Modeling the migration behavior and exploring the age-structured migratory connectivity of red kites (Milvus milvus) across the species' global range

GEO 511 Master's Thesis

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Abstract

Migration is a crucial part of the annual cycle for billions of animals. Understanding migratory connectivity (i.e., how breeding populations redistribute in space over the annual cycle) is essential to illuminate the intricate relationships in how migrating organisms link ecosystems and species across the globe and to inform evidence-based local and global conservation efforts. Most studies investigating migratory connectivity assume that no subgroups exist within populations, i.e., that populations mix randomly. Yet, many populations have sex or age-specific subgroups that differ in their migratory behavior, a phenomenon called differential migration, which is predicted to affect migratory connectivity.

Here, this rarely studied prediction is revised using a GPS movement dataset of unprecedented size and geographic coverage to derive a range-wide assessment of age-structured migration patterns and migratory connectivity in the red kite, a raptor species endemic to Europe. Daily GPS locations of 2440 complete annual cycles representing 1619 red kites were analyzed to identify age-specific migration strategies and links between breeding season and overwintering locations across the species' global range. By combining a novel continuous space Bayesian regression approach with a recent range-wide abundance map, five key results are derived:

First, calculations revealed that an estimated 54.4% of the total adult population is migrating to the western wintering grounds, while only 1.3% is migrating to the eastern wintering grounds and the remaining 44.4% remained resident throughout the annual cycle. Second, large variations in the migration strategies of individuals were found between breeding sites but also within a breeding population. Third, migration strategies of individuals changed with age, with younger birds generally showing a higher migration probability than adult birds. Importantly, the strength of this age-dependent differential migration varied substantially across the species range. Fourth, as predicted, migratory connectivity varied with age, with young birds exhibiting higher migratory connectivity (0.34) than adults (0.25). Hence, migratory connectivity of red kites was rather low. Fifth, a migration divide was discovered in eastern Europe, with migration distances to western wintering grounds being significantly longer than to eastern wintering grounds.

As one of the first studies, the effects of differential migration on migratory connectivity across an entire species range were empirically documented within this thesis. By analyzing this massive movement data set of one species, new insights into the overwintering and migratory behavior of red kites throughout the species' global range could be gained, thus helping to enhance the conservation of this bird species.

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1. Introduction

1.1. Motivation

Over the past decades, migratory birds have shown negative population trends (Rushing et al., 2020; Sanderson et al., 2006). Migration is a diverse behavior of repeated directed seasonal movements from the breeding to the non-breeding area and vice versa, often triggered by resource pulses (Fudickar et al., 2021; Marra et al., 2019). Until recently, there was a strong bias in research on migrating animals toward the breeding area (Marra et al., 2015). However, for instance, habitat degradation in the non-breeding area negatively affects the reproduction of birds in the breeding area (Kramer et al., 2018). Hence, there are seasonal interactions, whereby circumstances within one period of the annual cycle influence events or characteristics in a subsequent period. These seasonal interactions affect the population dynamics of migratory species (Webster et al., 2002). Thus, to understand the population dynamics of a species, migratory animals must be examined over their entire annual cycle, which means understanding the connections between the breeding season, the non-breeding season, and the migration routes (Marra et al., 2019). Migratory connectivity describes the individuals' and populations' spatial and temporal linkages between seasons resulting from migratory movements (Cohen et al., 2018: 514). Understanding the migratory connectivity is essential to assess the impact of, e.g., environmental changes on the species, be it from an ecological, evolutionary, or conservation perspective (Knight et al., 2018; Marra et al., 2019). As billions of animals migrate between their breeding and non-breeding grounds each year, crossing national borders, developing effective conservation strategies is a major challenge (Knight et al., 2018). Recent technological advances have made it possible to use long-lasting and relatively small GPS sensors to obtain highly accurate spatial and temporal locations of animals. These advances are the prerequisite for accurate and comprehensive migratory connectivity research.

Many studies assume that individuals of populations mix randomly. However, in many species, demographic subgroups of a population migrate separately or spend the nonbreeding season apart (Cristol et al., 1999). This phenomenon is described as differential migration, with the most common subgroups being gender and age. (Briedis & Bauer, 2018). Differential migration may cause demographic-specific vulnerability across the annual cycle, resulting in subgroup-specific mortality and thus affecting population dynamics. (Briedis & Bauer, 2018). Hence, environmental perturbations may affect population dynamics when a particular demographic group is exposed (Briedis & Bauer, 2018). Therefore, if young birds migrate differently than older birds and have a dissimilar mortality rate due to, for example, changing environmental conditions, there will be an effect on the breeding population with some delay. Whenever differential migration is identified, conservation actions should also be tailored to particularly vulnerable demographic subgroups to be most effective (Briedis & Bauer, 2018). As of now, how differential migration is affecting migratory connectivity has not been studied over a large area. Among the reasons is that young birds are usually not marked because failure rates are high and return rates are low, so the costs are correspondingly high. In this study, this problem was circumvented by collecting a vast collaborative data set on a study system with comparatively low juvenile mortality, combined with tracking sensors that did not require animals to be recaptured for data replication.

