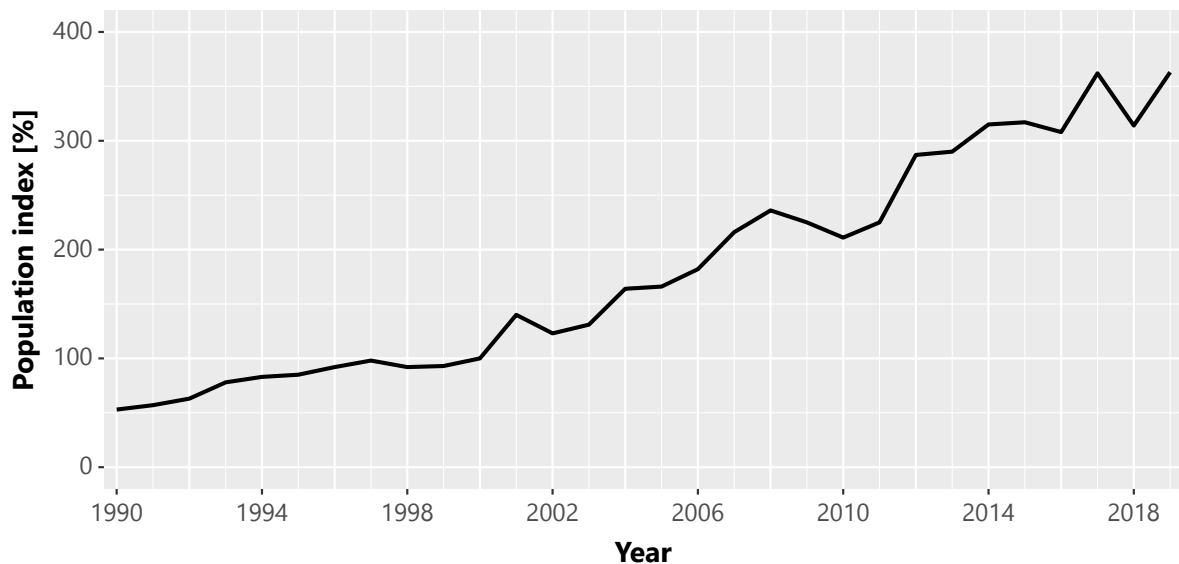
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# Introduction

## 1.1 Context and motivation

According to genetic analyses, red kites (*Milvus milvus*) most likely populated Central Europe after the Last Glacial Period (LGP), coming from Italy and Spain. However, it is assumed that the density of red kites was low, as large parts of Europe were still covered with forests some thousand years ago (Aebischer, 2009). With the beginning of anthropogenic deforestation in connection with increasing agricultural activities and livestock farming, the situation for red kites in terms of potential habitats began to change. Red kites were able to spread along suitable habitats that were continuously created, allowing red kites to become a common species (Carter, 2001). However, the breeding range of red kites has always been limited to the European continent, with only a few exceptions known (Aebischer, 2009; Urcun & Bried, 1998). During the nineteenth and the beginning of the twentieth century, the once frequently occurring red kites were strongly decimated due to hunting, poisoning and looting of nests. The persecution of red kites as well as other birds of prey found its origin in fears and superstitions of people during that time. Its beginning can be found in the seventeenth century and reached most considerable dimensions in the eighteenth century, with evidence of extinction in many places until the first half of the twentieth century (Bijleveld, 1974; Carter, 2001). As a result, red kites disappeared as a breeding species in large parts of Central Europe. Even though red kite populations slightly recovered from the 1870s towards the 1890s because of considerably less persecution, populations subsequently started to drop again. While a decline in food availability due to agricultural intensification was the main reason in the east of Germany, red kite populations in the northeast of France declined due to poisoning, which was intended to combat water voles (*Arvicola terrestris*). Illegal killing and partially poisoned baits intended for predators were the main reason for a severe population decline within Spain (Seoane et al., 2003). A further factor explaining the recent decline concerns the fewer bait places and open landfill sites based on a more conscious and complete understanding of the environment across

Europe that exist nowadays, which obviously has an impact on the food availability of red kites. The species is even classified as near threatened on the red list of the International Union for Conservation of Nature (IUCN), mainly because of persistent population declines in the major breeding areas of red kites, which are located within Germany, France and Spain (Aebischer, 2009; Cereghetti et al., 2019).



**Figure 1** – The red kite population index within Switzerland over time. The index was set to 100% for the year 2000. An index of 125% for the year 2002 therefore indicates an increase of 25% compared to the year 2000 (Knaus et al., 2018).

Over the course of the nineteenth century, a distinctive decline of the red kite population could also be observed within Switzerland, since also in Switzerland the persecution of birds of prey was practised. It was customary for the cantons as well as private parties such as ornithological associations to pay rewards per bird of prey that has been shot (Bijleveld, 1974). As a consequence, the geographical extent of the breeding area of red kites within Switzerland decreased to about two thirds of the natural state towards the beginning of the twentieth century (Aebischer, 2009). Although red kites and other species were put under protection by the Swiss authorities in 1925, it took decades until populations started to recover from human interventions in the system. While red kites were breeding even in the greater Alpine valleys during the nineteenth century, the breeding areas were limited to parts of the northern Jura and the cantons of Schaffhausen, Thurgau and Zurich around 1960. The absolute population was expected to lie only around 90 breeding pairs at the end of the 1960s (Aebischer, 2009). In the 1970s and 1980s the red kite population within Switzerland started to noticeably grow again. And so did the geographical extent of the breeding areas, which could be observed through a shift of the distribution

boundary towards the south and east of Switzerland, but also areas above 800 MASL are increasingly populated. Subsequently, the geographical extent of breeding areas doubled over the course of twenty years and the population was estimated to lie already between 800 and 1200 breeding pairs in 1998 (Aebischer, 2009). Nevertheless, there are still some regions, especially in the greater Alpine valleys, which used to serve as breeding areas for red kites in earlier times and have not been repopulated up to now (Aebischer, 2009; Knaus, 2010). The red kite population index of Switzerland increased from 1990 to 2020 (Figure 1). According to estimates, the population size of red kites within Switzerland has more than tripled, compared to the year 2000. As already mentioned, however, the red kite populations outside of Switzerland in the most important breeding and wintering areas have declined or only slightly increased in recent years, reducing the chances of these populations to recover in time Cereghetti et al. (2019). The current growth of the Swiss red kite population together with the confined range of the species on the European continent thus highlight two good reasons why the Swiss population is becoming increasingly important in terms of cross-national species conservation programmes.

Only a few decades ago, almost all Swiss red kites migrated towards the southwest of France or the Iberian Peninsula, due to scarce food availability and harsh conditions in Central Europe during the winter season (Aebischer, 2009). However, winter sightings of red kites in Central Europe started to increase from around 1960 onwards. Milder winters with in general less snow most likely favoured the behaviour of staying in the surroundings of breeding areas throughout the year. Active as well as passive anthropogenic feeding of red kites are another important reason, enhancing the chance of overwinter survival at higher latitudes, as food is provided even at days when a closed snow cover prevents the access to small mammals and other food (Aebischer, 2009; Cereghetti et al., 2019). For a better understanding of the current population growth within Switzerland, which seems to differ from the main breeding areas (France: Pinaud et al. (2009), Germany: Mammen (2009) and Spain: Cardiel (2006)), factors that affect survival rate, reproduction rate, immigration rate and emigration rate have to be investigated. Telemetry devices have the potential to provide high-resolution data from the full annual cycle on an individual level, thus providing insight into the ecology of a species rarely possible in the past (Cagnacci et al., 2010). Modern radiotelemetry devices mostly use the Global Positioning System (GPS) technology for positioning in space. In fact, the strong synergy between technology and science is rapidly shaping the structure of ecology itself. This opens up a wide range of new possibilities for research into the ecology of movement (Demšar et al., 2015), which obviously can also be applied to the red kite. Tracking red kites from the beginning of their lives to their death under ideal conditions will certainly provide new insights into their population dynamics.

## 1.2 Research objectives and questions

The growth of the red kite population in Switzerland over the past decades, together with the technological possibilities to track animals today, prompted the Swiss Ornithological Institute to launch a major scientific red kite project. The main goal of the project is to gain a better understanding of the factors that may explain the increase in population and the spread of the red kite in Switzerland. The Sense district in the canton of Fribourg was chosen as the study area, mainly due to its particularly high red kite density. In addition, the area has been well researched for 20 years thanks to a group of volunteer ornithologists including Adrian Aebischer and Laurent Broch, who regularly count the animals and, over time, ringed around 850 juvenile red kites in their nests. In this way, the development of the population could be well observed. Is it the climate, food supply or the fact that more and more red kites are deliberately fed with slaughterhouse waste by humans? When do they start their migration towards the wintering areas and why does a certain proportion of them winter in Switzerland? These and further questions should be clarified within the scope of the overall project. For this purpose, since 2015, mainly young animals have been equipped with GPS radiotelemetry devices, an essential component of the research methodology.

The following thesis is connected with the main project of the Swiss Ornithological Institute, whereby it is related to the section on migration behaviour. In general, there is a poor understanding of how vulnerability varies across different phases of the annual cycle of migrating birds (Mehlman et al., 2005). However, migration is considered to be the most vulnerable and unpredictable period of the annual cycle (Moore & Aborn, 2000). Preliminary results indicate that red kite mortality is increased outside the breeding area compared to the breeding grounds (personal communication M. Grüebl). While generally quite a lot is known about the breeding areas of migrating bird species, only little is known about the stopover ecology (Lindström, 1995). For this reason, wildlife managers and conservation practitioners often can promote efficient conservation measures in the breeding areas, but for the migration period it is even difficult to define areas of conservation priority. Thus, identifying and prioritising areas used by migrants *en route* is crucial for the creation of comprehensive conservation strategies (Mehlman et al., 2005). Red kites use places along their migration path to rest, sleep and forage before continuing their journey. In the following, these places will be referred to as stopover sites. In particular, juvenile red kites are highly dependent on stopover sites during their first migration, as they use them more often than adults, probably due to the need to improve their food acquisition skills (Maciorowski et al., 2019). It is therefore essential to understand where stopover sites are placed and what the key determinants of the placement behaviour are. This information can be used to protect sufficient suitable areas for red kites to stop during migration in the near future. In this context, densities of stopover sites can play an important role in identifying regions that are highly relevant for protection measures, as it can be assumed that regions with high

stopover site densities are most important for the migration of red kites. Knowing in what regions red kites preferably stop, it is also possible to better assess the threat situation within stopover sites. In addition, investigating stopover habitat selection can provide information on important habitat features at stopover sites. On the basis of these considerations, the following research questions have emerged, which are to be examined in the context of this thesis:

### **1 Identification of stopover sites**

Where are the stopover sites of migrating Swiss red kites located?

- (a) Does the density of stopover sites vary across geographical space?
- (b) Where are high densities of stopover sites to be found?
- (c) Is there a higher density of stopover sites near the north of the Pyrenees?

### **2 Determinants of stopover sites**

What are determinants of stopover sites of red kites within France?

- (a) What are the factors associated with stopover site selection?
- (b) What factors are related to the number of red kites using a stopover site?
- (c) Are red kites exposed to greater threats at stopover sites than elsewhere?



# Theoretical Background

## 2.1 Red kite ecology

### 2.1.1 Foraging

The red kite is said to be one of the most opportunistic feeders of all birds of prey. The diet consists of earthworms, insects, fishes, frogs, lizards, birds, small mammals, carcasses and anthropogenic waste, to name just the most common (Davis & Davis, 1981). Mentioning all proven prey animals would fill several pages. For a long time, red kites were thought to be notorious predators and acquired an unfair reputation with farmers and gamekeepers, since they often arrive first at perished animals. The fact is, however, that red kites only rarely kill by themselves (Aebischer, 2009). Since red kites are not noted for their strength, live prey is basically limited to invertebrates and other small or weak creatures. Leverets found in nests of red kites, were most of the times victims of mowing activities or killed on roads and not prey that has been caught alive. The diverse diet has enabled the red kite to exploit a wide range of habitats, from the hot and dry plains of the Iberian Peninsula to the rain-soaked hills of central Wales in Great Britain, everywhere depending on a very different diet (Carter, 2001). According to various studies investigating the diet composition of red kites, the share of mammals varies between 11% and 97%, the one of birds between three and 83% and amphibians and reptiles together never exceeded 3%. The share of fish can range from zero to 45%, whereby notably not only dead or diseased animals can be caught from the surface of the water (Aebischer, 2009). To be able to exploit a wide variety of both live prey and carrion, a range of foraging behaviours are required, which are described in the following according to Carter (2001) and Wildman et al. (1998). The type of flight seen when a bird is foraging differs distinctly from the one associated with travelling from one place to another, where movements usually follow a straight line. Using the wind or rising thermals enables red kites to soar effortlessly for long periods by circling high above the ground up to several hundred metres, without flapping even once. This so called

high circling is a very efficient method of searching for animal carcasses and allows to scan a large area in a rather short space of time. To detect animal carrion, red kites rely on their extremely sharp eyesight. As soon as potential food is located, it is gradually approached by descending in ever-tighter circles. Wherever possible, red kites do not favour landing, but rather snatch up the carcass and fly it to a safe feeding perch. They are not particularly agile on the ground, and are therefore vulnerable to ground predators. Large carcasses that are too heavy to lift are usually approached on foot by first landing a few metres away. For energy reasons, walking can sometimes also be observed while searching for invertebrates during cold periods and times with only little wind, which make flying more arduous. Another foraging behaviour is characterised by low circling, gliding and hovering just a few metres above the ground, typically to search for smaller carcasses and invertebrates. Earthworms are one of the most favourite food of red kites and a characteristic prey of such low-altitude flights. They may suddenly drop down from around 10 m above ground to take an earthworm only a few centimetres long, which further highlights their good eyesight. Active hunting is only rarely witnessed and especially observations of anything other than invertebrates that have been killed by a red kite are uncommon. Still, red kites are capable to pursue live prey by low gliding or flapping flights, at least over short distances. However, most live prey is taken by surprise. Since red kites are relatively weak and exhibit little aggression compared to Buzzards for instance, the size of animals that are taken is restricted. Instead, their lightweight frame allows them to remain in the air for long periods, which is well adapted to their dependence on carrion, which has to be searched actively. Food piracy is another foraging behaviour commonly seen for red kites and constitutes an important part of their food. In particular, birds from other species flying with a piece of meat get approached by rapid and agile aerial pursuits, as soon as a red kite realises its luck. The red kite's advantage in flying often leads the quarry to drop the food while trying to escape. The red kite then takes the falling food, sometimes even before it reached the ground. The goal is thereon to avoid the attention of conspecifics and corvids. Before the piece of food is finally consumed, it is usually changing hands for several times. This feeding strategy allows the relatively weak red kite to get a share of food even at carcasses, where more powerful scavengers are present and food might otherwise be unavailable (Carter, 2001; Wildman et al., 1998).

### 2.1.2 Migration in the annual cycle

Red kites are short-distance, partial migrants, meaning that there are both, resident as well as migratory individuals even within the same population (Jaffré et al., 2013). Harsh winters in Northern, Central and Eastern Europe are the main reason for red kites being mainly a migratory species, whereas populations in Southern Europe and Britain, where the moderating influence of the maritime climate means that winters are much less severe, are basically resident (Carter, 2001). In Switzerland, both behaviours occur (Aebischer, 2009), however in the following the focus will be laid on the

migrating fraction of the population. Even though warmer winters and anthropogenic bird feeding within Switzerland lead to decreased winter migration (Plummer et al., 2015), there is still a considerable number of migrating birds. To be worthwhile, the benefits of wintering in an area with a more temperate climate have of course to outweigh the costs involved in undertaking a distant migration (Carter, 2001). Survival is certainly easier in areas, where the conditions are less severe, since for instance less food must be consumed in order to maintain the required body temperature than in regions with harsh winters. Furthermore, the food availability may be reduced, as other species also migrate in order to escape the conditions or are inactive in winter (Aebischer, 2009). For a species that is so heavily dependent on carrion as the red kite, the potential of prolonged snow cover is particularly difficult, as due to the reliance of red kites on its keen eyesight to locate food, carcasses covered in snow are no longer accessible. But it could also be that the snow cover makes it easier for red kites to find carcasses, as they are better visible against a white background, which of course depends on how often it snows.

The annual cycle can mainly be categorised into four stages, which are: autumn migration, overwintering, spring migration, which is often also referred to as return migration, and breeding. The start of the migration period, the return date to the breeding area, but also the flight route often vary considerably from individual to individual, and even from year to year for the same individual (Aebischer, 2009). Nonetheless, there are some general patterns according to Carter (2001) that are noteworthy to mention here. First migratory movements can be observed in late summer, however, most red kites start migrating no earlier than the middle of September and no later than the end of October. In many cases, young birds start their journey slightly earlier than adults, although the arrival in the wintering areas does not seem to vary clearly. Some individuals, often older birds, may wait to move south until a longer period of poor weather arises, while other, often the younger birds, will begin to migrate south regardless of weather. Occasionally such movements take place even as late as February, not long before the usual onset of the spring migration. The destination of the migration are wintering areas, which are typically located in the south of France and the north of Spain (Aebischer, 2009). Red kites migrate both in small groups and individually. An often occurring phenomenon is the formation of groups in the north of the Pyrenees, due to bad weather. Once conditions get better, the potential of seeing a large group of red kites migrating over the Pyrenees is enhanced. Like other species of birds of prey, red kites accomplish their migrations predominantly by soaring on thermals and orographic updraughts during the day (Nourani et al., 2018). As a diurnal species, a period of sleeping or other inactivity at night is common, even during migration. Urcun & Bried (1998) found that the actual migration mostly took place between nine in the morning and three in the afternoon.

Red kites typically use stopover sites to rest, sleep and forage for a while before continuing their journey. The number of stops made along the migratory path as well as the distance in between consecutive stopover sites depends on various factors like the individual fitness or meteorological conditions (Maciorowski et al., 2019). A

pattern of age- and sex- dependent migration can be found for the spring migration period of red kites ([Aebischer, 2009](#); [Carter, 2001](#)). While young birds, which are not yet of breeding age, usually begin their migration at the earliest in March or even April, adult birds, especially the males, generally leave their wintering area much earlier. There are reports of cases of adult red kites that began their return migration to the breeding grounds from their wintering areas in the north of the Pyrenees as early as mid-January ([Aebischer, 2009](#)). A general trend towards earlier return to the breeding areas in spring, could be observed in the last decades. Besides the age-dependency also a gender-dependency of migration is expected, since males usually return earlier back to their breeding areas, increasing their chance of breeding success ([Carter, 2001](#)).

### 2.1.3 Physiology and Reproduction

The red kite (Figure 2) is the third largest native bird of prey within Switzerland, after the Bearded Vulture and the Golden Eagle ([Aebischer, 2009](#)). It is a synanthropic species, whose occurrence is linked to two conditions: trees to rest and breed as well as open landscapes for foraging ([Carter, 2001](#)). Despite the impressive wingspread of up to 170 cm and a body length of approximately 70 cm, red kites only weigh around one kilogram. Even though females are on average only slightly larger, the weight difference between the sexes is significant. While adult females can reach a weight of up to 1.4 kg, males are generally clearly lighter with a maximum of 1.2 kg ([Aebischer, 2009](#)).



**Figure 2** – The red kite (pictures downloaded from: [www.naturfoto-fahl.de](http://www.naturfoto-fahl.de)).

Most red kites breed at the age of three for the first time. Nonetheless, earlier breeding has been widely observed in regions with an abundance of resources, where the species is spreading ([Carter, 2001](#)). As mentioned in the previous section, some of the breeding pairs stay in close surrounding of their breeding area throughout the winter. The breeding pairs of the migrating fraction most of the times find themselves again in their territory after the winter, although they have not spent the cold

season together. Besides rare copulations in February, the usual mating period starts no earlier than March with shrill mewing sounds that can be heard, feeding of the female by the male, common nest building, copulations and characteristic acrobatic flights. However, according to [Carter \(2001\)](#) these mating flights are much more seldom than actual quarrels with conspecifics, which often get wrongly interpreted as the former. A further repeatedly observable flight pattern is the circling of the male above the nest, which can be interpreted as the manifestation of its territory, to mainly keep competitors away from the nest. As the time for laying approaches, female red kites continuously move less far away from the nest, relying more and more on the feeding of the male. At the same time, the number of copulations increases. [Mougeot \(2000\)](#) for instance found that copulations can take place even more than forty days before the first egg is laid. In this way, the male attempts to make sure that there is no rival male fertilizing the eggs, while he was away looking for food. Red kites usually mate with the same individual until the death of one of the pair. Breeding site fidelity is also a characteristic for the species and if red kites sometimes move to alternative breeding sites, it is mostly within 10 km, and often even much less ([Aebischer, 2009](#); [Carter, 2001](#)).

#### 2.1.4 Human influence on red kite populations

As already briefly discussed in the introduction, man has traditionally persecuted birds of prey into the twentieth century. Although birds of prey are now generally protected throughout Europe, more than three-quarters of known deaths are due to human activity. The range of direct and indirect influences of human actions on red kite populations are diverse, of which a large part of the known dangers will be presented in the following according to [Aebischer \(2009\)](#) and [Carter \(2001\)](#), unless another reference is indicated.

Modifications in agricultural practices over time can mean severe changes in habitats of red kites. A switch from pasture to rapeseed or winter wheat can for example have several consequences that affect the food availability of red kites, since the concentration of small mammals like hamsters very likely decreases and also the accessibility of them is reduced because of higher and more dense crops. In this context, it is also worth mentioning the closure of landfills, which served as the main source of food for various populations, with red kites preying on rodents living there or feeding on organic waste themselves.

Furthermore, various human infrastructures can pose a life-threatening danger to red kites. Simultaneously coming into contact with two conductive elements on a power line, or likewise a conductive power line and a grounded mast, can lead to an electric shock. Particularly endangered are bird species with large wingspans. In Switzerland too, dead animals are occasionally found due to electric shocks. Collisions with cables or masts are probably rather rare due to the relatively leisurely flight of red kites. Wind turbines, on the other hand, pose a major collision risk and have already led to many deaths, although their impact on populations is difficult to

assess according to experts (Hötker et al., 2017). Besides, wind farms usually change the structure of a habitat, so that these areas are subsequently avoided by red kites. However, some experts can also imagine that wind turbines attract red kites because they recognize that small birds are killed in the immediate vicinity of wind turbines, providing a food source.

Furthermore, road traffic can be dangerous for red kites, who often use roadkill as a food source. However, since they often do not land on the road to eat, but instead grab their prey in flight and carry it away to eat it somewhere more safe, there are fewer deaths than for other birds of prey. Human disturbance of red kites is particularly severe during the breeding season, but very often happens, for example through work or activities in the forest near the nest. Often they have to leave their eggs due to such disturbances. The shooting of red kites is still a fact of life today. Beside the trade of eggs or live as well as dead individuals among collectors, abandoned shot animals are found annually.

Finally, red kites are at risk of being poisoned by man-made pesticides, poisoned bait or heavy metals that may be present in carrion killed by lead shot. All these substances can affect the nervous system as well as the immune system or have effects on the hormone balance, which can result in reduced breeding success.

## 2.2 Movement ecology

The study of movement data is evolving rapidly within Geographic Information Science (GIScience) and is applied to manifold domains such as transportation, human mobility and ecology. For all domains, movement observations in the form of spatiotemporal signals constitute the fulcrum of the research. Movement ecology is therefore only one of several domains interested in the analysis of spatiotemporal data. In the case of movement ecology, the aim is to reveal why, how, where and when organisms of all kinds move (Nathan et al., 2008). Humans have tracked the movements of animals for thousands of years, first to survive and more recently to better understand, manage and protect wildlife (Fraser et al., 2018). Technological progress in satellite tracking technologies like the Global Positioning System (GPS) have resulted in an increased availability of highly accurate data on moving phenomena, outpacing the development of appropriate methods with which to analyse them (Dodge et al., 2016). Still, the tracking of moving entities has been a very cumbersome and costly undertaking for a long time (Gudmundsson et al., 2016). Over the years, however, tracking devices have become cheaper, smaller and more accessible, trends that will continue in the near future. The more efficient data download methodologies as well as the generally increased battery life of today's tags, allows to also increase the number and variety of sensors on tracking tags, which in the end leads to a more complete picture of the environment in which the object under investigation was moving (Cagnacci et al., 2010). All this is leading to more data being collected at even higher temporal and spatial resolutions. Movement ecology

has transformed itself from a data-poor discipline in the beginnings to a data-rich present and future, allowing to find new answers to burning research questions in animal ecology (Demšar et al., 2015).

In general, movement data consists of a discrete time series of observed locations that together form a trajectory (Cleasby et al., 2019), with the locations usually being collected in detailed temporal resolutions and according to specific time schedules (Demšar et al., 2015). The identification and understanding of movement patterns in trajectories is of crucial importance for movement ecology (Cleasby et al., 2019), as they can be viewed as an expression of behaviour (Gudmundsson et al., 2016). The movement of an individual organism is regarded as an interplay of four mechanistic components: its internal state, its motion capacity, its navigation capacity and external factors (Nathan et al., 2008). These components dynamically interact with each other at various spatiotemporal scales, which is consequently reflected in spatiotemporal patterns of movement data and constitutes the main motivation of ecologists in identifying these patterns. The search for patterns in the data is driven by different perspectives. While some are interested in the variation of patterns within individuals or groups over time, others are involved in the investigation of varying patterns between individuals, groups or populations, but also patterns between different species can be of interest. Both, similarity and differences in movement patterns can be of interest and further also their relationships to geographic space and time, depending on the scientific context (Demšar et al., 2015).

### 2.2.1 Trajectory segmentation

In this context, trajectory segmentation methods provide the basis for the detection of movement changes and the behavioural mechanisms driving them. There exist various approaches for trajectory segmentation from which according to Edelhoff et al. (2016) basically three groups of methods are considered for segmenting trajectories based on potential changes in underlying behaviour. The first group consists of topology-based approaches that quantitatively describe the geometric properties of a trajectory itself or of one or several signals calculated from the trajectory. Based on similar signals, movement steps are then assorted into groups that are relatively similar. A second group constitutes time-series methods that calculate signals from consecutive location points and treat them as time ordered observations. Most of these approaches attempt to find substantial change-points along the time axis of the signal sequence deduced from the movement trajectory. The third group comprises methods that intend to identify latent or hidden behavioural states based on the observed movement data, using the state-space modelling framework. The objective is to gain a deeper insight into the underlying processes by the formulation of a movement model that explains observed movement patterns. All these approaches model the future state of a system by a probabilistic model in such a way that it depends on its current state. An alternative classification of behavioural segmentation methods was proposed by Gurarie et al. (2016), who distinguish four classes of methods: met-

ric based, classification and segmentation, phenomenological time series analysis, and mechanistic movement modelling. The first and the last group of this classification corresponds to the first and the last group of the classification by [Edelhoff et al. \(2016\)](#), while [Gurarie et al. \(2016\)](#) split the second group of [Edelhoff et al. \(2016\)](#) into two classes.

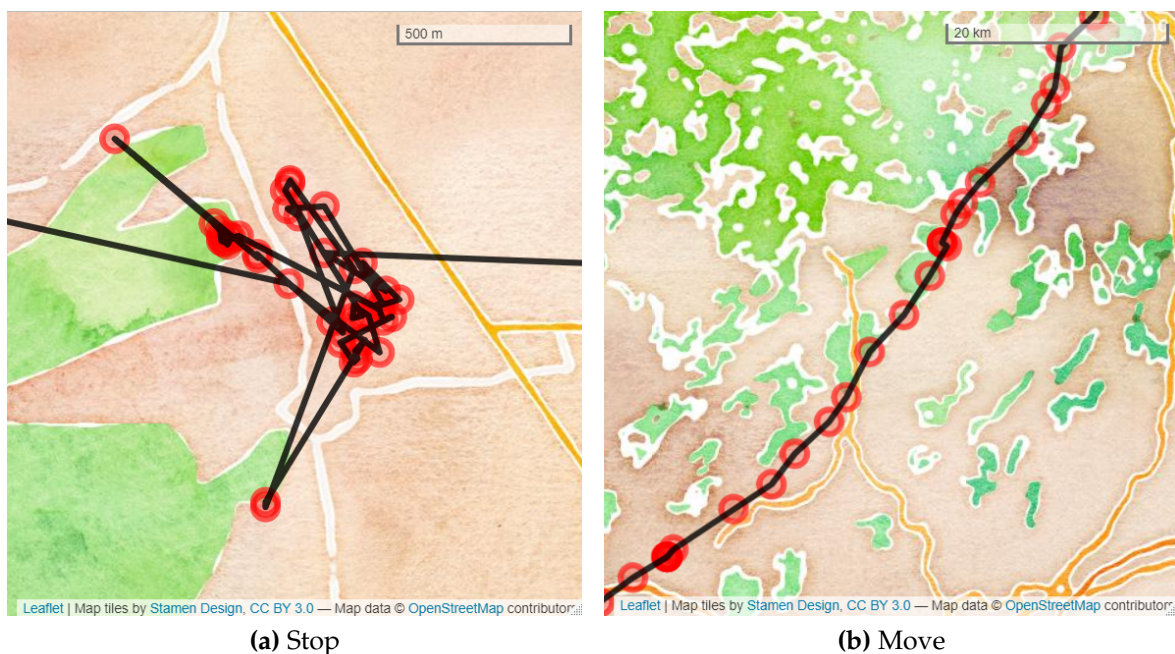
### 2.2.2 Stop detection in the context of migration

Migration can be defined as the repetitive movements of individuals over long distances ([Heylen & Nachtsheim, 2018](#)). In the context of wild animal migration, these movements are mostly strongly directional and seasonally reversible. The identification of such routines or regular returns in movement data is nevertheless a major challenge. In order to investigate migration behaviour, movement trajectories are segmented into sub-trajectories on different spatiotemporal scales. In most cases, geometric segmentation methods are used in which each resulting sub-trajectory fulfils a geometric criterion that characterises a behaviour of a moving animal ([Demšar et al., 2015](#)). [Buchin et al. \(2013\)](#) for instance looked at different types of bird movement such as (flying, foraging and resting) and linked them to different types of geometric properties of trajectories. On the basis of these geometric properties, they were subsequently able to develop a method that automatically segments the trajectories into segments of distinct types of movement. The results of such algorithms are trajectories with certain semantics attached, which allow the movements of the animals to be further studied and ecologically analysed. In general, there are various geometric properties that can be derived from trajectories, of which location, speed, angular range and heading are only a few. ([Demšar et al., 2015](#)). Since travelling objects do not *per se* move continuously during a displacement, trajectories themselves can be semantically segmented by determining temporal sequences of subintervals in which the object position alternately changes and remains fixed, better known as stops and moves. Thus, a trajectory can also be seen as a sequence of stops separating the moves ([Spaccapietra et al., 2008](#)). Figure 3 shows an exemplary illustration of the characteristic difference in the course of trajectories between stop and movement phases in the context of migration. Detecting the occurrence or absence of movement is one of the most fundamental tasks of segmentation, which is why different solutions have been developed in a variety of scientific fields ([Nogueira et al., 2017](#)). Especially to locate and analyse the places where objects stop can lead to interesting findings ([Bak et al., 2012](#)), be it cars, animals or people. Stops are usually seen as the more important parts of trajectories compared to moves, because the object has stayed there for a certain amount of time ([Alvares et al., 2007](#)). However, stops can be defined differently depending on the research context.

While some researchers have attempted to identify stops in a single step, others have developed two-step procedures, identifying all stops in a first step and refining them in a second ([Gong et al., 2015](#)). Depending on the variety of available sensors a tracking device has, some solutions even use accelerometer data to detect stops



(Ohashi et al., 2016)). In order to get an overview of the various approaches to detect stops, three groups of conceptual methods can basically be formed. The first group represents methods that either use only geometric criteria, which were mentioned earlier in this section, or additional temporal criteria introduced amongst others in Buchin et al. (2013), Collins et al. (1995) and Montoliu et al. (2013). A second group of methods focuses on the determination of stops based on the presence of spatial accumulations of localisations. Consequently, the individual GPS points are not considered sequentially as in the first group, but rather used to generate a density surface. From variations of the DBSCAN algorithm (density-based spatial clustering of applications with noise) (Gong et al., 2015; Palma et al., 2008) to kernel density approaches (Thierry et al., 2013), there are already various methods for building density surfaces based on positioning. Such density-based methods have the advantage that they can handle GPS noise better than methods from the first group, which potentially improves the quality of the locations obtained (Kami et al., 2010). This is of particular importance since data derived from tracking devices are often noisy and the actual state of moving objects cannot always be determined (Nogueira et al., 2017). The third group of methods integrates context information to detect stops (Baglioni et al., 2009; Stenneth et al., 2011). To give an example, Alvares et al. (2007) determined candidate regions in advance of the actual stop detection that can at all be considered for stops. This approach allows to find stops within these predefined regions by means of geometric queries.



**Figure 3** – Characteristic movement patterns in migration trajectories. While a clustered pattern can be observed during (a) stops, a much more directed movement pattern can be observed during (b) movements.

### 2.2.3 Stopover sites during bird migration

Population declines and the associated species conservation are two important reasons, why researchers are investigating what constitutes important characteristics of habitats of a threatened species. In that context, the research focus is often placed on breeding and wintering areas of migratory species and associated events (Buler & Moore, 2011). That is why only little is known about the actually so dramatic migration phase (Hutto, 1998), in particular about stopover site ecology (Moore & Aborn, 2000). Stopover sites are defined as places where migratory birds can briefly rest and forage, usually for more than a few hours before continuing their journey. They are necessary because the migration route would be too long, both in terms of time and energy, to cover it without stopping (Mehlman et al., 2005). According to Buler & Moore (2011), the importance of habitat during migration has been widely overlooked in the development of conservation strategies. The findings of Klaassen et al. (2014) further support this view. Using GPS telemetry, the authors investigated the migratory behaviour of three species of birds of prey, finding that the mortality rate during migration is about six times higher than during stationary phases. Mortality during migration is even higher for juvenile birds compared to adults, as they have to cope with enduring and risky journeys shortly after fledging (Rotics et al., 2016). Mehlman et al. (2005) therefore suggest that conservation of migratory landbirds requires a network of stopover sites along migration routes.

There are mainly two components that make a stopover site important for migratory birds. On the one hand a site has a certain function. Stopover site functions can range from shelter, in case of sudden harsh weather, to recover after passing a geographical barrier. On the other hand all sites have a relative value within a category (Mehlman et al., 2005), which means that, for example, a stopover site that was used by different red kites for several days can be considered more important than a site that was only used by a single individual during one day. These two components illustrate the difficult task of classifying the importance of stopover sites, because a final evaluation of functions is not necessarily trivial. Is for example a stopover site selected primarily because of unfavourable weather conditions and for immediate survival less important than one chosen because of good food prospects? Further, it is clearly more difficult to identify and conserve important stopover sites than important breeding or wintering areas, as the function of a particular stopover site is highly dynamic in space and time and is based on both intrinsic (e.g. food supply) and extrinsic (e.g. weather) factors, combined with the physiological condition of individuals (Buler & Moore, 2011). It is evident that there is stopover site habitat selection during migration; the question is rather how exactly stops are chosen. Moore & Aborn (2000) expect the choice to rely on a sequence of hierarchically ordered decisions that depend on different criteria. A migratory bird might initially settle because of decisions on gross habitat features such as vegetation density together with the avoidance or choice of areas that bear some resemblance to previously experienced habitat. The decision whether resources are actually searched for within the confined area or whether local movement will continue, probably depends on

more specific habitat features or the behaviour of other migrants. Food availability (Buler et al., 2007) as well as gross habitat features (Leutner et al., 2017) seem to be key factors shaping the distribution of birds during stopover. However, it is expected that the social attraction of other migratory species already present at a stopover site, in particular conspecifics, is also relatively important when choosing a habitat. Finally also predation represents a considerable danger for migratory birds. The decision to use a particular habitat therefore also depends on the perception of the predation risk of a migratory bird (Moore & Aborn, 2000). Since red kites are rarely attacked by one of their few natural enemies such as hawks, the Eurasian eagle owl (*Bubo bubo*) or the Spanish imperial eagle (*Aquila adalberti*), it can be assumed, at least in their case, that the predator risk only plays a minor role in their decision to choose a stopover site or not (Aebischer, 2009). Shiu et al. (2007) showed for two buzzard species that there is site fidelity to several, but not all stopover sites in successive years, even though the sites differed between spring and autumn migration. They also observed that if a migratory bird stays at a stopover site for a longer period, usually more than five days, it shows fidelity to that site and revisits it the following year. In contrast, stopover sites that are only used for short periods of time may be due to unfavourable weather or other short-term factors and will not be used in subsequent years.

## Data sets and data preprocessing

### 3.1 Red kite movement data

The entire red kite GPS location data set has been made available by the Swiss Ornithological Institute. Data collection for the red kite project started in the year 2015 and is still ongoing. The tagging of birds is restricted to the Sense district in the canton of Fribourg, since the population increase within that area is regarded as extraordinary. The solar-powered GPS telemetry devices of the manufacturers Ecotone Telemetry (Gdynia, Poland) and Milsar (Cluj Napoca, Romania) are placed on the back of the animals and programmed to periodically record the location of an individual as longitude and latitude positions according to a predetermined temporal resolution. In addition to the location, the corresponding timestamp, the identification number of the animal as well as an event identification number is stored for every single record (Table 1).

**Table 1** – Extract of the raw movement data set, showing the relevant attributes of each record, namely: an event and red kite identifier, a timestamp, and the localisation given as longitude and latitude.

Event-ID	Timestamp	Longitude	Latitude	Red kite-ID
4722570718	"2017-11-02 07:00:08.000"	4.121982	45.151866	72
4722570719	"2017-11-02 08:00:09.000"	4.056166	45.132949	72
4722570720	"2017-11-02 09:00:19.000"	3.980183	45.122116	72
4722570721	"2017-11-02 10:00:10.000"	3.965516	45.123666	72
4722570722	"2017-11-02 11:00:42.000"	3.802266	45.056366	72
4722570723	"2017-11-02 12:00:03.000"	3.667766	45.040666	72

In total, the raw data set consists of 3'869'580 localisations from 400 individual red kites, of which more than 80% were tagged as juveniles (Table 2). The temporal resolution of the location data varies from five minutes up to several hours, depending on the sensor type and the research focus of sub-projects conducted at the Swiss Ornithological Institute. Occasionally the temporal resolution has been adjusted to best suit the purpose of the recording at a particular time. A much finer resolution is for instance favourably used to study the home range of red kites during the breeding season, whereas for tracing the migration path a coarser resolution is most of the times sufficient. A continuous recording of the localisations would certainly be the ideal case, but it rarely corresponds to reality. Also in this data set there are some red kites with shorter or longer interruptions of the recording of the localisations from single hours up to several weeks, which can be attributed to different causes, such as faulty hardware. To save energy and since red kites are typically not active during the night anyway, no data is recorded during the night, although the start and end times of the night are adjusted from time to time to reflect the changing length of the day. Besides the actual movement data, complementary data sets exist in the form of a compilation of georeferenced nest sites and the associated attributes, such as tree species or height above the ground on which the nest was built. But also the individual life history of the transmitter-equipped red kites is continuously documented in a data set that is as complete as possible with attributes such as hatching date, tagging year, sex or the nest site location identifiers of the individual breeding seasons.