The red kite (*Milvus milvus*) is a medium-large bird of prey endemic to Europe. While the global population has declined in recent decades due to increased mortality, with poisoning as the primary cause (Aebischer, 2009; BirdLife International, 2022; Knott et al., 2009; Mateo-Tomás et al., 2020; Mattsson et al., 2022), the breeding population has recovered and increased again in recent years (Aebischer & Scherler, 2021; BirdLife International, 2022). Single-population studies indicate that red kites exhibit a diverse migratory behavior. While many northern birds are migrating to southwestern Europe (García-Macía, De La Puente, et al., 2022; García-Macía, Vidal-Mateo, et al., 2022; Maciorowski et al., 2019; Spatz et al., 2022), others migrate to southeastern Europe (Literák et al., 2018, 2019; Panter et al., 2020, 2022) or remain resident year-round (Heredia et al., 1991). The phenomenon in which some individuals of a population migrate while others remain resident throughout the year is called partial migration (Hegemann et al., 2015). Thus, the red kite is considered a partial short-distance migrant.

Recent studies have examined red kite migration routes and showed high variabilities of the red kites' migration behavior. However, all migration studies have focused on small sample sizes of specific populations (García-Macía, Vidal-Mateo, et al., 2022; Literák et al., 2022; Maciorowski et al., 2019), ignoring the comparison of the migration strategy over large breeding ranges. Currently, neither the spatial variation in the red kites' migratory behavior nor the migratory strategies of any bird species have been studied continuously across the breeding range. Evidence was found that age influences the migratory behavior of red kites since the migration distances, timing, and duration were dependent on the birds' age (García-Macía, Vidal-Mateo, et al., 2022; Literák et al., 2022). Thus, the migration strategies of red kites may vary spatially with the breeding site, and differential migration could potentially occur due to age. Whether, where, and how age affects the red kites' migration strategy remains unexplored. Further, age-dependent migration strategies would imply differential migration and have significant implications for the red kite ecology.

Quantifying the migratory connectivity of species is of great importance (Marra et al., 2019), so the hitherto unexplored migratory connectivity of the red kite needs to be assessed. Consequently, differential migration triggered by age groups would be expected to affect the migratory connectivity of a species. Thus, migratory connectivity must be approached from an age perspective. In this thesis, the age-structured spatial aspects of migration strategies and migratory connectivity of red kites were examined in detail to increase the understanding of the diverse migration behavior of red kites. This thesis aims to determine the migratory connectivity across different stages of the annual cycle to better assess the impact of habitat changes, such as climate change, on the red kite population and to enable effective conservation measures in the future. This in-depth analysis was made possible by compiling a unique dataset of tracking data for one bird species distributed over nearly the entire species' range.

1.2. Research questions and hypotheses

According to the research gaps described in the previous section, this master's thesis looks at the age-structured migration strategies and the migratory connectivity of red kites across the species range.

Research question 1: *How does the migration strategy of red kites differ with their breeding season location and age?*
Previous studies showed a diversity of overwintering strategies, such as full-year residents and migration to western and eastern wintering sites. However, where and with what probability red kites follow a particular migration strategy and what influence age has on the choice of migration strategy has not yet been investigated over the breeding range. The migration strategy of an individual is expected to depend on the location of the breeding season and on the birds' age.

Research question 2: *What is the age-specific migratory connectivity of red kites between breeding sites and wintering sites?*
For the first time, the migratory connectivity of the red kite is evaluated and in addition it will be assessed whether age affects the migratory connectivity. As red kites are expected to have large intra-population variability in migration strategies, migratory connectivity is expected to be relatively low. In addition, migratory connectivity is expected to vary with bird age, since some migration characteristics differ between younger and older birds.