**Table 2** – Basic information about the movement data set.

Period covered by data set	10 June 2015 to 01 July 2019
Total number of localisations	3'869'580
Number of individuals in the data set (of which juveniles at the time of tagging)	400 (322)
Total number of entirely available autumn migration trajectories	271
Number of individuals tagged over:	
- 1 autumn migration period	147
- 2 autumn migration periods	92
- 3 autumn migration periods	43
- 4 autumn migration periods	5

### 3.1.1 Pre-processing

In a first step, spatial outliers were identified and removed, by selecting localisations clearly lying outside of a conservatively defined study area extent. By deriving the velocity from the temporal and spatial difference for all consecutive localisations of a

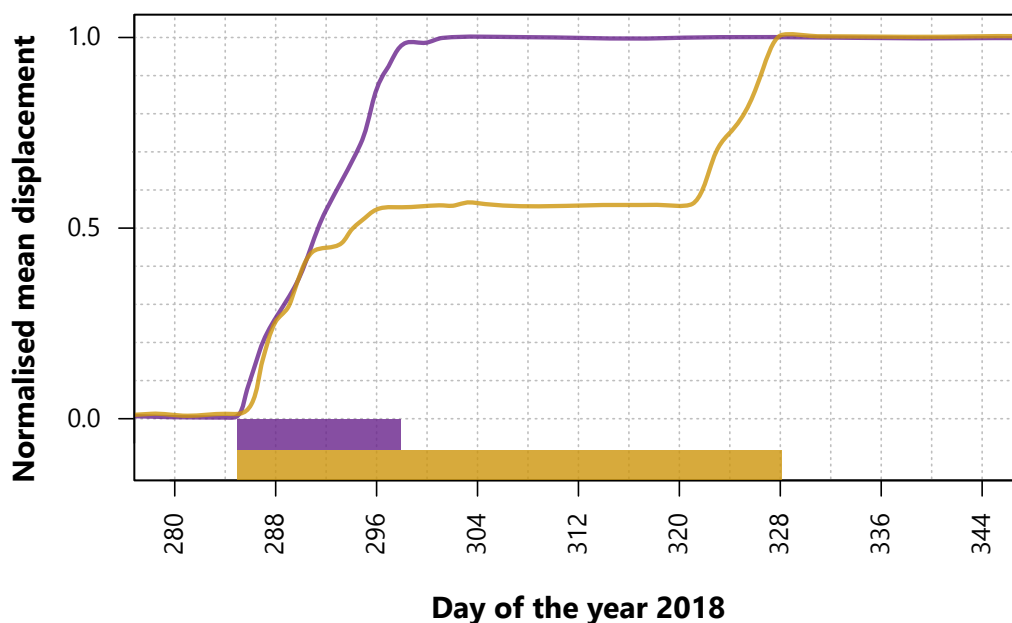
red kite, about five hundred location points with unrealistically high velocities could be excluded from the data set in a second step, using a clearly conservative threshold value of 180 km/h. The reason why this very conservative threshold was chosen is that the aim of this thesis is the identification of stopover sites, where high velocities are untypical anyway. Kochert et al. (2011), for example, defined the maximum rate of movement to be much lower with 90 km/h for a buzzard species. The third step was based on the knowledge about the general inactivity of red kites during night, which is why all localisations recorded at a time without daylight have been removed. The R-package *suncalc* by Thieurmél & Elmarhraoui (2019) was used to get the starting time of the sunrise respectively the end time of the sunset for all localisations at the given point in time. Although the locating devices were set up in the way that they do not record any data at night to save battery lifetime, approximately 861'344 localisations (22%) had to be removed. Since the temporal resolution of the raw data varied from several minutes up to a few hours, the data was set to a maximum temporal resolution of one hour, which means that for animals equipped with a GPS transmitter recording at a resolution of ten minutes, only every sixth location point in the sample was retained.

### 3.1.2 Determination of autumn migration period

In order to perform stop detection, the start and end points of the autumn migration periods had to be defined individually to ensure that no stops of other phases of the annual cycle of the animals were considered as stopover sites of migration movements. To do so, the distance of all localisations to the nest an individual used during the preceding breeding season was calculated. For juvenile red kites which hatched in the current year, the nest of origin was used as the fixed point. The same applies for juveniles of the previous year that return to the surroundings of their place of birth after a whole migration cycle, but do not build a nest in the first year and are much more likely to explore the wider environment. In the following, the distance to the nest has been normalized to the maximum distance to the nest of an individual in the current migration period. In this way, the relative change in distance to the nest over time could be graphed to determine the start and end points of a migration period for each individual. Since the migration behaviour of red kites is quite diverse and can exhibit various special cases, the determination of the migration periods could not be fully automated. This applied method of segmenting trajectories is very similar to the net squared displacement method developed by Bunnenfeld et al. (2011) that allows to separate migration from other movement behaviours.

In addition to the juveniles, which usually have an undirected exploratory phase in the somewhat wider surroundings of their nest of origin before the actual migration, a relatively frequent phenomenon found were longer stopovers north of the Pyrenees, which made automatisisation difficult. The stopovers north of the Pyrenees had for instance per definition not to be treated as end points of the migration period, but only as longer stopovers. In contrast, stops south of the Pyrenees last-

ing two days or more were already determined as the end of the migration period, which obviously could not be determined purely on the basis of the normalised distances to the nest graphs. The yellow graph in Figure 4 shows an example of an individual with a prolonged stopover after day ten of migration, which had to be located in geographic space to check whether the stopover site was north or south of the Pyrenees and therefore represented the end of migration or not (Figure 5). These circumstances consequently led in a semi-automatic procedure in which migration period localisations were plotted on a map, to see whether the determined end of migration localisations would lie south or north of the Pyrenees, in the sense of a visual verification process. Altogether 698 autumn migrations of 381 individual red kites could be determined for the migration periods of the years 2015 to 2018.



**Figure 4** – Normalized mean displacement to the nest of origin for two individual red kites, showing a clearly different migration behaviour in the autumn migration period 2018. A normalised displacement value of zero means that the individual is still in the close vicinity of the nest, while a value of one means that the individual has reached the maximum distance from the nest for the current migration period. The migration period duration of red kite 40 (yellow) lasts 43 days with a longer stopover of around 24 days north of the Pyrenees. In contrast the migration period duration of red kite 254 (purple) only lasts around 13 days with an almost continuously increasing normalised displacement value over time.

A closer look at the temporal resolution of the filtered data of the determined migration periods revealed that there were both time series without gaps and others with various gaps of up to several days without a recorded localisation. The propor-

tion of time series with gaps was 65%, all of which were retained in the sample. One reason for keeping the patchy time series in the sample was that the stop detection algorithm subsequently applied on the time series was able to handle gaps, further details of which are described in Section 4.2. Another reason was that this approach ensured that the number of stopover sites detected thereafter could be maximised. If the primary interest had been, for example, to investigate the number of stopover sites of red kites during a single migration period or to compare the duration of migration periods among years, the incomplete time series should have been excluded. However, since the aim of this thesis was to characterise stopover site habitat in general, as many stopover sites as possible were desirable, regardless of whether they originated from patchy migration period time series or not.



**Figure 5** – Map of localisations of red kites 40 (yellow) and 254 (purple) during the autumn migration period 2018.

In green the start points of migration within the Sense district are highlighted; the end points of migration are displayed in red. The potential end point of the migration of red kite 40 in the north of the Pyrenees is indicated as an enlarged end point.

## 3.2 Context data

From the ecology of red kites discussed in Section 2.1, various potential determinants of stopover sites can be derived. Before the actual implementation of attribute data of the stopover sites, the first step was to obtain context data for the relatively large study region in the case of France. Even if access to suitable data sets was rather difficult or such simply did not exist, a solution was finally found for the most important factors. Table 3 provides an overview of the data sets used and further characterises them with regard to spatial accuracy and completeness. A more detailed description of the data sets is additionally given in the following Subsections 3.2.1 to 3.2.5.



**Table 3** – Overview of the context data sets used for the analysis of the stop-over sites. The data sets are evaluated with regard to the two properties spatial accuracy (Sp. acc.) and completeness (Compl.), using the following qualitative grading: good (+), moderate (0) and poor (-).

Data set	Source	Date	Sp. acc.	Compl.
Illegal landfills	FMESD**	Jun. 2005	(-)	(-)
Composting sites	FAEE***	Feb. 2005	(-)	(-)
CORINE Land Cover	Copernicus	2017-2018	(0)	(0)
Digital Elevation Model	EEA*	unknown	(0)	(+)
Natura 2000 protected areas	EEA*	2018	(+)	(+)
Power supply lines	OpenStreetMap	Feb. 2020	(+)	(0)
Railway network	OpenStreetMap	Feb. 2020	(+)	(0)
Road network	OpenStreetMap	Feb. 2020	(+)	(0)
Wind turbines	OpenStreetMap	Feb. 2020	(+)	(0)

\* European Environment Agency

\*\* French Ministry of Ecology and Sustainable Development

\*\*\* French Agency for the Environment and Energy

### 3.2.1 Illegal landfills and composting sites

Both data sets (illegal landfills and composting sites) are derived from the data used by Laurian (2008), whose research focus was on the investigation of the environmental injustice in France, where inter alia the spatial distribution of waste loads in relation to the size of the local population was considered. Countless classes of toxic sites have been compiled by the author for this purpose, among them 884 illegal landfills and 438 composting sites, which could be used on explicit permission of the authorship. The sites had to be georeferenced since the data set only included a unique code of the corresponding commune used by the National Institute of Statistics and Economic Studies of France (INSEE), which could be regarded as an implicit location. The use of the vector data set of the communes in France from OpenStreetMap (2020), allowed to assign illegal the landfills and composting sites to communes, using the INSEE code. Although the more than 36'000 communes of France lead to a moderate spatial resolution, the spatial accuracy of the data set has to be put into perspective. It is quite obvious that the area of a single landfill is only a small proportion of the total area of the commune (average commune area: 15 km<sup>2</sup>), yet the whole commune is given the attribute that a landfill exists. In addition, it must be taken into account that the data are more than ten years old and therefore a relatively large attribute error must be assumed, which leads to a rather poor judgement regarding the completeness of the data set. Nevertheless, the data set is considered for a later analysis of the determinants of red kite stopover sites, as it is expected that this is an important factor and that no better data is available or even exists.

### 3.2.2 CORINE Land Cover

The CORINE Land Cover programme is coordinated by the European Environment Agency (EEA) and part of the Copernicus system for monitoring the Earth, providing consistent information on both land cover and land cover changes across Europe. The CORINE Land Cover products are based on the interpretation of remote sensing data by national teams of the participating countries of the programme. The national land cover inventories are subsequently integrated into a seamless pan-European map, based on standard methodology and nomenclature. In total there are 44 land cover classes in a hierarchical three level nomenclature, whereby the degree of detail increases from level-1 to level-3 (Table 4).

**Table 4** – Excerpt of the Corine Land Cover nomenclature level-1 classes 2 *Agricultural areas* and 3 *Forests and semi natural areas* of the EEA.

Level-1	Level-2	Level-3	
2 Agricultural areas	21 Arable Land	211 Non-irrigated arable land	
		212 Permanently irrigated land	
		213 Rice fields	
	22 Permanent crops	221 Vineyards	
		222 Fruit trees and berry plantations	
		223 Olive grooves	
	23 Pastures	231 Pastures	
	24 Heterogeneous agricult. areas	241 Annual crops associated with permanent crops	242 Complex cultivation patterns
			243 Land principally occupied by agriculture, with sign. areas of natural vegetation
			244 Agro-forestry areas
3 Forests and semi natural areas	31 Forests	311 Broad-leaved forest	
		312 Coniferous forest	
		313 Mixed forest	
	32 Scrub and/or herbaceous veg. associations	321 Natural grasslands	322 Moors and heathland
			323 Sclerophyllous vegetation
			324 Transitional woodland-shrub
	33 Open spaces with little or no vegetation	331 Beaches, dunes, sands	332 Bare rocks
			333 Sparsely vegetated areas
			334 Burnt areas
335 Glaciers and perpetual snow			

Artificial surfaces, agricultural areas, forests and semi-natural areas, wetlands and water bodies are the five level-1 categories (Büttner et al., 2004). The raster data set used has a spatial resolution of 100 m, which is quite good. However, the minimum mapping unit of 25 hectares and the minimum width of the linear elements of 100 m are only partially satisfactory, as smaller areas may be missed in the scope of the data set. All in all, though, the uniformly compiled data for the entire study area provide a good basis for the subsequent analyses.

### 3.2.3 Digital Elevation Model

The Digital Elevation Model of Europe (EU-DEM) is another EEA product. The data set is made available as GeoTIFF, subdivided into 1000 × 1000 km tiles at a spatial resolution of 25 m. For the analysis of the stopover sites, the R-package *elevatr* by Hollister & Shah (2017) was used to access the data set. The package allows easy and efficient handling of the relatively large partial data sets, since only the data of the bounding box of the input spatial data is retrieved from a web service at a time and returned as a raster object, rather than having to store the entire data set locally.

### 3.2.4 Natura 2000 protected areas

The growing awareness of environmental problems, including the loss of habitats and species in the second half of the twentieth century, has led to many national and international initiatives (Evans, 2012). Natura 2000 was established during these movements and represents a network of protected sites throughout the European Union for selected species and habitats listed in the Directive on the Conservation of Natural Habitats (European Union, 1992) and the Directive on the Conservation of Wild Birds (European Union, 2010), which also mentions the red kite species as a subject of special conservation. The vector data set provided by the EEA and used in this thesis is a compilation of the data submitted by the Member States to the European Union and is updated once a year. Only Special Protection Areas (SPAs) designated under the birds directive and Special Areas of Conservation (SACs) designated under the habitats directive have been extracted for the analysis, where it is believed that they most accurately reflect the needs of red kites.

### 3.2.5 OpenStreetMap

OpenStreetMap (2020) is based on Volunteered Geographic Information (VGI), the collection and sharing of geographic data by volunteers. The reduced cost of modern handheld devices equipped with satellite navigation has enabled people to collect geographical data with ease of use and with a precision that was previously simply out of reach of non-professional users. Moreover, the progress of the Internet has led to the development of a participatory approach, making collaborative efforts to produce and share content of different kinds very frequent (Helbich et al., 2012).

The geometric primitives of the spatial data are of the types: points (called *nodes*), polylines (called *ways*) and relations, whereas polygons are represented as closed polylines.

**Table 5** – Overview of the OpenStreetMap data sets used. For the purpose of reproducibility, the tags, consisting of key and value, used for querying the database are given as well as the number of objects returned at the time of the query for the bounding box (WGS84: -3.9; 42.3; 7.8; 47.8).

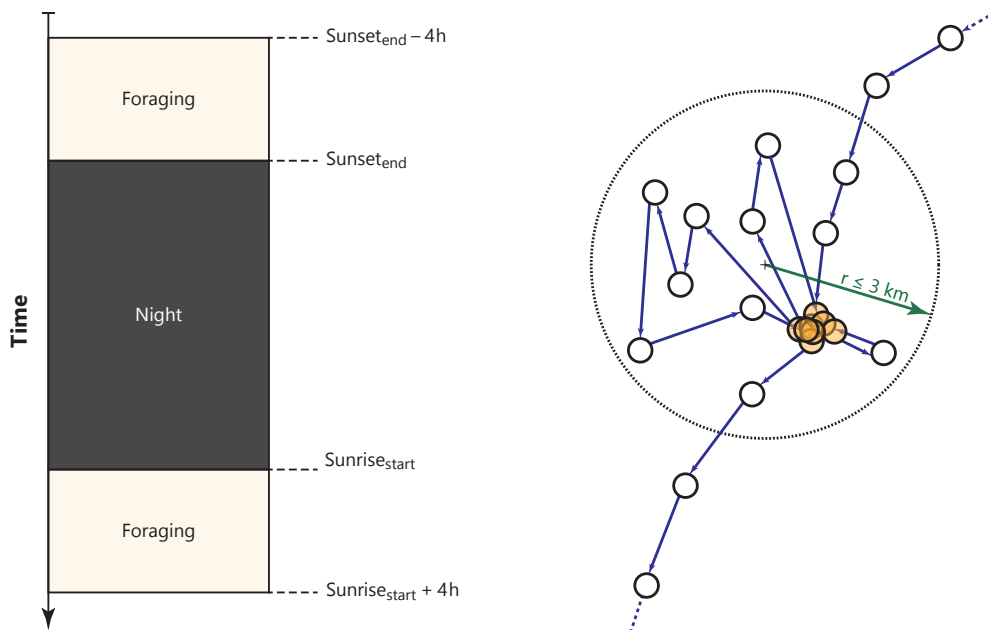
Data set	Geometry	Values = keys	Objects	Date of query
Power supply lines	Polyline	power = line	25'253	19 Feb. 2020
Railway network	Polyline	railway = rail	54'868	18 Feb. 2020
Road network	Polyline	highway = motorway highway = trunk highway = primary	176'427	27 Feb. 2020
Wind turbines	Multipoint	power = generator: source = wind	19'607	18 Feb. 2020

Since OpenStreetMap does not include a formal quality control process of the user-generated content, its accuracy (semantic and spatial) as well as completeness may be variable. Completeness becomes more problematic in rural areas compared to urban areas as was shown by [Girres & Touya \(2010\)](#) for France. [Haklay \(2010\)](#) called it moreover the disadvantaged areas that were less covered, as for instance places with a large number of tourists. Even a recent study by [Zhang & Malczewski \(2018\)](#) still pointed to a rather spatial heterogeneity regarding the completeness of OpenStreetMap data, even though they considered the overall quality of the data to be comparable to commercial reference data sets. [Jackson et al. \(2013\)](#), however, found an overall completeness of OpenStreetMap data of 70% for a study area that included both rural and urban areas. Regarding spatial accuracy, the authors found that 96% of the objects were within 150 m of the objects in the reference data set, which was considered as ground truth. [Brovelli et al. \(2016\)](#) even found a better spatial accuracy of the OpenStreetMap data for the road network of Paris compared to the data of the national institute, which may further corroborate the spatial accuracy of OpenStreetMap data. For this reason, despite possible limitations of the OpenStreetMap data, the polyline elements power supply lines, railway network, road network as well as point data of wind turbines were obtained using the *Overpass turbo* API. Free access to the data has been considered a major advantage, with the previously mentioned classes being regarded as being more likely to be captured by contributors ([Girres & Touya, 2010](#)). Table 5 lists the tags consisting of keys and values that have been included in the data sets. While all classes of power lines, railway lines and generators with the energy source wind were included in the respective data sets, only motorways, trunk roads and primary roads were included into the road network.

## Methods

### 4.1 Stopover site definition

There are different approaches to the definition of a stopover site, whereby the concepts should be adapted to the species-specific migration behaviour. The vague definition of a stop as a place where a bird can recover for a short time and recharge its energy reserves (Mehlman et al., 2005) is not sufficient, if the intention is to explicitly differentiate between roosts and stopover sites, for example. For this purpose definitions have to be more specific such as the one of Kochert et al. (2011), who defined stopover sites of an American long-distance migrating buzzard species as movements of less than 150 km within at least 24 hours before and after movements of at least 150 km per duty cycle. A similar definition was provided by Shiu et al. (2007), who investigated stopover site fidelity of a European as well as an Asian migratory buzzard species. They specified a stopover site to be an area where a buzzard stayed within an area less than 30 km in diameter and for at least 24 hours. As there was no existing definition of stopover sites of red kites that was widely accepted in the literature or existed at all, a new one based on established definitions of other migratory bird of prey species and existing knowledge in the literature on the migratory behaviour of red kites had to be developed. In the further course of the thesis, a stopover site of a red kite is therefore considered to be an area where an individual stayed for a minimum of one night and was foraging for at least four hours the same afternoon or the following morning before continuing its migration. However, stopovers where a red kite has only passed the night without previous or subsequent foraging are distinguished from stopover sites and considered to be a roost. At stopover sites GPS positions are usually dispersed in different directions and locally concentrated in an area with a radius of up to 3 km (Figure 6).



**Figure 6** – Temporal and spatial illustration of the stopover site definition. For a stopover site to be identified as such, a red kite has to forage for at least four hours in the preceding afternoon before the end of the sunset or in the subsequent morning after the beginning of the sunrise, besides staying at the site all night (left). Further, at stopover sites GPS positions are dispersed in different directions and locally concentrated in an area with a radius of up to 3 km (right).

## 4.2 Stop detection

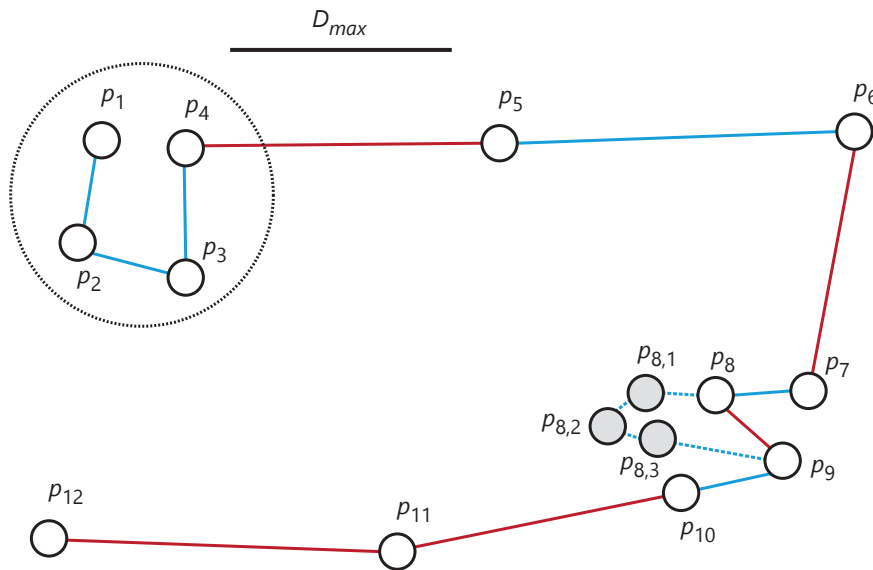
### 4.2.1 Detection of candidate stops

On the basis of the already defined autumn migration periods (Section 3.1.2), the resulting sub-trajectories can subsequently be examined for stops. For this purpose the algorithm developed by [Montoliu et al. \(2013\)](#) was applied, even if, as seen in Section 2.2.2, there were many other possible approaches. One of the main advantages of this algorithm is its capability of dealing with temporal gaps in between consecutive location points ([Fillekes et al., 2019](#)), a characteristic of the data set to be used. The algorithm was developed in the field of human mobility research and considers two levels of clustering for the detection of the so called stay regions ([Toader et al., 2017](#)). First, location points are grouped using a time- and distance-based clustering method, which discovers stay points. In the second level, the stay points are grouped into stay regions by means of a grid-based clustering algorithm. A stay region is consequently a cluster of stay points, which may have taken place on different days and a single stay point can be regarded as a stopover site in the context of bird migration. Hence, only the first-level algorithm was required for the stop detection in the red kite migration trajectories, as a certain distance between successive stopover sites is

to be expected and a possible aggregation to stay regions in the special case of very close stopover sites would have led to larger areas, which would have affected the accuracy of the stopover site characteristics.

The first-level algorithm requires a list of consecutive location points per individual  $l_p = (p_1, p_2, p_3, \dots, p_N)$  as input, where  $N$  represents the total number of location points of that individual during the autumn migration period under investigation. Every location  $p_i$  is defined as a triple consisting of geographical latitude, longitude and a corresponding timestamp ( $p_i = (lat, lon, T)$ ). The objective of the algorithm is to obtain a list of stay points  $l_{sp} = (sp_1, sp_2, \dots, sp_M)$  using the list of consecutive locations  $l_p$  of an individual, where  $M$  is the number of stay points of an individual. Every stay point  $sp_j$  is defined as a quadruple  $sp_j = (lat, lon, T^{start}, T^{end})$  containing the location as well as the time when the stay point started respectively ended. A stay point is defined as a geographic region in which an individual stays for a while in case certain constraints are fulfilled. Formally a stay point is determined from a start location point  $p_s$  to an end location point  $p_e$ . In total there are three constraints, two temporal and one spatial.  $SpaceDistance(p_s, p_e) < D_{max}$  is the spatial constraint, ensuring that the distance between the start and end point of a stay point does not exceed  $D_{max}$ . A stay point is only identified as such, if a particular minimum temporal duration is exceeded, defined as  $TimeDifference(p_s, p_e) > T_{min}$ , which is the first temporal constraint.  $TimeDifference(p_k, p_{k+1}) < T_{max}$  is the second temporal constraint, ensuring that the time difference between two consecutive location points does not exceed a certain value. The three intuitive constraints can be adjusted by the user, as  $(D_{max}, T_{min}, T_{max})$  are the three input parameters of the algorithm. Figure 7 exemplarily illustrates the behaviour of the algorithm on a sequence of location points in a latitude-longitude coordinate space. To best meet the definition of the stopover sites (Section 4.1), the input parameters of the stop detection algorithm were set as follows:

- $T_{max} = 16$  h: In view of the fact that daylight is continuously becoming scarcer during the autumn migration period and therefore the period during which no positioning is recorded is becoming increasingly longer,  $T_{max}$  had to be determined very conservatively with 16 hours in order to ensure that important stopover sites are not lost due to long recording breaks.
- $T_{min} = 12$  h: A very conservative choice, intended to detect all stay points that lasted longer than 12 hours in a first step and only in a second step to distinguish between roosts and stopover sites, using the effective sunrise and sunset times at the respective locations of the stopover sites (Section 4.2.2).
- $D_{max} = 4$  km: Based on a sensitivity analysis with regard to this parameter, it turned out to be the best value to meet the criterion of the maximum radius of a stopover site of 3 km (Section 4.1).



**Figure 7** – Illustration of the first-level of the algorithm by [Montoliu et al. \(2013\)](#). Two consecutive location points are connected with a blue line if the time difference between the two connected location points is less than  $T_{max}$  and it is red otherwise. A stay point is detected in the set  $(p_1, p_2, p_3, p_4)$ , since also the distance from  $p_1$  to  $p_4$  is smaller than  $D_{max}$ . For the points in the set  $(p_7, p_8, p_9, p_{10})$ , there are two individual detected stay points, since  $T_{max}$  has been exceeded between  $p_8$  and  $p_9$ . One stay point consisting of points  $p_7$  and  $p_8$  and another one of  $p_9$  and  $p_{10}$ . Assuming that the three location points  $(p_{8.1}, p_{8.2}, p_{8.3})$ , which are lying between  $p_8$  and  $p_9$ , were actually detected by the sensor, a single stay point from  $p_7$  to  $p_{10}$  (indicated by the blue dashed lines) would have resulted, since  $T_{max}$  would no longer be exceeded in the consecutive point set  $(p_7, p_8, p_{8.1}, p_{8.2}, p_{8.3}, p_9, p_{10})$ .

### 4.2.2 Differentiating stopover sites and roosts within France

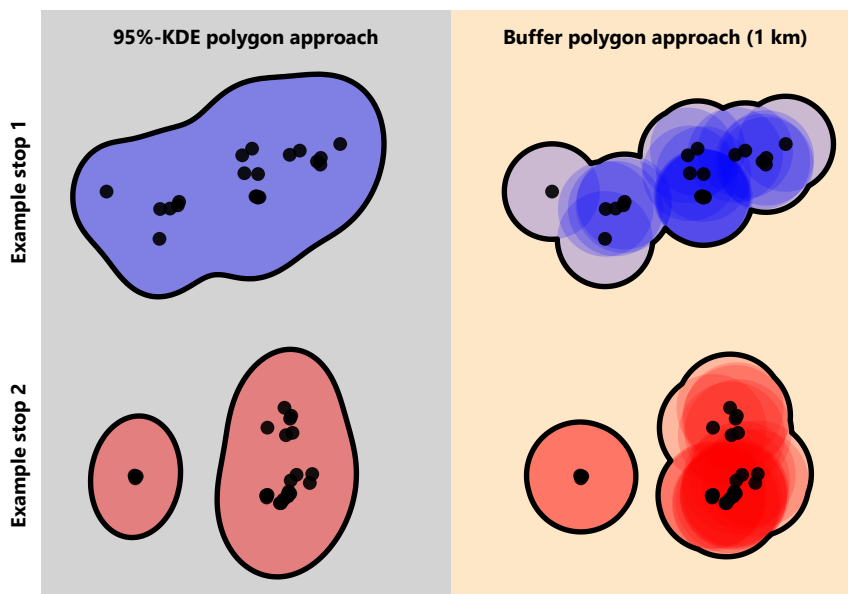
After the stops (stay points) had been detected, all those located outside France were eliminated. By considering only stops within France, the distinctive differences in landscape between the north and the south of the Pyrenees was taken into account. Moreover, the main route of the red kite migration is expected to pass through France, which is particularly evident from the fact that most stops are situated within France. The remaining French stops were subsequently analysed with regard to the criterion that a red kite must be foraging for at least four hours either on the day of arrival or the morning after in case of a stopover site. This dynamic definition required that for all stops the exact times of sunrise and sunset had to be calculated at the time of the actual stops at the given location. For this purpose, the R-package *suncalc* by [Thieurmel & Elmarhraoui \(2019\)](#) was used, whose *getSunlightTimes* function allows to retrieve all kinds of times connected to sunlight for a given point in time at a specific location requiring merely longitude, latitude, a date as well a desired time zone



of the results as input. The exact solar stages of the stops were determined using the centroids of the location points of each stop and the averaged underlying date of the stop. Based on these local solar stage times, stops that fulfilled the temporal foraging constraint could be separated from roosts as stopover sites, by comparing the time stamps of the start point of a stop with the ending time of sunset and the end point of a stop with the beginning of sunrise. If in one of the cases the temporal constraint of four hours was met, the stop was subsequently considered a stopover site. Otherwise, it was regarded a roost and discarded from further analysis.

### 4.3 Generation of a stopover site area

To analyse the characteristics of a stopover site, an area had to be generated somehow from the individual location points constituting a stop. This intention meets a widespread need of ecologists, since the estimation of ranges, such as the home ranges of individuals or geographic ranges of species, is a major challenge in both wildlife management and conservation biology (Fleming & Calabrese, 2017). Due to the relatively small number of location points per detected stop in the underlying study, it would have been easiest to create a polygon of the merged buffers created around the location points of every stop to obtain an area (Figure 8).



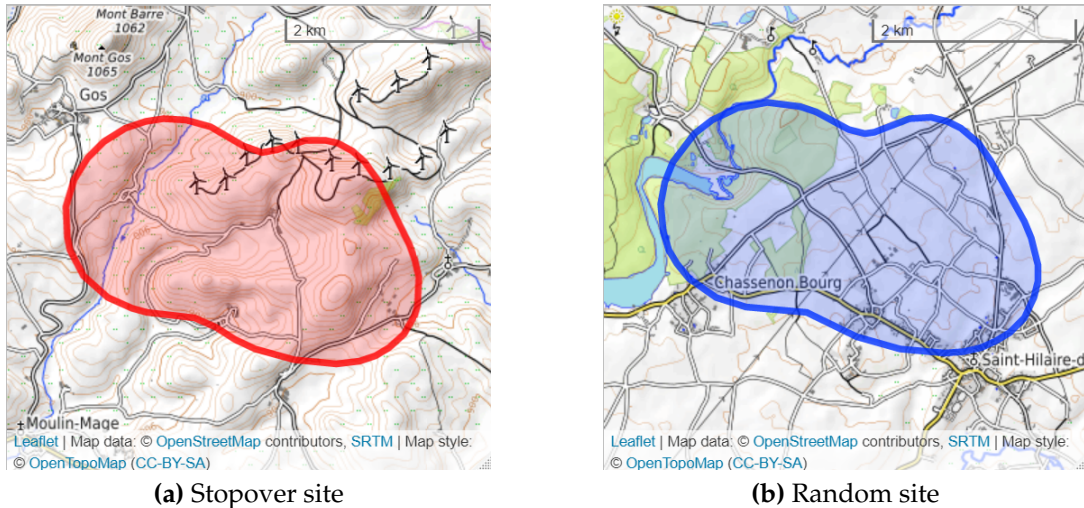
**Figure 8** – Illustration of the two approaches 95% KDE and buffer polygons for two exemplary stopover sites (stop 1: 21 points; stop 2: 24 points). For the KDE, the reference bandwidth selector has been applied as smoothing parameter and the spatial resolution of the grid was set to 30 m. The distance value of the buffer in the corresponding examples on the right was set to 1 km. It can clearly be seen that the polygons obtained from the two approaches differ only slightly in terms of shape and size.

However, this would not have taken into account the existing point density. For this reason, non-parametric density estimators are often used to assess unknown distributions, as they can account for irregular structures without requiring an understanding of the biological mechanisms. Kernel density estimation (KDE) methods are widely used in this context (Fleming & Calabrese, 2017) and also represent the method used in this thesis. However, these methods are sensitive to outlying points that are regarded as exploratory movements of animals and therefore should be omitted, when for example a home range is estimated. That is why it is common to use the 95% volume isopleth of a density surface to delimit home ranges to deal with outlying points, while the 50% isopleth is used to delimit the most important part of a home range, known as the core area (Getz et al., 2007). Figure 8 shows an example of 95% isopleth polygons for two example stopover sites and provides the results of the buffer approach for the same stops for comparison. To generate the kernel density estimation, the R-package *adehabitatHR* by Calenge (2006) was used. More specifically, the *kernelUD* function was first used to create a density surface of the location points of a stopover. A kernel density estimation can only be calculated based on at least five location points, thus stops that did not meet this constraint had to be removed from the sample. For the smoothing parameter ( $h$ ), required by the *kernelUD* function, the reference bandwidth of each stop was used, while for the parameter grid, defining the size of the grid, the input was implemented in such a way that the size of the raster cell was always 30 m. The third required parameter (extent) was chosen sufficiently large in order to be able to generate the isopleths. These 95% isopleths of the stopover sites were then determined using the function *getverticeshr*, which used the density surface of the previously applied *kernelUD* function as input.

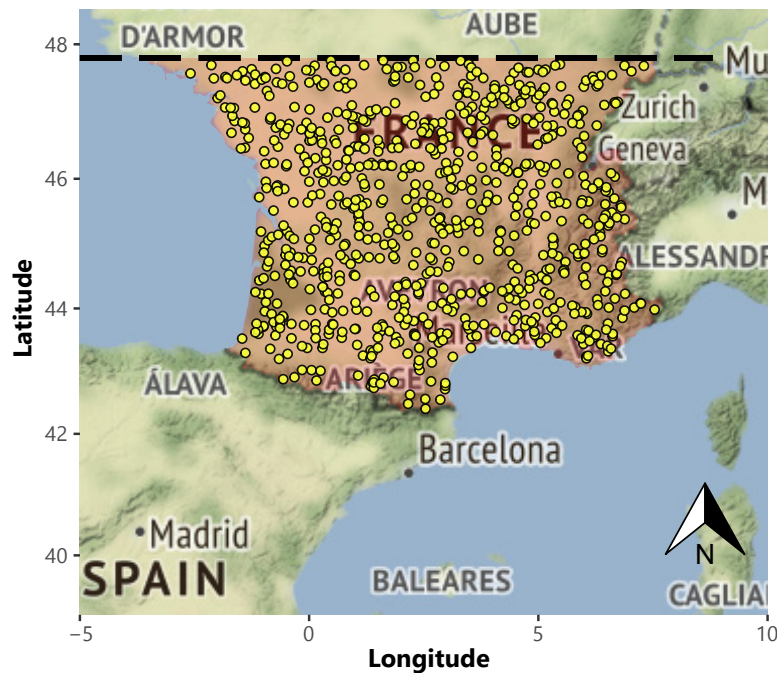
## 4.4 Random sites generation

In order to statistically investigate the characteristics of the stopover sites in the form of a presence/absence model (Section 4.6), random sites had to be generated for which it was assumed that they were not stopover sites. These random sites were determined by displacing the geometric shapes of the 792 stopover sites to 792 random locations (Figure 9), which consequently resulted in the sample consisting of equal numbers of random sites and stopover sites. This further meant that the same geometric shapes of the 95% KDE polygons once appeared at a random location. The potential region for random sites was limited to a predefined extent, which was the territory of France south of the northernmost point of Switzerland (47°48' N). The northernmost point was chosen because the autumn migration of red kites is usually directed towards southwest and the territory of France in the north of Switzerland therefore could be ignored as potential stopover site area. As the southern border of France runs basically along the mountain ridge of the Pyrenees and a certain smaller proportion of the red kites from the Sense district migrate to Spain, the national border was chosen as the southern limit of the potential stopover site area. Figure 10

illustrates these random sites generated within the specified extent. The determination of the random locations within the given extent was coded such that there was no overlap with the 95% KDE polygons of the actual stopover sites.



**Figure 9** – Example of (a) a stopover site that was displaced to (b) a random location within the predefined extent, retaining the geometry shape of the 95% KDE polygon of the stopover site and ensuring that there was no overlap of random sites with stopover sites.



**Figure 10** – Distribution of the random sites (yellow points) within the defined extent, which was the territory of France south of the northernmost point of Switzerland, highlighted in light red, whereby the geometries of the actual stopover sites were displaced to the generated random locations.

## 4.5 Generation of stopover site attributes

On the basis of the stopover site 95% KDE polygons, attributes both of the stopover sites and the random sites could now be generated. The first step was to identify possible determinants that could make a stopover site for red kites favourable or unfavourable and for whose implementation a data set of the study area of France could be found. Table 6 shows an overview of the feasible determinants investigated in this thesis, with the considerations and methods for obtaining the determinants being documented in Sections 4.5.1 to 4.5.6.

**Table 6** – Summary over the implemented attributes of the stopover sites. A total of 15 attributes of the stopover sites as well as the random sites have been implemented, which are listed here with a short description, data type, and levels or range, respectively.

Attribute	Description	Type	Levels/range
<i>elevat</i>	Mean elevation of the stopover site	Numeric	[-1.6,2872.9]
<i>slope</i>	Mean slope of the stopover site	Numeric	[0.0,0.6]
<i>land_L</i>	Occurrence of illegal landfill or composting site in vicinity	Binary	{0,1}
<i>LC_For</i>	Forest area share	Numeric	[0.0,1.0]
<i>LC_Pas</i>	Pasture area share	Numeric	[0.0,1.0]
<i>mot_L</i>	Occurrence of road (primary or higher)	Binary	{0,1}
<i>mot_D</i>	Shortest distance to road (primary or higher)	Numeric	[0.0,24085.9]
<i>natu_L</i>	Occurrence of conservation area	Binary	{0,1}
<i>natu_D</i>	Shortest distance to conservation area	Numeric	[0.0,107960.9]
<i>pow_L</i>	Occurrence of electric power line	Binary	{0,1}
<i>pow_D</i>	Shortest distance to electric power line	Numeric	[0.0,18686.3]
<i>rail_L</i>	Occurrence of railway line	Binary	{0,1}
<i>rail_D</i>	Shortest distance to railway line	Numeric	[0.0,48063.1]
<i>wind_L</i>	Occurrence of wind turbine	Binary	{0,1}
<i>wind_D</i>	Shortest distance to wind turbine	Numeric	[0.0,832779.9]

### 4.5.1 Elevation and slope

Within Switzerland red kites prefer habitats located at up to 800 MASL, especially during the breeding season. For that reason it was assumed that elevation also plays an important role during migration and stopover sites below 800 MASL are therefore preferred. To generate the attribute mean elevation (*elevat*), the Digital Elevation

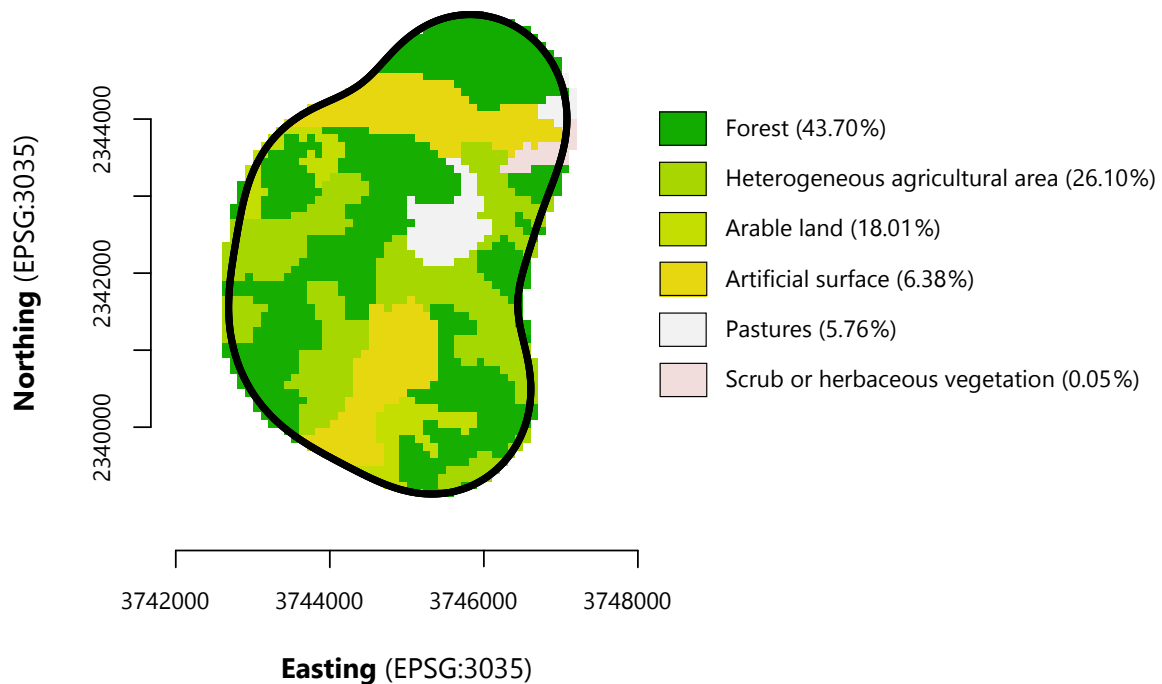
Model (DEM) of Europe was accessed using the R-package *elevatr* (Hollister & Shah, 2017). For each stopover site an extent covering the 95% KDE polygon was retrieved and intersected with the DEM to calculate the mean elevation. On the basis of the elevation model it was possible to derive a second attribute, the mean slope *slope* within the stopover site, as a proxy for surface roughness. Regarding the mean slope attribute, it is assumed that areas with smooth topography should be more attractive to red kites than those with rugged topography.