2. Theoretical Background

2.1. Movement ecology

2.1.1. Movement ecology and migration

Organisms moving from one place to another is a fundamental feature of life (Nathan et al., 2008). Movement can be described as the position of an object over successive points in time (Dodge et al., 2008). Further, movement ecology deals with the central question of why, how, when, and where animals move by looking at the internal state, the motion capacity, the navigation capacities of the individual, and external factors affecting the movement (Nathan et al., 2008). Animal movement consists of internal and external factors interacting on different spatio-temporal scales and is caused by physiological and environmental changes (Brum-Bastos et al., 2022; Nathan et al., 2008) due to the strong dependency on habitat and resource availability (Newton, 2007; van Bemmelen et al., 2019). Capturing animal movements through tracking devices is one approach to quantifying movements. Recent technological advances are providing new opportunities for animal tracking, which has led to a tremendous increase in tracking data and is about to revolutionize the knowledge of animal ecology (Kays et al., 2015). Not only is the sheer volume of tracking data increasing, but equally important, spatial accuracy and temporal resolution are also increasing.

An important subfield of movement ecology is the study of animal migration, firstly because it covers large spatial and temporal scales and secondly because the animals are particularly endangered during migration. Migration is a diverse behavior found in many animal species, such as mammals, fishes, and birds (Fudickar et al., 2021; Marra et al., 2019). As a term, migration mainly refers to a movement from one area to another, often triggered by resource impulses and commonly involving a return to the point of origin (Fudickar et al., 2021). Or more specifically, migration can be described as a repeated directed seasonal movement from the breeding to the non-breeding area and vice versa (Marra et al., 2019). Research on animal migration within movement ecology has gained a substantial increase in interest (Fudickar et al., 2021). Severe environmental changes significantly impact a species' distribution, behavior, and interactions (Walther et al., 2002). Since migration occurs over large areas and is triggered by resource availability, the whole system is susceptible to change. This also applies to migratory birds, whose survival rate and population dynamics are affected by changing environmental conditions, raising concerns about the effectiveness of current species conservation (Franklin et al., 2022). The effects of ecological changes on the migratory system are still largely unresolved, which is the main challenge for conservationists (Franklin et al., 2022). Understanding animal migration and, thus, the cyclical movements of individuals between different sites throughout the annual cycle is challenging yet essential for effective conservation (Vickers et al., 2021).

2.1.2. Migratory connectivity

A thorough understanding of the biology of any animal requires knowledge of how events interact at different stages of the annual cycle, on both an individual and population level (Webster et al., 2002). The concept of migratory connectivity was introduced to describe the degree to which individuals from different breeding areas mix in the nonbreeding areas, whereby migratory connectivity ranges from weak to strong (Webster et al., 2002). The strength of migratory connectivity has implications on the population dynamics and knowledge of the migratory connectivity of a species, thus enabling effective conservation measures. Low migration connectivity often indicates strong mixing between populations (Finch et al., 2017). For a species with an extensive distribution and weak migratory connectivity, changes in the availability or quality of nonbreeding habitats have diffuse but far-reaching effects on a species' breeding populations (Finch et al., 2017; Taylor & Norris, 2010). Strong migratory connectivity implies that individuals have population-specific wintering areas, and thus little mixing occurs. Therefore, individual populations are also more vulnerable if the quality of the wintering area deteriorates, as a large proportion of individuals are affected.

Hence, studies in migratory connectivity depend on knowing where individuals of different populations are in their annual cycle. The phases of the annual cycle, such as breeding, migration, and overwintering, are connected for migrating animals but are mostly poorly understood (Marra et al., 2006). The information about the bird locations can come from different sources, such as ringing, feather isotope analysis, light-level geolocators, or GPS and GSM tracking technologies (Marra et al., 2019). With GPS sensors becoming lighter and cheaper over the past few years, they enable more comprehensive studies with high spatial and temporal resolution (Marra et al., 2019). At the same time, the amount of tracking data collected is increasing each year, further driving research on migratory connectivity.