### 4.5.2 Illegal landfills and composting sites

Unfortunately, as already mentioned in Section 3.2.1, the illegal landfills and composting sites (*land.L*) could not be georeferenced precisely because the data sets only mentioned the name of the commune in which a site was located and the sites could therefore only be assigned to the polygons of the communes. But since this attribute is regarded as eminently important for the stopover site selection of red kites and no other data set was available, it had to be implemented somehow based on this data set, with the given limitations. By intersecting each 95% KDE polygon of the stopovers with the commune vector data set, the communes contained in the polygon could first be determined. In a second step it could be checked whether one of the identified communes contained either an illegal landfill or a composting site. If this was the case, the value 1 (true) was assigned to the stopover site, otherwise the value 0 (false).

### 4.5.3 Proportions of land cover classes forest and pasture

Since red kites prefer foraging near pasture areas and furthermore tend to roost in the vicinity of edges of forests, the two attributes proportion of pastures (*LC\_Pas*) and forests (*LC\_For*) have been implemented using the CORINE Land Cover data set. Pastures and forests represent two individual CORINE Land Cover level-2 categories, the latter consisting of the three level-3 categories broad-leaved, coniferous and mixed forests, which have been integrated into a single category (Table 4 in Section 3.2.2). The 95% KDE polygons of the stopovers were intersected with the land cover raster data set and the number of raster cells of each category were summed up. Based on the total number of raster cells per stopover site, the relative share of each land cover category could be calculated. Figure 11 shows an example plot of a stopover site that was intersected with the land cover layer. Of course, in a first step, other land cover classes important in connection with the red kite were also considered, such as arable land. However, it was found that the shares of different land cover classes correlated strongly with each other. For example, it is very likely that arable land and pastures are generally negatively correlated, since in a region with a high share of arable land, fewer pastures will be present.



**Figure 11** – Relative CORINE Land Cover proportions expressed as a percentage for an example stopover site using the CORINE Land Cover raster data set with a spatial resolution of 100 m.

#### 4.5.4 Natura 2000 conservation areas

It was assumed that conservation areas clearly favour the characteristics of a stopover site due to expected increased availability of food. The Natura 2000 conservation areas were available as polygons in a vector data set. Both a binary (*natu\_L*) and a shortest distance attribute (*natu\_D*) were generated for all stopover sites. The binary attribute was obtained using the *over* function of the R-package *sp* by [Bivand et al. \(2013\)](#) and [Pebesma & Bivand \(2005\)](#). Again, the shortest distance was calculated between the centroid of a stopover site and the nearest protected areas polygon by means of the *dist2Line* function, where the distance was set to zero for stopover sites whose area had parts of a conservation area.

#### 4.5.5 Road, power line and railway line network

The reasons why the individual attributes were considered important for stopover sites of red kites vary slightly. It is assumed that the presence of roads and railway lines can have a positive effect on the food supply of red kites, due to the carcasses of small mammals that have been run over. Besides, roads and railway lines should normally not pose a danger to red kites, as they usually grab their prey in flight and carry it away to a safe place, which should minimise the risk of collision with

a vehicle (Aebischer, 2009). By contrast, it is somewhat more complex to assess the effects of the presence of power lines. They can pose a danger (Maciorowski et al., 2019) as well as improve food availability, as other bird species collide with the infrastructure or die from electric shock. While collisions are rather unlikely due to the normally leisurely flight of red kites, the danger of an electric shock also exists for them, which does not allow for a firm hypothesis on the advantages or disadvantages of the occurrence of power lines for red kites.

However, since the three data sets road, power line and railway line network are all vector data sets consisting of line elements, the methodology for deriving the corresponding attributes is described jointly. In a first step, the *gIntersects* function of the R-package *rgeos* by Bivand & Rundel (2019) was used to generate a binary attribute for each of the three data sets (*road\_L*, *pow\_L* and *rail\_L*), where the question was whether a stopover site contained the feature or not. In addition to the binary attribute, the shortest distance between a stopover site and an element of the underlying network was calculated in a second step (*road\_D*, *pow\_D*, *rail\_D*). More specifically, the shortest path between the centroid of the 95% KDE polygon of each stopover site to the network was calculated using the *dist2Line* function of the R-package *geosphere* by Hijmans (2019). If a stopover site contained either a road, a power line or a railway line, the shortest distance attribute for that stop was set to zero.

### 4.5.6 Wind turbines

The binary attribute, whether a stopover site contains a wind turbine or not (*wind\_L*), was determined in a first step using again the *over* function of the R-package *sp* by Bivand et al. (2013) and Pebesma & Bivand (2005). To determine the distance to the nearest wind turbine (*wind\_D*), the *dist2Line* function of the R-package *geosphere* by Hijmans (2019) was used. If a stopover site contained a wind turbine, the shortest distance was defined as zero. As in the case of power lines, it is not possible to make a conclusive hypothesis on the advantages or disadvantages of the occurrence of wind turbines. Although the availability of food in the immediate vicinity of wind turbines may be increased due to collision victims, this does not rule out the possibility that red kites themselves collide with the rapidly rotating rotors, as occasional findings prove.

## 4.6 Generalised linear model

### 4.6.1 Background

A generalised linear model (GLM) was set up to evaluate the determined attributes of the stopover sites with regard to their statistical significance in the selection of stopover sites of red kites. Generalised linear models use distributions other than the normal distribution and are required if the assumption of normally distributed

residuals cannot be fulfilled, as is often the case if the nature of the outcome variable is binary, a proportion or a count that cannot have negative values. In the case of the red kite stopover sites, the outcome variable can only take one of two values (*stopover site* or *no stopover site*), which obviously makes it a binary variable. For this reason, a generalized linear model with binomial error distribution was used, in which there is one trial at a time and the probability of obtaining a true stopover site is equal to  $p$ , which basically corresponds to a binary logistic regression (Korner-Nievergelt et al., 2015).

**Table 7** – Pearson correlation coefficients of the stopover site determinants.

	LC_Pas	LC_For	rail_D	elevat	slope	pow_L	natu_L	wind_D	mot_D	land_L
LC_Pas	1.00	-0.24	0.04	0.13	-0.11	-0.07	0.04	0.10	-0.02	0.01
LC_For	-0.24	1.00	0.06	0.18	0.43	-0.08	0.04	-0.08	0.10	-0.01
rail_D	0.04	0.06	1.00	0.23	0.22	-0.12	-0.10	0.03	0.39	-0.01
elevat	0.13	0.18	0.23	1.00	0.66	-0.05	0.00	0.01	0.23	0.09
slope	-0.11	0.43	0.22	0.66	1.00	-0.05	0.04	0.17	0.18	0.05
pow_L	-0.07	-0.08	-0.12	-0.05	-0.05	1.00	0.08	-0.01	-0.11	0.08
natu_L	0.04	0.04	-0.10	0.00	0.04	0.08	1.00	0.16	-0.09	0.00
wind_D	0.10	-0.08	0.03	0.01	0.17	-0.01	0.16	1.00	0.03	-0.02
mot_D	-0.02	0.10	0.39	0.23	0.18	-0.11	-0.09	0.03	1.00	-0.06
land_L	0.01	-0.01	-0.01	0.09	0.05	0.08	0.00	-0.02	-0.06	1.00

## 4.6.2 Explanatory variables

For the attributes related to the road, power line and railway line networks as well as the Natura 2000 conservation areas and the wind turbines, a binary and a numeric attribute was generated for each stopover site. Naturally it would not make sense to include both the binary and the numeric attribute of the same characteristic for the further analysis, which is why the following consideration was made in order to decide which of the two attributes should be kept. If at least one third of the actual stopover sites contained a feature under consideration, the binary attribute was retained, which was the case for the power line network and the Natura 2000 conservation areas with 39 and 40% respectively. Consequently, the numeric attribute of the minimum distance was used for the wind turbines, the railway lines and the road network. In a further step, the Pearson correlation coefficients were calculated to check whether certain attribute pairs are closely related (Table 7). Due to the relatively strong correlation between elevation and slope (Pearson's  $r = 0.66$ ), it was decided not to include slope as an explanatory variable in the generalised linear model. All explanatory variables that were finally included in the generalised linear model are listed in Table 8.

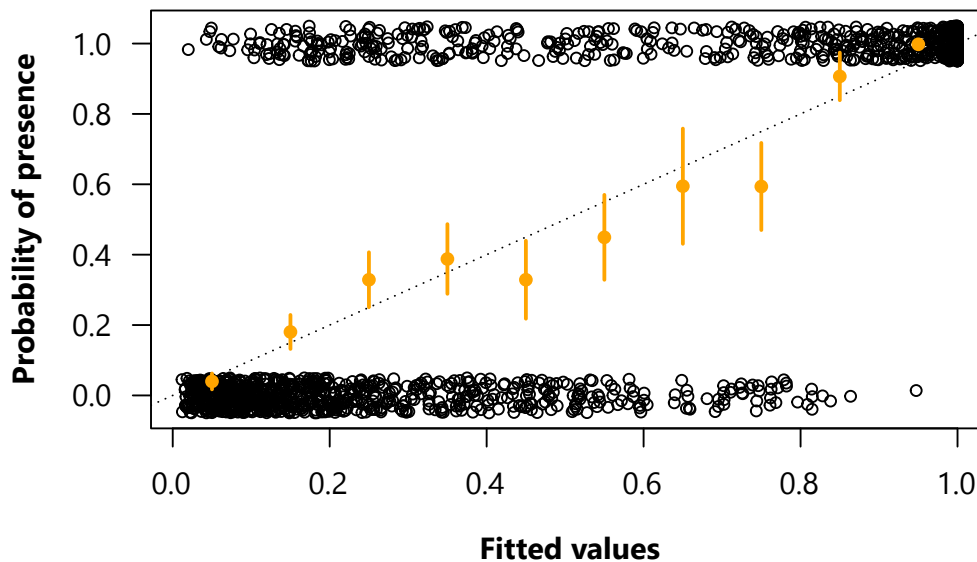


**Table 8** – Overview of the explanatory variables (Expl. var.) included in the generalised linear model with a brief description of what was analysed.

Expl. var.	Description	Type
<i>elevat</i>	Mean elevation of the stopover site	Numeric
<i>land_L</i>	Occurrence of landfill or composting site in vicinity	Binary
<i>LC_Pas</i>	Pasture area share	Numeric
<i>LC_For</i>	Forest area share	Numeric
<i>natu_L</i>	Occurrence of Natura 2000 conservation area	Binary
<i>mot_D</i>	Shortest distance to road (primary or higher)	Numeric
<i>pow_L</i>	Occurrence of electric power line	Binary
<i>rail_D</i>	Shortest distance to railway line	Numeric
<i>wind_D</i>	Shortest distance to wind turbine	Numeric

### 4.6.3 Visual evaluation of model fitting

The model fitting has been controlled by comparing the fitted values with the observed values in a plot (Figure 12). Since the mean values were more or less distributed along the  $y = x$ -line, it was assumed that the model fits the data well (Korner-Nievergelt et al., 2015).



**Figure 12** – Goodness of fit plot of the generalised linear model. The orange dots represent the mean (and 95% confidence intervals given as vertical bars) of the observations within classes of width 0.1 along the x-axis. The dotted line indicates perfect coincidence between observation and fitted values.

## Results

### 5.1 Stop detection

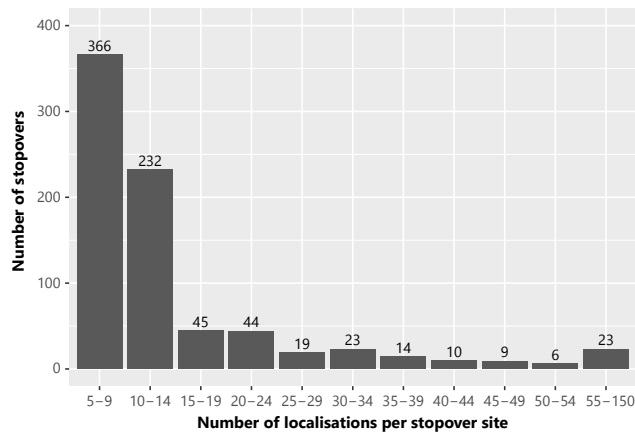
A total of 4048 stops were identified within the trajectories of the autumn migration periods, of which 1073 fulfilled the requirements of stopover sites described in Section 4.1, and 2975 by definition represented roosts. Another 189 stopover sites had to be removed from the sample because they were not located within France and further 92 since they did not consist of at least five localisations, which would not have allowed to generate a kernel density estimation. Altogether 792 stopover sites resulted and could be used for further analysis, which corresponds to 20% of all stops detected within the migration trajectories (Table 9).

**Table 9** – Reduction steps from the stop sample to the stopover sites sample.

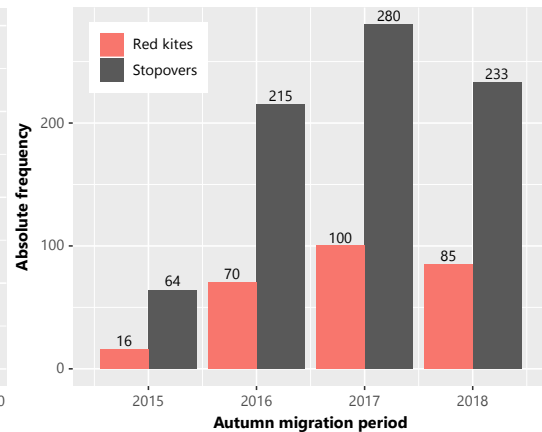
Number of stops detected	4048	(100%)
<b>Reduction steps</b>		
1. Roosts per definition	-2975	(-73%)
2. Stopover sites not located within France	-189	(-5%)
3. Stopover sites not consisting of at least five localisations	-92	(-2%)
<b>Total number of stopover sites within France</b>	<b>792</b>	<b>(20%)</b>

About 90% of the stopover sites consisted of less than 30 and 75% respectively of less than 15 localisations (Figure 13). The detected stopover sites originated from 202 individual red kites, with a maximum of 20 stopover sites from a single animal. During the autumn migration period 2015, the number of detected stopover sites, with 64 detected stopover sites, was considerably lower than for the autumn migration periods of the years 2016 to 2018, in which more than 200 stopover sites were detected in each year. There was generally a high degree of agreement between the number of stopover sites per migration period and the number of red kites per migration period in the sample (Figure 14). While for the year 2015 the stopover

sites were derived from the movement data of 16 individual red kites, the stopover sites of the year 2016 were already based on the trajectories of 70 red kites and even 100 in 2017, whereby the number was again slightly lower in 2018 with 85 birds. The mean number of stopover sites per individual differed only slightly between the years (2015: 4.0 sites per indiv.  $\pm$  2.9 SD; 2016: 3.1 sites per indiv.  $\pm$  2.2 SD; 2017: 2.8 sites per indiv.  $\pm$  2.1 SD; 2018: 2.7 sites per indiv.  $\pm$  2.6 SD).



**Figure 13** – Number of localisations captured per stopover site of the final sample (N = 792 stopover sites of 202 red kites).

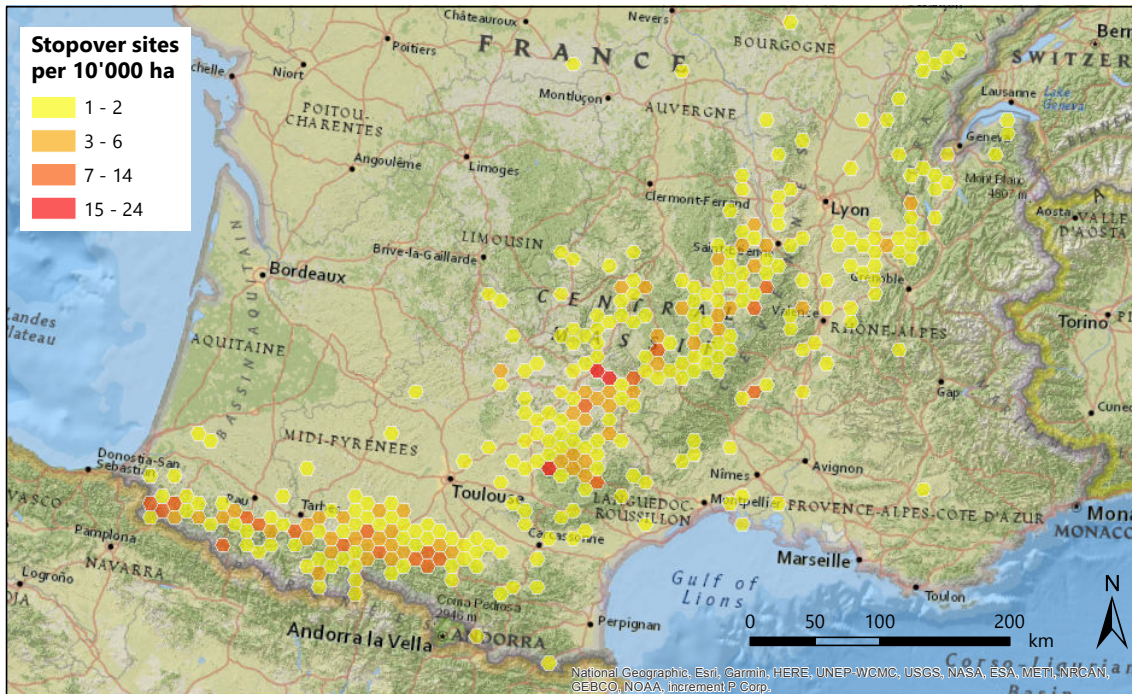


**Figure 14** – Number of stopover sites and red kites per autumn migration period (N = 792 stopover sites of 202 red kites).

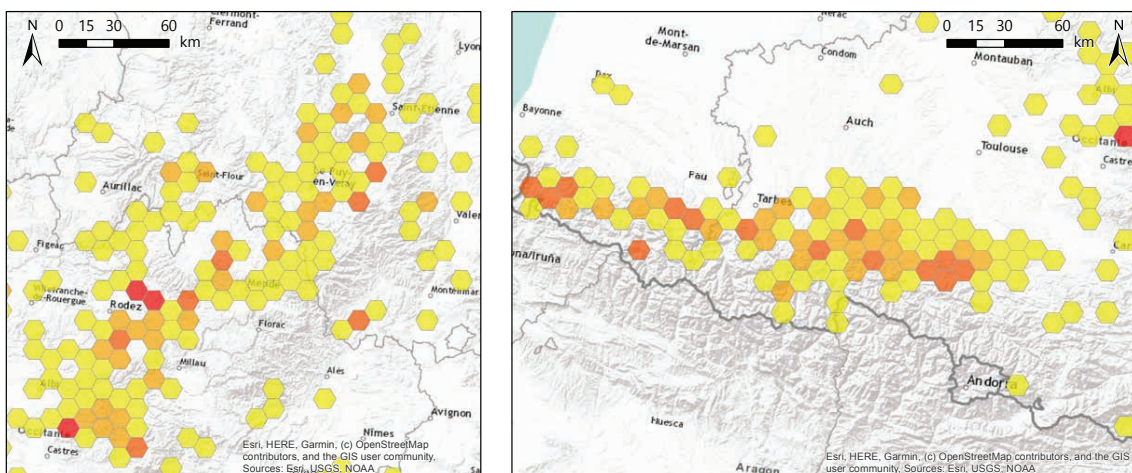
## 5.2 Spatial distribution of the stopover sites

The stopover sites were not evenly distributed over the whole territory of France (Figure 15). Instead, an accumulation of stopover sites was found along a southwest directed corridor between Switzerland and Spain, mainly in the region of the Massif Central (Figure 16a), as well as north of the Pyrenees, where there were many stopover sites on a large section from east to west at a distance of about 50 to 100 km along the main divide of the Pyrenees (Figure 16b). There were few exceptions of stopover sites outside of these regions. An additional consideration of the kernel density estimation of the centroids of the stopover sites showed that the spatial distribution of the stopover sites was even more structured (Figure 17). In fact, most of the stopover sites fell within a southwest-facing corridor of approximately 80 to 120 km width. The major part of this corridor was located in the Massif Central, with hotspots on the southern central slope in the region around Rodez and Castres. The east-west running band north of the Pyrenees extended over an east-west distance of less than 300 km and a north-south extent of mostly less than 100 km. Within the east-west band north of the Pyrenees, a large hotspot of stopover sites southwest of Toulouse was identified. Finally, a third region with high densities of stopover sites was found on the northwestern edge of the Alps south of the narrows between

the Jura and the Alps in the region west of Chambéry. Between these three regions with high densities of stopover sites, gaps with few stopover sites were found both between the Alps and the Massif Central and the Massif Central and the Pyrenees.



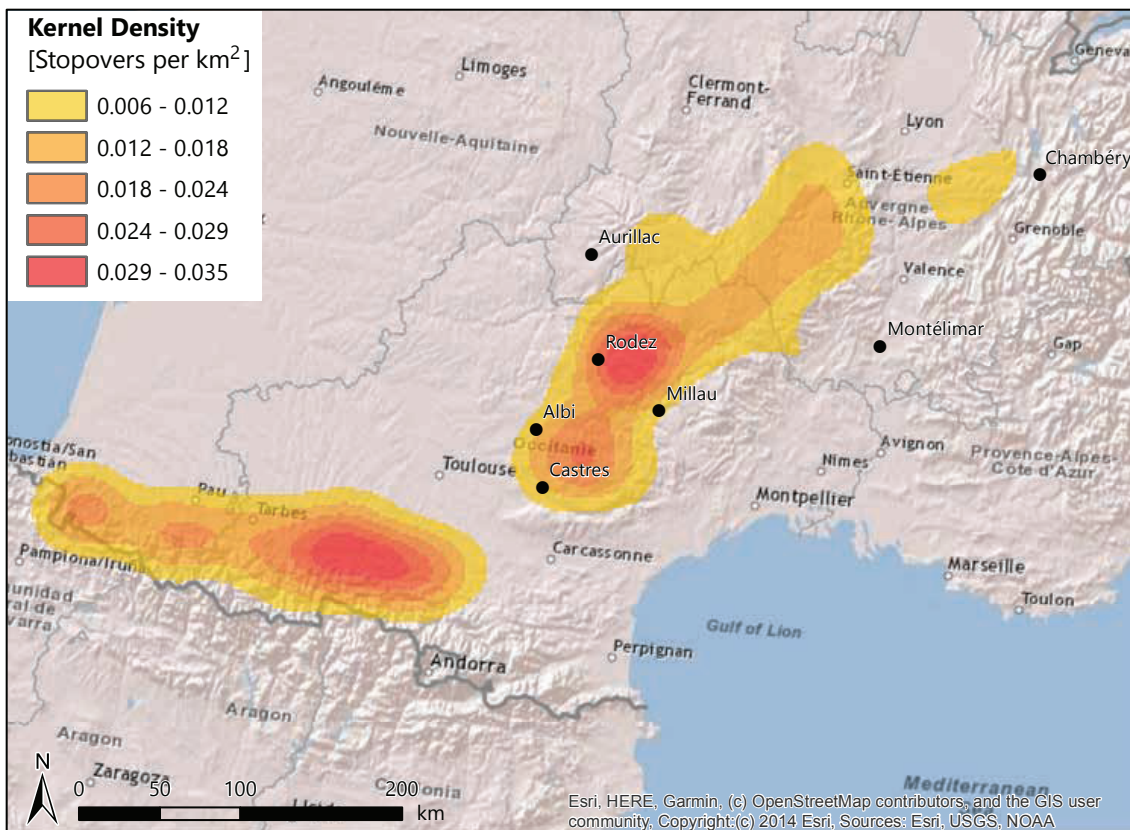
**Figure 15** – Spatial distribution of the stopover sites within France. A single hexagon corresponds to an area of 10'000 hectares, with the colour gradient indicating the different number of stopover sites per hexagon.



(a) Massif Central

(b) The Pyrenees

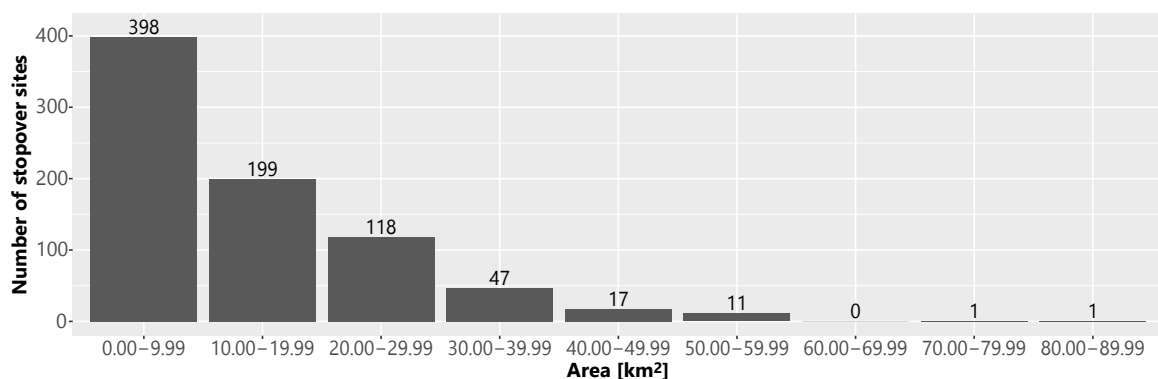
**Figure 16** – Spatial distribution of the stopover sites in the region of the (a) Massif Central and (b) the Pyrenees. A single hexagon corresponds to an area of 10'000 hectares, with the colour gradient indicating the different number of stopover sites per hexagon. Same legend as in Figure 15 applies.



**Figure 17** – Kernel density of the stopover sites within France with the three resulting hotspot regions in the northwest of the Alps west of Chambéry, the Massif Central and north of the Pyrenees.

### 5.3 Areas of the stopover sites

The area of the stopover sites generated using kernel density estimation varied greatly in size ranging from 12'000 m<sup>2</sup> to 82 km<sup>2</sup>. However, with about 75% of stopover sites having an area of less than 20 km<sup>2</sup>, there was a clear accumulation of relatively small stopover site areas (Figure 18).



**Figure 18** – Frequency distribution of the size of stopover sites.

A relationship between the number of localisations per stopover site and the area of a stopover site was not found (Figure 19). There were both small stopover site areas consisting of many localisations and large areas made up of relatively few localisations. However, the interquartile ranges of all area classes varied in a similar range between 5 and 45 localisations, which was consistent with the distribution of the number of localisations per stopover site (Figure 13).

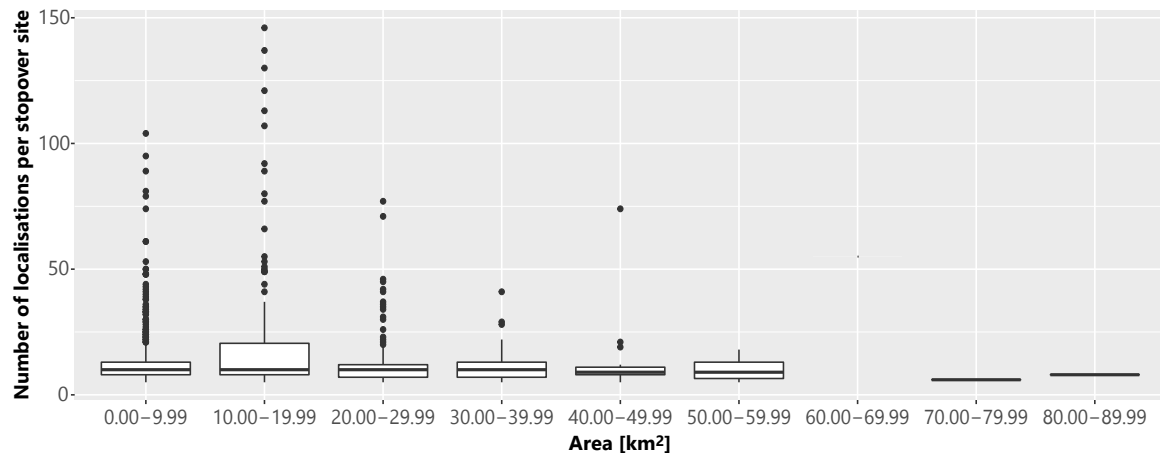


Figure 19 – Number of localisations per stopover site in relation to its area.

## 5.4 Stopover site determinants

The share of pasture varied between complete coverage and total absence in both the stopover sites and the random sites (Table 10). However, the mean proportion of pastures occurring in the stopover sites was found to be more than 10% higher than in the random sites. The forest shares also varied between complete coverage and total absence in the stopover sites as well as the random sites. Though, the mean proportion of forest at random sites was more than 8% higher than at stopover sites. The mean shortest distance from the centroid of each stopover site to the next railway line was within a similar range for both the random sites and the stopover sites. The mean elevation of the random sites and the stopover sites differed mainly regarding the maximum and mean values. While the maximum value for the random sites was almost 3000 MASL, the stopover sites were located at a maximum of 1800 MASL. Nevertheless, the mean elevation of the stopover sites was found to be about 150 m higher than that of the random sites. For the shortest distance from a stopover site to the nearest wind turbine, there was a considerable difference between the random sites and the stopover sites, with the mean shortest distance from a random site to a wind turbine being  $33.5 \text{ km} \pm 28.4 \text{ SD}$ , which was more than six times less than for the stopover sites. The values determined for the distance to the nearest road hardly differed for the random sites and the stopover sites with mean values of around 4 km for both random sites and stopover sites. The differences in the mean values of the numeric site determinants between random and stopover sites were all highly significant, except for the distance of the sites to the nearest road (Table 10).

**Table 10** – Numeric site determinants. Minimum, maximum and mean values of the numerical determinants shortest distance to railway lines, wind turbines and roads, mean elevation and the land cover class shares of pasture and forest, for both the stopover sites and the random sites. Further, the statistical significance of differences in mean values between random and stopover sites is given, using a Mann-Whitney-Wilcoxon test.

	Stopover sites (N = 792)			Random sites (N = 792)		
	min	max	mean $\pm$ SD	min	max	mean $\pm$ SD
Pasture share [%]	0.0	100.0	28.7 $\pm$ 23.2	0.0	100.0	16.4 $\pm$ 20.9 ***
Forest share [%]	0.0	100.0	19.8 $\pm$ 16.8	0.0	100.0	28.2 $\pm$ 26.5 ***
Dist. to railway line [km]	0.0	36.6	10.3 $\pm$ 8.5	0.0	48.1	9.0 $\pm$ 7.7 **
Mean elevation [MASL]	-1.0	1816.6	569.9 $\pm$ 280.3	-1.7	2872.9	424.1 $\pm$ 478.7 ***
Dist. to wind turbine [km]	0.0	832.8	203.7 $\pm$ 163.9	0.0	128.7	33.5 $\pm$ 28.4 ***
Distance to road [km]	0.0	22.2	4.3 $\pm$ 4.8	0.0	24.1	4.1 $\pm$ 4.4

\*\* $p < 0.01$ , \*\*\* $p < 0.001$

**Table 11** – Binary site determinants. Occurrence of power line, Natura 2000 conservation area or illegal landfill respectively composting site at the site. Further, the statistical significance of differences in the occurrence of the binary determinants between the random and the stopover sites is given, using a  $\chi^2$  test of independence.

	Stopover sites (N = 792)		Random sites (N = 792)	
	Present	Absent	Present	Absent
Power line	308	484	289	503
Natura 2000 conservation area*	319	479	279	513
Illegal landfill or composting site	131	661	120	672

\* $p < 0.05$

For the binary stopover site determinants, the differences between stopover sites and random sites were generally found to be less noticeable than for the numerical determinants (Table 11). Compared to the random sites, stopover sites more often included a power line with 308 cases versus 289, a difference of about 2.5%. Natura 2000 conservation areas were more common at stopover sites than at random sites, with 319 and 279 cases respectively, a discrepancy of around 5%. Almost identical *absent* and *present* proportions were found for the occurrence of illegal landfills or composting plants within the stopover site areas. With 131 *present* values for the stopover sites and 120 for the random sites, the share of sites with an illegal landfill or composting site for the stopover sites was only 1.5% higher than for the random sites. In general, however, for all three binary stopover site determinants it was observed that well over half of the stopover sites did not contain the relevant feature. Only for the binary site determinant occurrence of Natura 2000 conservation area, a significant difference in frequencies between the random and stopover sites was

found (Table 11). Figures 26 and 25 of the Appendix A provide an additional visual summary of the site determinants data for both the random sites and the stopover sites.

The explanatory variables pasture share, mean elevation, occurrence of power lines and the shortest distance to wind turbines had a positive effect on the probability of a site being selected as a stopover site, while the forest share at a site had a negative effect (Table 12). The effect of the shortest distance of a site to a wind turbine represented both the strongest positive and the strongest overall effect of the model. The null deviance of 2195.9 on 1583 degrees of freedom is essentially increased compared to the residual deviance of 1065.6 on 1574 degrees of freedom. Including the independent variables decreased the residual deviance by 1130.3 with a loss of nine degrees of freedom. The generalised linear model therefore predicted the response variable considerably better than a model that only includes the grand mean (i.e., the intercept).

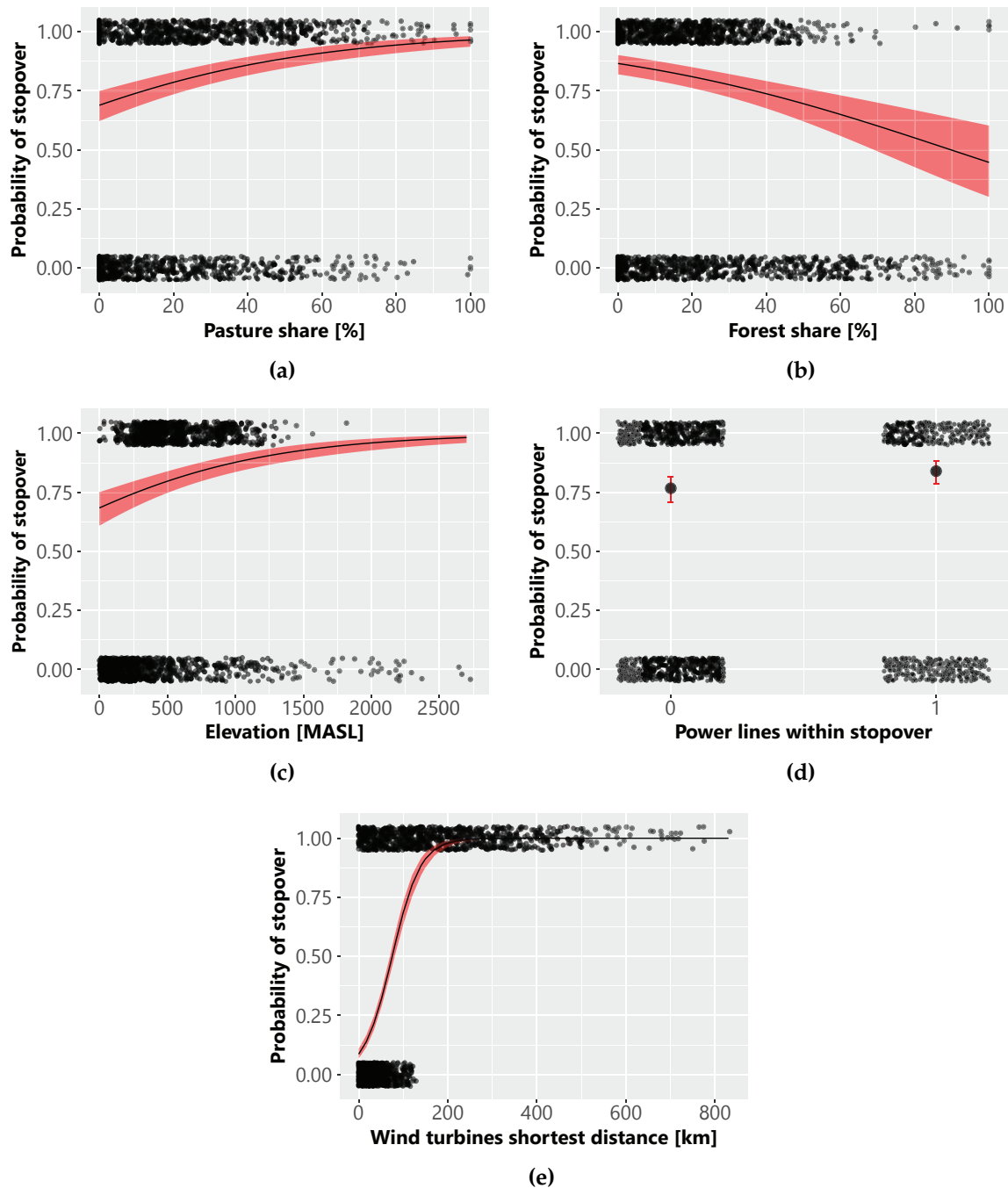
**Table 12** – Generalised linear model summary.

Explanatory variable	Estimate	Std. Error	Z-value
Intercept	1.208	0.165	7.329***
Pasture share	0.579	0.078	7.390***
Forest share	-0.468	0.088	-5.300***
Shortest distance to railway line	-0.060	0.086	-0.706
Mean elevation	0.475	0.072	6.628***
Presence of power line	0.462	0.162	2.848**
Presence of Natura 2000 conservation area	-0.080	0.165	-0.485
Shortest distance to wind turbine	4.560	0.279	16.368***
Shortest distance to road	-0.059	0.085	-0.698
Presence of illegal landfill or composting site	0.091	0.205	0.444

\*\* $p < 0.01$ , \*\*\* $p < 0.001$

According to the generalised linear model, an increasing share of pasture on the total area of a stopover site was associated with an enhanced probability of stopover site selection, whereby the probability was found to be close to 1.0 for pasture shares greater than 80% (Figure 20a). For the share of forest in the total area of a stopover site, an inverse relationship was found, since the probability of stopover site selection decreased significantly with increasing forest share (Figure 20b). In the case of total absence of forest, the probability of stopover site selection was approximately 0.8. The probability that a site was selected as a stopover site increased with increasing elevation. However, in the relatively large range from 0 MASL to 2750 MASL, the probability increased only from slightly below 0.75 to 1 (Figure 20c). The only significant binary variable revealed that the probability of power lines at stopover sites was slightly increased (Figure 20d). With increasing distance of sites to wind turbines, the probability that a site was used as a stopover site increased significantly, whereby the probability at a distance of 200 km settled at 1.0 (Figure 20e).





**Figure 20** – The effect of (a) proportion of pastures, (b) the proportion of forests, (c) the elevation of sites, (d) the presence of power lines, and (e) the distance to wind turbines on the probability of stopover site selection. 95% credible intervals are given in red. Black points represent the raw data.

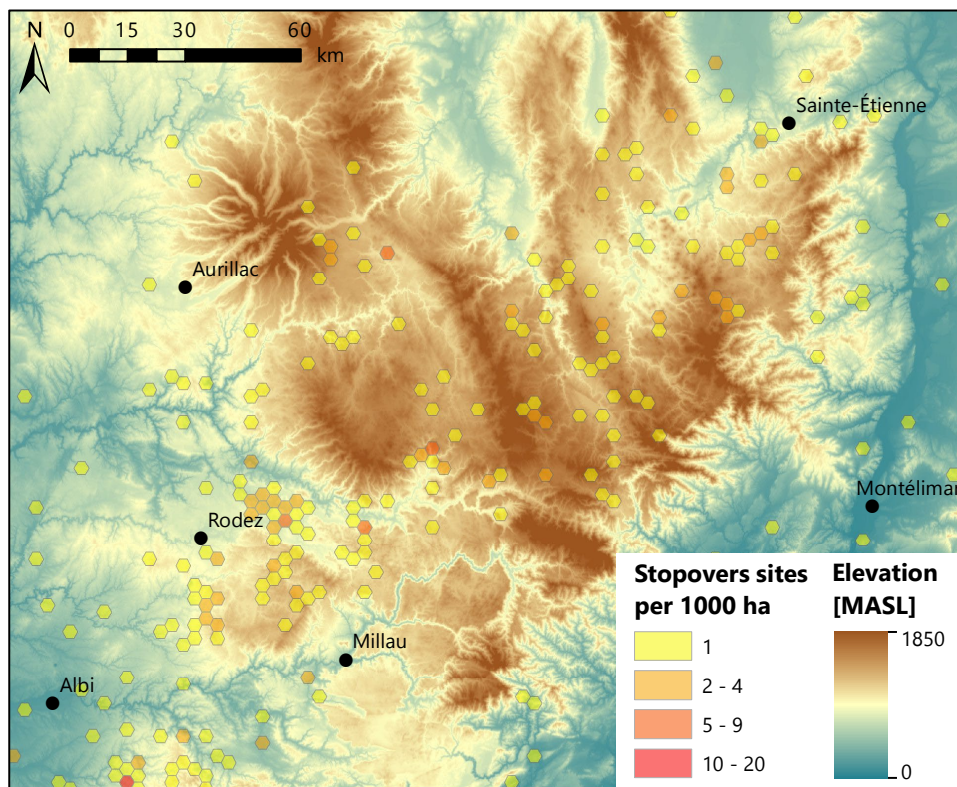
## Discussion

This study identified stopover sites of red kites used during the autumn migration period and examined their possible determinants. It was shown that there were high densities of stopover sites mainly in three regions between Switzerland and Spain. Besides the two large hotspot regions of the Massif Central and the area north of the Pyrenees, a third area with a relatively high density of stopover sites was identified on the northwestern edge of the Alps south of the narrows between the Jura and the Alps. Many of the stopover sites were located on the edge of mountains or in valleys, with the highest elevations of the passed land rarely being used. Furthermore, it was shown that the characteristics of high proportion of pasture, elevated altitude, presence of power lines and increasing distance to wind turbines of a site had a positive effect on the probability of a site being used as a stopping point. An increasing proportion of forest at a site, by contrast, had a negative effect on the probability that this site was used as a stopover site. The following Sections 6.1 and 6.2 address the two research questions posed in Section 1.2, while the methodology used in this thesis is discussed in Section 6.3.