Many studies analyzed how migration routes and the timing varied between different populations and their impact on migratory connectivity (Bauer et al., 2016; Briedis et al., 2020; Briedis & Bauer, 2018; Trierweiler et al., 2014). Migratory connectivity can also be studied by comparing, for example, the longitudes of the breeding area, the sea crossing, and the wintering area of different populations (Trierweiler et al., 2014). Most studies evaluated the strength of migratory connectivity of a species by performing a Mantel correlation test (r_M) on a pairwise distance matrix from the breeding and wintering site of individuals (Ambrosini et al., 2009). The Mantel correlation coefficient has values between −1 and +1, where a strong positive r_M indicates that close-by breeding individuals also tend to spend the non-breeding season nearby and vice versa. Finch *et al.* (2017) examined the population spread and inter-population mixing of land bird migrants of 98 populations from 45 species. They figured migration strategies based on determinism are ineffective due to the high population spread (Finch et al., 2017). Cohen *et al.* (2018) extended the often-used Mantel correlation method to measure the strength of migratory connectivity with population-specific transition probabilities, supporting uneven sampling by including the breeding bird abundance. Since not only the geographical locations are essential, but also the temporal aspect of the locations, the concept of migratory connectivity was extended by the temporal aspect (Bauer et al., 2016). While most studies only compare breeding and wintering sites in the context of migratory connectivity, Knight *et al.* (2018) built a migratory network across the annual cycle. There are two crucial spatial components to migration connectivity; "population spread" refers to the extent to which individuals of a single breeding population disperse during the non-breeding season, while "interpopulation mixing" on non-breeding sites refers to the extent to which individuals from different breeding populations mix (Finch et al., 2017).

The sampling strategy usually describes the spatial distribution of tagged individuals of a species for a particular study. Sampling strategies have an impact on migratory connectivity. Vickers *et al.* (2021) have extensively studied the bias of the sampling strategy on the Mantel correlation coefficient. As such, the strength of migratory connectivity is underestimated when global connectivity of a species is analyzed based on sampling in spatially limited sub-areas (Vickers et al., 2021). Further, a sample size of less than 100 significantly affects migration connectivity, whereas a sample size of 1000 makes the error negligible (Vickers et al., 2021).

2.2. Red kite ecology

The red kite (*Milvus milvus*) is a medium-large bird of prey whose global range is restricted to Europe. Despite the low weight of about 1 kg, their wingspan can reach more than 1.5 meters (Aebischer & Scherler, 2021). Their primary color is rusty brown, with the head standing out from the rest with its light color (Aebischer & Scherler, 2021). The tail is narrow at the base, broader towards the back, and the bifurcation at the end is typical for red kites. They can circle for hours with their narrow, long wings, constantly twisting their long, forked tail. Red kites nest in tall trees, preferably on forest edges or in field copses (Aebischer & Scherler, 2021). They are food opportunists, with a diet ranging from small mammals to birds and carcasses (Aebischer & Scherler, 2021). Red kites inhabit richly structured landscapes with open land and forest.

In the wild, red kites can live up to 29 years, with an average life expectancy of just over three years (Pfeiffer, 2009; Scherler, 2020). Breeding usually begins between the second and fourth year of life, although most birds have their first brood by the age of three (Aebischer & Scherler, 2021; Mougeot et al., 2011).

Figure 1: The red kite © Marcel Burkhardt

Red kites show a wide variety of overwintering strategies. While most northern birds migrate to the South for overwintering, some individuals stay resident all year round. The annual cycle of migrating red kites can be split into four phases: breeding, autumn migration, overwintering, and spring migration. In contrast, resident birds do not exhibit the migratory phases. The breeding phase begins with nest building around March, then the eggs are usually laid and incubated in March and April until the chicks hatch after 31 days (Mougeot et al., 2011). Chicks typically fledge around June and early July after 47 to 60 days of age (Aebischer & Scherler, 2021; Mougeot et al., 2011). Red kites migrate toward their wintering sites between August to November. From November to January, red kites spend their winter at the wintering grounds before migrating back to the breeding grounds in late January and February.

Red kites inhabit large parts of the European continent, breeding in almost 30 countries from Portugal to the Baltic countries (*Figure 2*). The global breeding population is estimated to be between 33’500 and 39’000 breeding pairs (Aebischer & Scherler, 2021). The largest breeding populations are in Germany, Great Britain, Sweden, Switzerland, France, and Spain, accounting for about 90% of the red kite population. (Aebischer, 2009; Aebischer & Scherler, 2021). While the global population decreased in the past decades due to persecution and poisoning, the global population stabilized and has increased again in the last few years. (Aebischer, 2009; Aebischer & Scherler, 2021; BirdLife International, 2022; Mattsson et al., 2022). Other essential factors of red kite mortality are collisions with power lines, vehicles, and wind turbines, illegal hunting, habit loss, and reduced availability of human-mediated food (Mattsson et al., 2022). The increase in population size was partly due to successful reintroduction (e.g., Scotland and southern England) (Evans et al., 1999; Stevens et al., 2020) but also due to an increase in breeding density (e.g., Switzerland) (Aebischer & Scherler, 2021; Knaus et al., 2018). A project is currently in progress to study red kite mortality in numerous breeding and wintering areas (LIFE EUROKITE, 2021). Various actions have been taken to protect the red kite across different scales of its range, especially to mitigate the major threats such as poisoning and collisions (Mattsson et al., 2022). Recently, the red kite conservation status was updated from “near threatened” to “least concern” in response to the recovery of the global breeding population (BirdLife International, 2022).