### 6.1 Identification of stopover sites

The overall spatial distribution of the identified stopover sites led to the conclusion that the migration route of the Swiss red kites ran through the centre of the Massif Central region (Figure 21). As a clear majority of the stopover sites were found in this region, it can therefore be assumed that the Massif Central does not represent a major barrier for red kites along their migration path. Rather, these high densities of detected stopover sites indicated that the greater region of the Massif Central, which has a maximum of 1885 MASL, held important stopover site habitat for red kites. In the elevated areas of the Massif Central there were significantly higher densities of stopover sites than in the lower regions of the Rhone valley, which extends north and south of Montélimar and would in principle guarantee a barrier-free route to

the Pyrenees. On closer inspection, it was found that the stopover sites were often located at the edge of mountains as well as at the bottom of valleys, with only few exceptions where areas above 1000 MASL were selected. The almost complete absence of stopover sites in the Cévennes, the most southeastern part of the Massif Central, which lies to the west of the Rhone valley, was also striking. Also in the Aubrac plateau area southeast of Aurillac and northeast of Rodez hardly any stopover sites were detected. Why this passage through the Massif Central is generally chosen and why there is a higher density of stopover sites at the southern central edge of the Massif Central has not yet been investigated, which only allows for assumptions. Possible reasons could be a generally increased availability of food or land use in these regions that is more compatible with red kite foraging, compared for example with the Rhone valley.

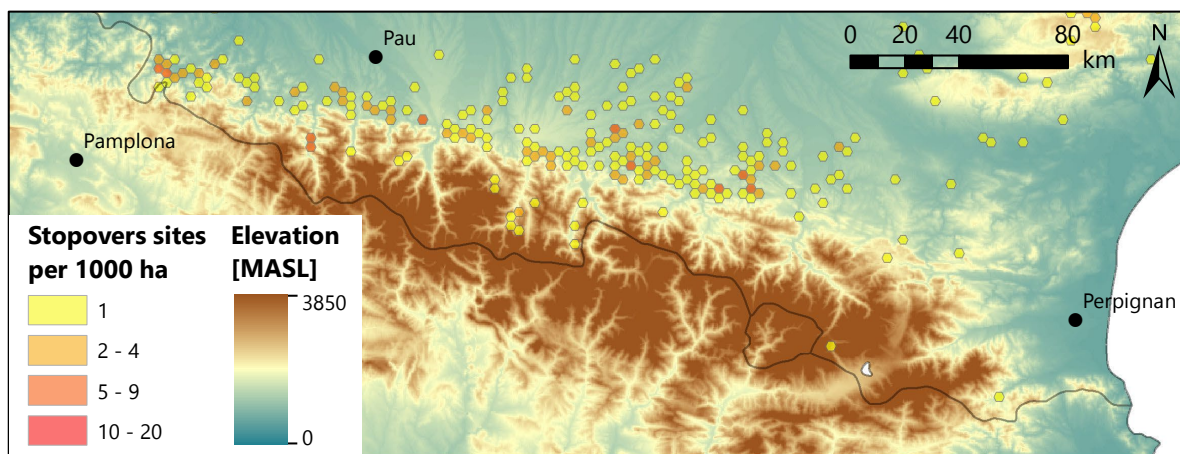


**Figure 21** – Spatial distribution of the stopover sites in the Massif Central region with respect to the digital elevation model.

The function of the Massif Central as an important element for the orientation of red kites along their migration route could also have an influence on this route selection. The high densities of stopover sites in the region around Rodez, Millau and south of Albi, in the southern foothills of the Massif Central, could on the one hand indicate that there is a certain need to recharge energy reserves after passing through the more elevated regions. On the other hand, it could also be due to favourable conditions for staying in these regions for some time. It is quite possible that in

reality it is even a combination of both considerations. These areas, located on the southern central edge of the Massif Central, would therefore be areas of interest for a more thorough investigation, also in view of the possible recurrence of birds over the years.

Given the high density of stopover sites north of the Pyrenees at a distance of about 50 to 100 km from the main divide ranging from east to west, it is possible that the Pyrenees represent a geographical barrier to red kites along their migration routes, as [Urcun & Bried \(1998\)](#) suggested. However, there would be an almost barrier-free passage towards Spain in the very east in the area of the Mediterranean coast as well as in areas in the west, which are at similar elevations as the stopover sites within the Massif Central, which somewhat undermines the barrier effect hypothesis of the Pyrenees (Figure 22).

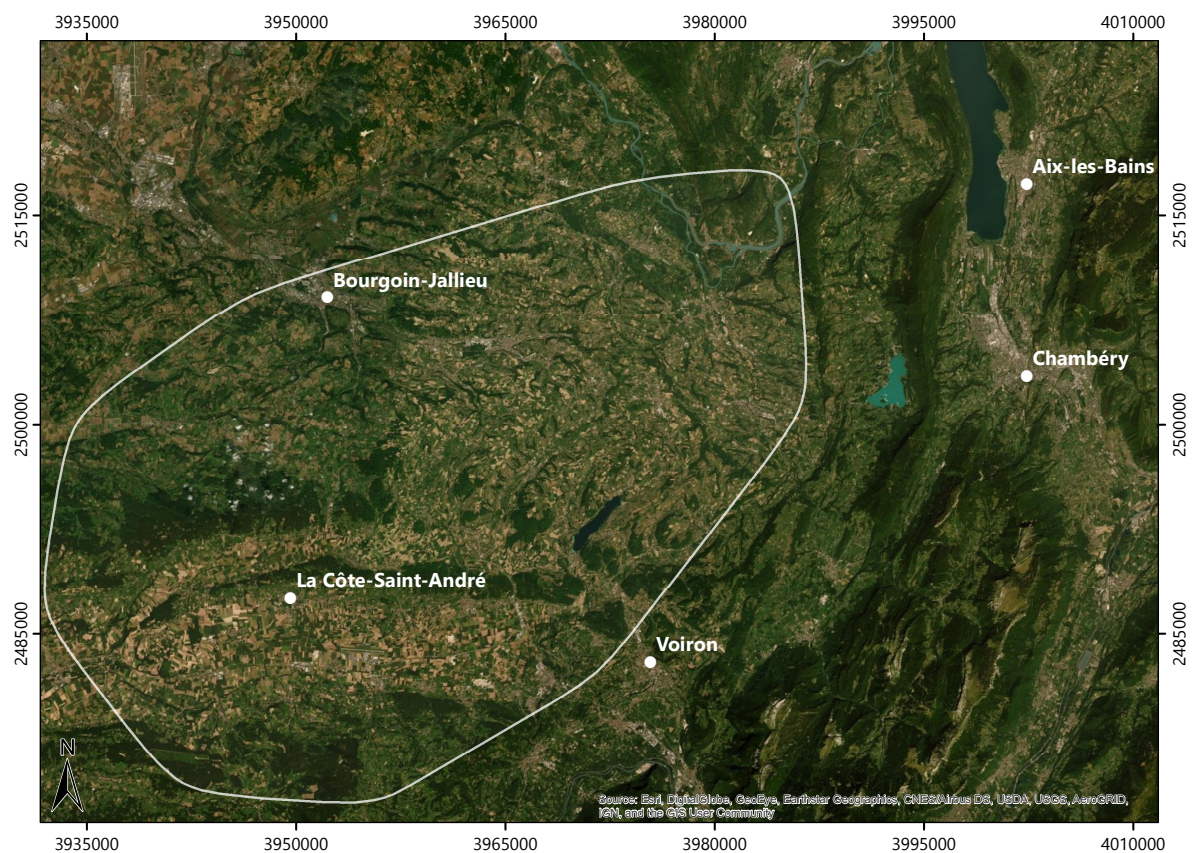


**Figure 22** – Spatial distribution of the stopover sites north of the Pyrenees with respect to the digital elevation model. The stopover sites are clearly concentrated in the west along the northern foot of the Pyrenees, while in the east, in a much lower region along the Mediterranean coast, there are hardly any.

According to [Urcun & Bried \(1998\)](#), red kites reached Spain most frequently in the provinces of Navarre and the Basque region on the southwestern edge of the Pyrenees, after passing them. In their study about the red kite migration through the Pyrenees that was based on extensive observations, they further found that only about 1% of the red kites migrating to Spain cross the central or eastern Pyrenees to Spain. Based on their observations they found that the majority of the birds migrated along the Pyrenees until they found a valley that runs approximately south and where meteorological conditions, the main factor in the decision of where and when red kites cross the Pyrenees, allowed them to easily reach the Spanish side. Furthermore, the major areas of occurrence of the red kite within Spain, determined on the basis of population surveys, were located mainly on the southwestern edge of the Pyrenees and in the two adjacent autonomous communities Aragon, Castile and León and the region of Extremadura ([Cardiel, 2006](#)). In contrast, large parts of central, eastern and southeastern Spain were sparsely or not at all populated. Both,

the observation that red kites more often pass the Pyrenees in the west than in the east, and the spatially varying abundance of red kites within Spain with large areas in the east where only few red kites were ever sighted, could be corroborated by the detected spatial distribution of stopover sites in the north of the Pyrenees.

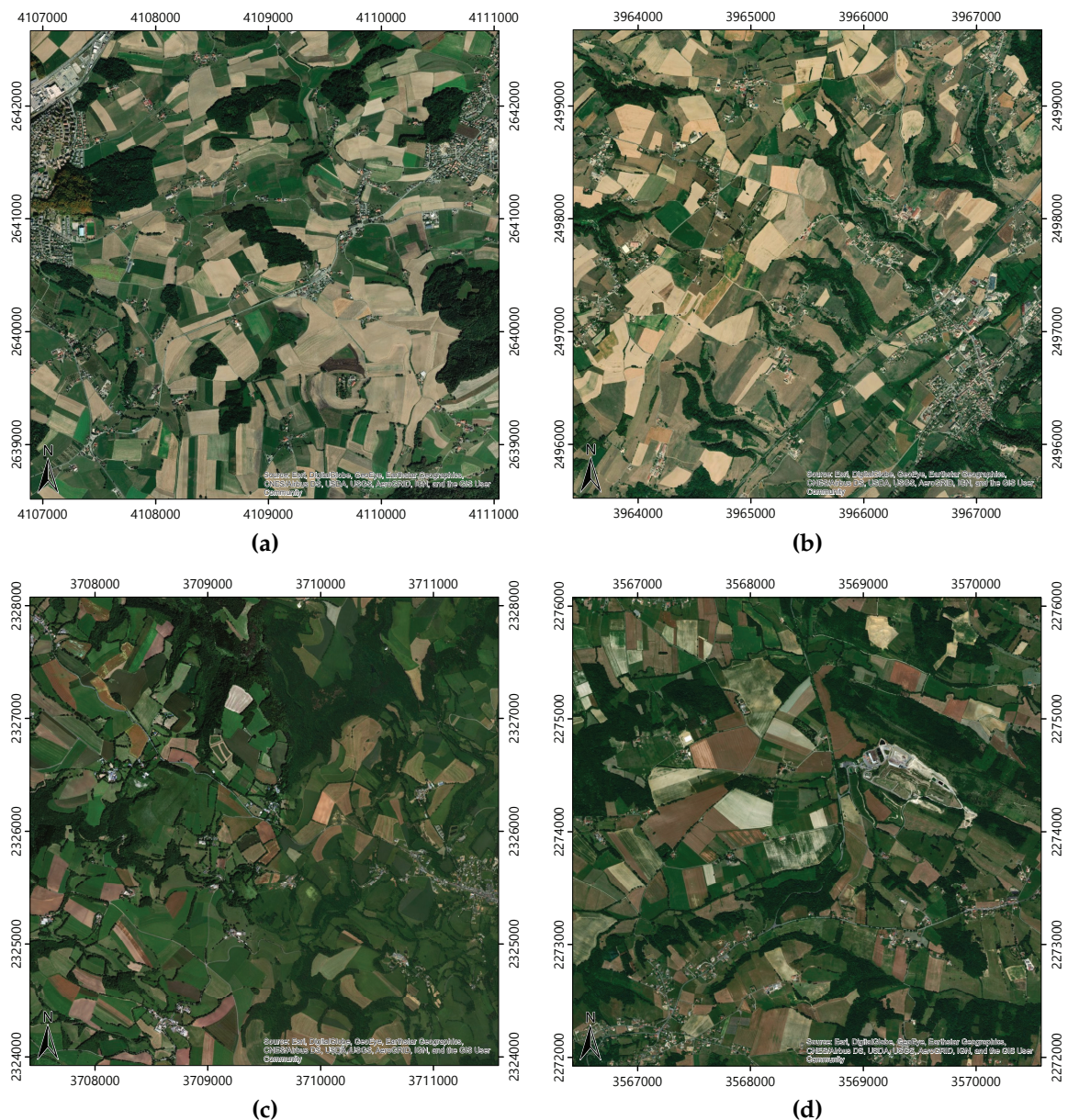
Another hotspot area of stopover sites was identified south of the narrows of the Jura and the Alps at the northwestern edge of the Alps, about 200 km southwest of the breeding areas of most birds under investigation in the Sense district (Figure 23). Its extent was estimated to an east-west dimension of around 50 km and a north-south dimension of 30 km. Even if it was the least pronounced and smallest hotspot identified, its relevance for red kite migration should not be diminished and has to be considered in future conservation measures.



**Figure 23** – Hotspot area of stopover sites at the northwestern edge of the Alps (cf. Figure 17). The actual hotspot estimated according to kernel density is indicated by the white polygon outline. Coordinates are given in metres (EPSG:3035).

In general, these three hotspot regions revealed that stopover sites tend to be found at the edge of mountains and partly in valleys. To what extent this is related to the fact that the breeding areas of the red kites of the investigated population are also located along mountain slopes, the northern slopes of the Alps and the southern foot of the Jura, is not known. However, it is quite conceivable that the characteristics of the three hotspot regions are similar to the breeding area characteristics, which

could be shown with aerial images of the three excerpts of the hotspot regions and the breeding area, respectively (Figure 24). All hotspot areas as well as a section of the breeding area in the Sense district showed strongly structured cultivated landscapes, with the proportion of pastures being slightly higher than that of arable land. In addition, the landscapes in the images under consideration all included both relatively small fragmented forest areas and rural settlement areas.



**Figure 24** – Aerial image excerpts of (a) the breeding area and the three stopover site hotspot regions (b) at the northwestern slope of the Alps, (c) the southern central slope of the Massif Central and (d) the north of the Pyrenees. Coordinates are given in metres (EPSG:3035).

## 6.2 Determinants of stopover sites

In the following, the explanatory variables that were significant according to the generalised linear model are discussed. A detailed discussion of the non-significant variables shortest distance to railway lines as well as roads and the occurrence of Natura 2000 conservation areas, illegal landfills or composting sites is not included. However, this should not put into question their individual importance for red kites. It is well documented that anthropogenic infrastructure such as railway lines or roads lead to large numbers of fatalities (Barrientos et al., 2018), which on the one hand can represent potential food for red kites, but on the other hand also poses threats to red kites. However, the non-significance of both railway lines and roads in the model suggests that the threat at stopover sites of the investigated sample was no higher than elsewhere. Surprisingly, the occurrence of conservation areas and illegal landfills or composting sites in the stopover site areas was also not significant. The hypothesis was clear that both elements have a positive influence on the availability of food and are therefore relevant for the selection of stopover sites for red kites. However, no such relationship could be identified with the underlying sample, possibly owing to low data quality, at least for the landfills. Figure 25 of the Appendix A shows a visualisation of the distributions of all determinant data variables.

### 6.2.1 Environmental factors

The investigation of the stopover sites and the random sites showed that the area of the forest played an important role in the composition of the stopover site areas. Forest edges and groups of trees hold preferred roosts for red kites (Aebischer, 2009), which means that although they should occur at a stopover site, their share of the area does not need to be enormously large. This is shown with the decreasing probability for a site being used as a stopover site with increasing forest share. Much more relevant, especially in search for food, is the occurrence of open landscapes with rather low-growing vegetation allowing easier location of prey such as voles and invertebrates. Pastures are one such landscape fulfilling these criteria (Carter, 2001). The analysis performed in this study showed that an increasing proportion of pastures indeed favours an area to be used as a stopover site. Seoane et al. (2003) came to a similar conclusion regarding the relevance of pastures for red kites. Although they investigated the distribution of red kites in Spain and Portugal and not explicitly their stopover sites, their finding that areas with less than 30% pasture are more likely to be avoided by red kites confirm the findings of this study. It is important to note, though, that the pastures land cover class itself covers a relatively wide range of land cover types. However, a common feature of all associated land cover types is that these areas are regularly either grazed or mechanically harvested, which does not allow a natural development of the native composition of herbaceous species. The fact that the height of the vegetation changes regularly, nevertheless clearly indicates that these areas are ideal feeding areas for red kites. Since also increasing

elevation had a positive influence on the stopover site probability, it could be that similar landscape features can rather be found at higher elevations within France, depending on the region and its local conditions and land use practises. While many stopover sites in the Massif Central were identified at higher elevations, there was a clear gap with hardly any stopover sites as far as the northern foothills of the Pyrenees, although these areas north of the Pyrenees were again at much lower elevations compared to the Massif Central. The CORINE Land Cover map in the area around Toulouse revealed that this gap contained large areas of arable land and permanent crops such as fruit trees or vines and hardly any pastures, of course all land cover types that do not particularly favour foraging for red kites.

**Table 13** – The proportions of the CORINE Land Cover classes of (a) a typical breeding area within the Sense district compared to the three hotspot regions (b) at the northwestern slope of the Alps, (c) the southern central slope of the Massif Central and (d) north of the Pyrenees. A uniform area size of 8 km<sup>2</sup> was examined for the breeding area as well as for a core area of each stopover site hotspot, which correspond to the image sections in Figure 24. The area of 8 km<sup>2</sup> represents roughly the median of the stopover site areas.

CORINE LC Class	(a) Breeding area (CH)	(b) NW of the Alps	(c) Southern Massif Central	(d) North of Pyrenees
Forests [%]	7.9	7.4	17.0	12.7
Pastures [%]	–	11.2	30.9	13.5
Arable land [%]	66.0	33.5	5.3	32.1
Heterogeneous agricultural areas [%]	25.0	43.8	46.8	31.3
Artificial surfaces [%]	1.1	4.1	–	5.5
Scrub and/or herbaceous vegetation assoc. [%]	–	–	–	4.8

Looking at the proportions of the individual land cover classes of the three hotspot areas as well as the characteristic breeding area in the Sense district, it was found that these areas show similarities (Table 13). While the proportion of forest land did not exceed 20% in any case, the importance of land used for agriculture was clearly demonstrated. Pastures were found in all hotspot areas, but none in the breeding area, where the proportion of all land cover classes in connection with agricultural activities together was also very high with 91%, but no land was classified as pasture. It is possible that the different crops grown in the breeding area complement each other so well in their chronological sequence that there is always enough area available with ideal foraging conditions for the red kites. In addition, it should be noted that the land cover class heterogeneous agricultural areas may to a certain extent also include pastures, especially smaller areas, which presumably means that there is also a small proportion of pasture-like areas in the breeding area. This must be the case, as there is definitely quite a lot of pastures in the southern part of the study area within the Sense district.



### 6.2.2 Potential threats at stopover sites

The occurrence of power lines was found to have a positive effect on the probability of a location being selected as a stopover site. Therefore, there is a slightly increased threat from power lines at stopover sites, although this could also mean that the availability of food at stopover sites is increased, as red kites themselves are thought to be rarely victims of electric shocks or collisions with the infrastructure of power lines (Aebischer, 2009). However, the small differences in occurrence between the random sites (36%) and the stopover sites (39%) suggest that stopover sites in general have only slightly higher risks from power lines than other areas. However, Maciorowski et al. (2019) found that the power line infrastructure at stopover sites played the most important role as a source of mortality for juvenile red kites on their migration route. According to the generalised linear model, wind turbines had a much greater effect than power lines, which was also shown by the strongly deviating value for the mean distance to the nearest wind turbine from random sites ( $33.5 \text{ km} \pm 28.4 \text{ SD}$ ) to stopover sites ( $203.7 \text{ km} \pm 163.9 \text{ SD}$ ). However, this positive effect is certainly also beneficial for the red kite population, since according to these findings it can be assumed that stopover sites do not pose an increased risk from wind turbines. Nevertheless, wind turbines still represent a fundamental threat to red kites. Attractive areas within wind farms, such as those being mown or harvested, proved to be critical factors increasing the collision risk of red kites with turbines (Hötker et al., 2017).

## 6.3 Methodology evaluation

In the following, the methodology used in this thesis will be critically reflected upon, which should also be considered when interpreting the results.

Although the GPS transmitters were programmed to send out one location per hour, there were still some large gaps of several hours or even days within the individual data series. Furthermore, several GPS transmitters exhibited faulty behaviour and recorded a location only every three hours. These gaps in the time series as well as differing temporal resolutions have the potential to lead to biased results. On the one hand, stops potentially could not be detected because the location data was not available, on the other hand the geometric accuracy of the detected stopover site polygons suffered from lower temporal resolutions of the data. Even the maximum available temporal resolution of one hour provides only a rough estimation of stopover site shape and size, considering that a red kite can cover many kilometres during a single hour. While a higher temporal resolution and more constant data would certainly have resulted in more accurate stopover site areas being detected, the one-hour recording rate was chosen as a trade-off to gain as much consistent long-term data as possible and still meet the charging limitations of the solar-powered GPS transmitter. Furthermore, it is expected that due to some missing localisations in

time series the shape change of a 95% KDE polygon is relatively small. Hence, both the fact that stopover sites of a random selection of red kites could not be identified and the change in shape of the 95% KDE polygons are not of concern for the conclusions of this thesis. There was no systematic exclusion from the sample which could have distorted the overall picture.

However, the general need for more continuous localisation time series exists, as it would allow for further, more specific questions in the field of investigating the migratory behaviour of red kites. For example, it would be interesting to relate the number of stopover sites per individual to its fitness, age, or total migration distance, which is already possible, but only for a subsample of individuals with consistent time series during the migration periods. However, this was not the focus of the thesis. In the context of the stop detection it is also important to mention that some sites defined as roosts seem to have been located not too far from a stopover site of one and the same individual and have only fallen through the mesh due to the spatial and temporal constraints of the stopover site definition. Consequently, it is quite possible that an important stopover site was not recorded, because the red kite flew overnight to a more suitable roost further than, for instance, 4 km away, in order to return to the actual stopover site the next morning to forage. As the results indicate, about three quarters, 2975 stops in absolute numbers, of all stops identified in a first run had to be removed from the sample and defined as roosts, as they did not fully meet the definition of stopover sites. An individual analysis of these roosts would be useful for further analysis of this data set, as this could further enhance the representativity of the sample. However, due to the fact that the roosts were excluded, it is possible that a certain type of stopover site that possibly has different characteristics, was systematically excluded from the sample or only incompletely captured. Specifically, it is conceivable that there are stopover sites where the roost was further away from a part of the stopover site area that was highly suitable for foraging. As a result, it is possible that such stopover sites were systematically excluded in this study due to the methodology applied. In this context, the question arises whether it would not have made more sense to define at least the spatial constraint of the stopover site definition less conservatively, which would allow larger areas of stopover sites and thus potentially better reproduce the actual stopover site habitats used by the red kites along their migration route. However, the reason for using this restrictive spatial constraint in the definition of stopover sites can be explained by the assumption that, on the basis of this approach, only stopover sites are covered and not all small-scale, tortuous movements or even exploratory behaviour that may not have been part of a stopover site.

Even though the results show that more than 90% of the stopover site areas are smaller than 30 km<sup>2</sup>, a comparison of area sizes between the stopover sites cannot be made, because the reference bandwidth was used to estimate the kernel density for each stopover site rather than a fixed kernel across the data. Hence, a larger kernel density area does not necessarily say anything about the quality of the stopover site habitat (Boyle et al., 2009; Gregory, 2017). A possible methodology, which would

also have allowed the comparison of the areas between the stopover sites, would have been the use of minimum convex polygons, which according to [Row & Blouin-Demers \(2006\)](#) are more suitable for this purpose than the kernel density estimations. For the analysis of the spatial use of a stopover site, however, the kernel density estimation should then be applied again, whereby the smoothing parameter must be chosen so that the 95% KDE polygons correspond as closely as possible to the shape of the minimum convex polygons. However, since the main interest in this thesis was to investigate stopover site characteristics rather than to draw conclusions about their quality based on stopover site extent, the 95% KDE polygon solution was chosen. This allowed to get from the individual localisation points to a weighted surface that better reflects the use within the area than minimum convex polygons.

Concerning the determination of the random sites that served as pseudo-absence sites for the generalised linear model, it can be said that there would certainly have been other approaches than to consider the entire territory of France south of the northernmost point of Switzerland as potential stopover site habitat. Based on the knowledge that the migration routes of the Swiss red kites generally follow a southwest-oriented migration corridor between Switzerland and Spain, the randomness of possible locations could have been limited to such a corridor rather than to the whole territory as far as the Atlantic Ocean. However, it can be assumed that red kite populations from Sweden or Germany also move through areas further to the west on their migration routes, which justifies the determination of random sites in this region as well. Furthermore, in the case of the approach used in this study, it was examined whether the stopover sites throughout France differ in their large-scale characteristics and not where the stopover sites are preferably located in the area of the typical migration routes, which would have been the case if random sites within the migration path area had been determined. Nevertheless, it is important to note that the choice of pseudo-absence sites is always subject to relatively large uncertainties and involves the potential for biased results. An issue that arises when a species is declared absent from a site is according to [MacKenzie \(2005\)](#) that the species has simply not been recorded using the prescribed sampling methods. The same applies to the detection of stopover sites from trajectories, as it is not guaranteed that a random site has never been used as a stopover site by a conspecific without GPS transmitter.

Some of the data sets used to define the examined stopover site characteristics in this study should be treated with caution, as they may be incomplete or outdated. Particularly, the OpenStreetMap data is not subject to an independent verification process, such that it can only be assumed that the object classes that have been investigated (motorways, wind turbines, power and railway lines) are considered attractive to OpenStreetMap users and, therefore, have a satisfactory level of accuracy ([Girres & Touya, 2010](#)). However, more recent studies on the quality of OpenStreetMap data have pointed out that they are often even more accurate and complete than commercial data sets ([Brovelli et al., 2016](#); [Zhang & Malczewski, 2018](#)), which does not raise major concerns about the data quality of the OpenStreetMap data used in

this thesis. Furthermore, reliable and complete data sets can be assumed for the digital elevation model and the Natura 2000 conservation areas vector data set. Both data sets derive from the European Environment Agency, where they are subject to systematic data collection, with changes in conservation areas also being updated promptly. The CORINE Land Cover data sets are also subject to a systematic recording methodology and show a relatively good temporal accuracy with a new release every six years. By analysing only forest and pasture shares of the stopover site areas, the issue of the minimum mapping unit of 25 hectares of the land cover data set could partly be avoided, as forest and pasture are usually relatively large areas, and should therefore be well reflected in the data set. The data set, which is most questionable in terms of completeness, spatial accuracy and actuality, is certainly that of the illegal landfills and composting sites. However, since no data set of better quality was available, it was necessary to make the best of the existing one, as red kites indeed like to forage around landfills, and ignoring this factor completely could have added bias to the overall results. Even in 21st century Europe, it can be assumed that illegal landfills have not yet completely disappeared. However, their documentation might not be a priority for the authorities, and getting accurate data could also be challenging due to the sensitivity of the subject matter. Furthermore, the publication of such data may be undesirable from the perspective of potential imitation of the offence.

It is certainly possible that the random selection of pseudo-absence site locations, where it cannot be excluded that they never served as stopover site habitat of red kites, as well as the incomplete detection of stops from the movement data trajectories in general had an influence on the quality of the informative value of the generalised linear model, as the parameter estimates may be biased (MacKenzie, 2005). While it is true that in the present case it would have been methodologically feasible to determine actual absence sites by determining true stopover sites and true absence sites along the movement data trajectories of the individual birds, this would have answered another question. Namely, how the characteristics between stopover sites and non-stopover sites differ within the migration path of red kites. Therefore, the chosen approach is considered to be a good approximation of the actual absence sites, with the aim of studying the determinants of stopover sites on a large scale. Given the relatively large sample size of both 792 random sites and stopover sites, the model results can furthermore be considered robust overall (Korner-Nievergelt et al., 2015).

## 6.4 Conclusion

### 6.4.1 Contributions

The findings of this thesis suggest that hotspot areas of particular value for red kite stopover site selection can be clearly identified, as stopover sites of migrating Swiss red kites were not evenly distributed between Switzerland and Spain. On the contrary, the identified stopover sites were located mainly in three hotspot regions: (1) at the northwestern edge of the Alps 20 km west of Chambéry, south of the narrows between the Alps and the Jura, (2) in the Massif Central with especially high densities north of the Cévennes and south of the Aubrac high plateau and (3) at the northern foot of the Pyrenees, mainly to the southwest of Toulouse. Both between the hotspot at the northwestern edge of the Alps and the Massif Central, and between the Massif Central and the hotspot north of the Pyrenees, gaps were found with only very few identified stopover sites. Thus, all these identified hotspot areas of the stopover sites represent target areas of great importance for conservation measures to reduce the anthropogenic mortality threat during migration such as accidents, illegal poisoning or poaching.

The analysis of characteristics of the stopover sites showed on the one hand that a high area share of pasture is clearly preferred. On the other hand, an ideal stopover site landscape of red kites should contain a small proportion of forest areas that allow overnight stays in the same area. With regard to the elevation of the stopover sites, it was found that, although this varied greatly depending on the region, there was a general trend towards higher elevations at stopover sites. This is probably related to the fact that, depending on the region, preferred stopover site habitat with similar landscape features exists at different elevations. In France, however, they are more likely to be found at higher elevations than other agricultural landscapes. Furthermore, similarities between landscapes of the three hotspot regions among each other and the breeding areas in the Sense district were shown. Stopover site habitat should therefore, in addition to the requirement for pasture land, preferably include strongly structured agricultural areas, which are presumably farmed in a crop rotation regime and are surrounded by smaller rural settlements.

Concerning the occurrence of threats at stopover sites from infrastructure facilities it was shown that power lines are only slightly more likely to be at or near stopover sites than elsewhere within France. Wind turbines were even located at a much greater distance from the stopover sites than from the random sites. On the basis of the findings of this thesis, it can therefore be assumed that red kites are not exposed to significantly greater threats at stopover sites due to human infrastructure.

### 6.4.2 Limitations

The conclusions of this thesis are based on a specific population of red kites from the Sense district. Therefore, they may not be fully applicable to other populations

and should be applied in this awareness, nevertheless it is not to be expected that other populations, such as red kites with breeding areas in Germany, will select stopover sites based on other characteristics. For this reason, the findings can certainly provide a good insight into the overall red kite migration through the area under investigation, and any measures to protect the identified stopover site habitats will certainly benefit other red kites.

The lack of existing previous studies in the field of investigating stopover site habitats of migrating birds of prey based on GPS movement data had a limiting effect on the foundation of the underlying research and was challenging, especially with regard to developing the methodology.

### 6.4.3 Outlook

The focus of this thesis was the investigation of stopover site habitats during the autumn migration period. However, at the beginning of spring, red kites migrate the entire distance from their winter habitats in Spain or southern France in the opposite direction back to their breeding grounds in the north. To investigate whether the important areas to stop during autumn migration are also used during spring migration might be interesting, leading to a more complete picture of the stopover site habitats. According to [Carter \(2001\)](#) it is known that red kites in spring generally seek to return to their breeding areas as quickly as possible to re-establish territories, which may indicate that red kites make fewer stops during spring migration. However, little is known about whether and to what extent the selection of stopover site habitats differs between autumn and spring migration due to these altered circumstances.

In order to ensure the best possible and most efficient conservation of stopover site habitat of red kites, it would be desirable to have a better knowledge of the functions of the individual stopover sites. This could be achieved, in particular, by including environmental data such as weather data in the analysis. Of course, a stopover site visited due to bad weather is not *per se* less important for the conservation of red kites. However, functional groups of stopover sites, such as shelter during bad weather or recovery after passing a geographical barrier, could be used to classify the importance of the stopover sites in more detail, thus promoting more selective protection of particularly valuable and important habitats. For this purpose, one could also look at which sites are frequently visited by different individuals during a migration period, but also over several years, or for how long a site usually serves as a stopover site, which could further provide information about the quality of a stopover site habitat. On the basis of such an in-depth analysis of the elementary characteristics of stopover sites, a suitability map for stopover site habitat could then be generated for a larger geographical scope using the information obtained, which could be made available for use by local nature conservation organisations and local authorities.

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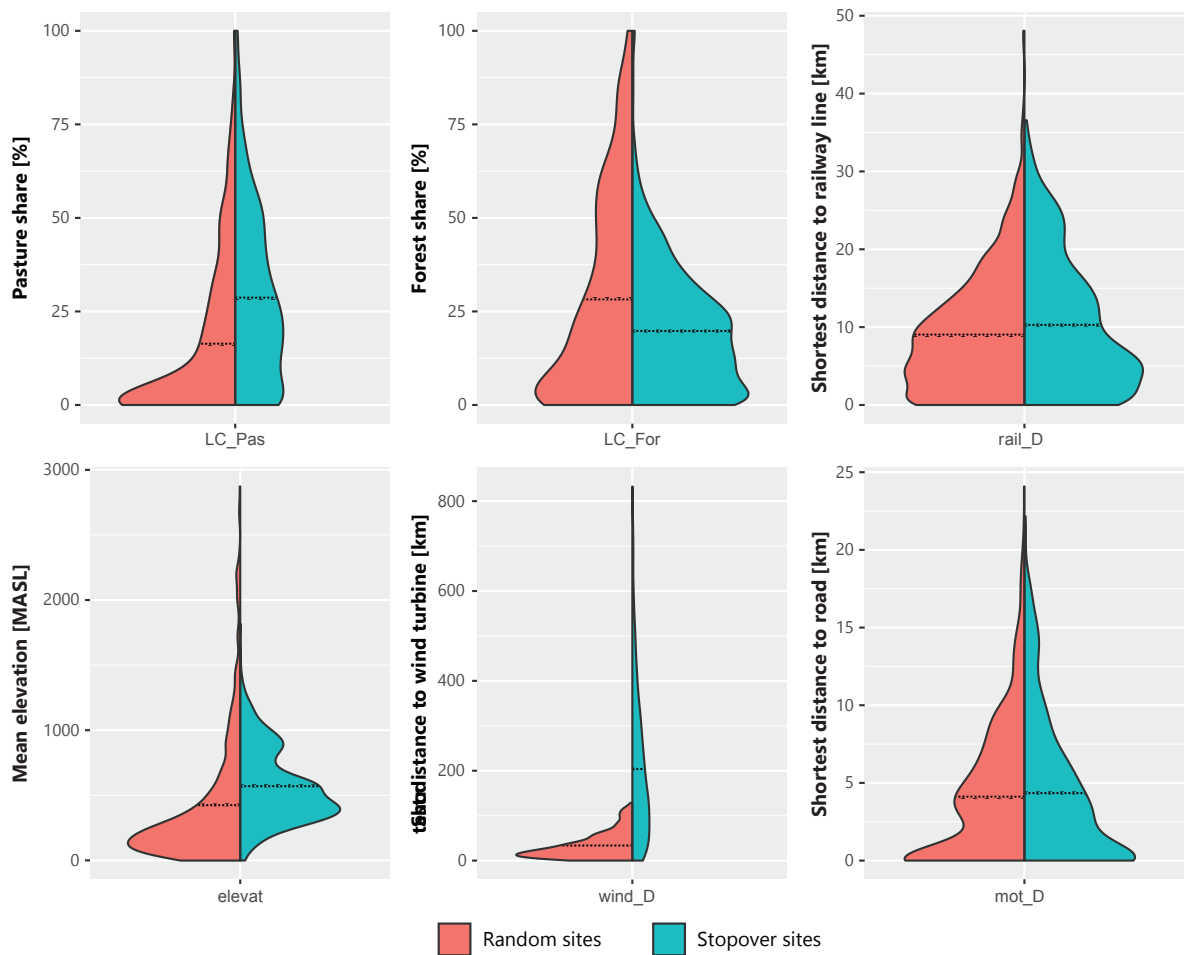
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# Appendices

## Visualisation of the determinants data

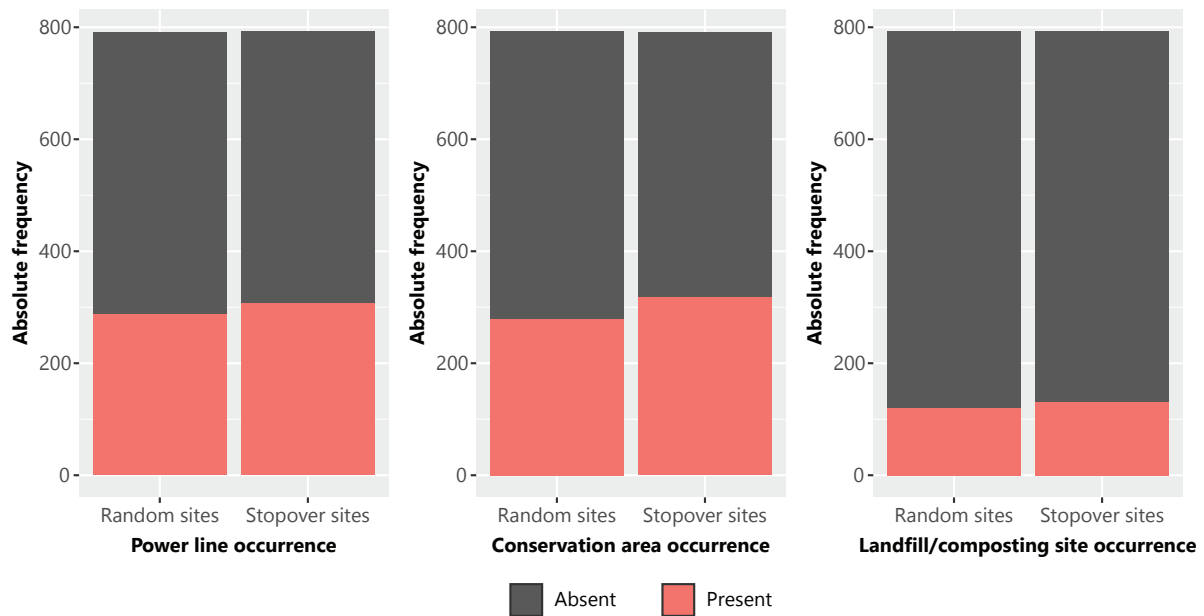
### A.1 Numeric determinants



**Figure 25** – Data on the numeric site determinants for both the random sites (N = 792) and the stopover sites (N = 792). Mean values indicated by dotted lines.



## A.2 Binary determinants



**Figure 26** – Overview of the binary determinants for both the random sites (N=792) and the stopover sites (N=792). For all three binary determinants, it can be observed that they occur somewhat more frequently at stopover sites compared to the random sites.

## Generalised linear model output

```
Call:
glm(formula = trueStop ~ scale(LC_Pas) + scale(LC_For) +
scale(rail_D) + scale(elevat) + pow_L + natu_L + scale(wind_D) +
scale(mot_D) + land_L, family = "binomial",
data = stopsSummaryStatistics)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.42636	-0.55618	-0.07715	0.26620	2.80068

Coefficients:

Estimate	Std. Error	z value	Pr(> z )
(Intercept)	1.20754	0.16475	7.329 2.31e-13 ***
scale(LC_Pas)	0.57914	0.07837	7.390 1.47e-13 ***
scale(LC_For)	-0.46875	0.08845	-5.300 1.16e-07 ***
scale(rail_D)	-0.06087	0.08617	-0.706 0.47993
scale(elevat)	0.47503	0.07167	6.628 3.40e-11 ***
pow_L	0.46197	0.16223	2.848 0.00441 **
natu_L	-0.08021	0.16543	-0.485 0.62777
scale(wind_D)	4.56071	0.27863	16.368 < 2e-16 ***
scale(mot_D)	-0.05948	0.08520	-0.698 0.48515
land_L	0.09103	0.20512	0.444 0.65719

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 2195.9 on 1583 degrees of freedom  
Residual deviance: 1065.6 on 1574 degrees of freedom  
AIC: 1085.6

Number of Fisher Scoring iterations: 7

## 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.

*Zurich, 30 April 2020*  
Place, date



Signature of the author