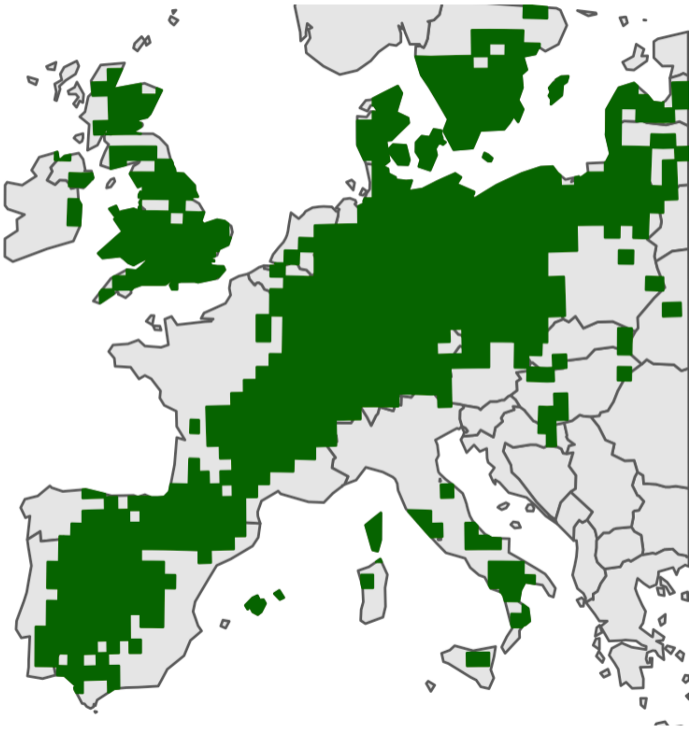

Figure 2: Breeding range of red kites, provided by the European Breeding Bird Atlas (Keller et al., 2020).

Red kites exhibit a great intra-specific variability of migration strategies. Different migration strategies can occur within a red kite population so that year-round residents exist alongside migratory animals, known as partial migration. The migration of birds can be primarily divided into two main migration routes: the western and eastern migration routes. In the fall, most northern birds migrate southwest to their wintering sites in southern France and the Iberian Peninsula (García-Macía et al., 2021; Panter et al., 2020). However, some birds are also known to migrate southeast to Italy, Greece, and the Balkans (Literák et al., 2018, 2019; Maciorowski et al., 2019; Panter et al., 2020). Yet, how migration behavior differs within the breeding range has not yet been studied.

3. Data sets and preprocessing

3.1. Movement data

The Swiss Ornithological Institute started to equip red kites with GPS transmitters in the scope of an ornithology research project in 2015 and steadily increased the number of tracked individuals. At the same time, several independent institutions and volunteers in many other European countries have started to equip red kites with GPS trackers so that tracking data of almost the whole species' global range is available. Although each organization has tagged red kites for different scientific purposes, the data can still be used in the field of migratory connectivity. Movement data were collected by solar-powered GPS telemetry devices placed on the animals' backs. The GPS telemetry devices record the location of an individual as longitude and latitude position, the corresponding timestamp, the animal identification, and an event identification (*Table 1*). Moreover, reference data about the bird's characteristics, such as its sex, age, and deployment time, were available (*Table 2*).

As the red kite tracking data were collected and stored independently by the various organizations, the data import also needed to be handled separately for each data set. Some organizations store their data in the Movebank data repository (movebank.org), which is an online database of animal tracking data. The `move` R-package was used to access the Movebank data. Other institutions use Anitra (app.anitra.cz), another platform for animal movement data. Anitra provides a python API for downloading the movement data, which was modified to serve our purpose. Further, some tracking data are stored in databases or were supplied as CSV files. Thus, the different data sources were combined into one data set of movement data and one reference data set. Since some animals occur on multiple datasets, duplicates were replaced during data processing.

Table 1: Relevant attributes of the movement data records.

Event-ID	Timestamp	Longitude	Latitude	Animal-ID
1205567	2017-06-25 17:05:01	46.26137	7.25535	1392936313
1205568	2017-06-25 18:00:10	46.28137	7.25531	1392936313
1205569	2017-06-25 19:01:02	46.28152	7.25627	1392936313

Table 2: Relevant attributes of the reference data of red kite animals.

Animal-ID	Age of deployment	Sex	Date of deployment	Study-ID
1392936313	Juvenile	m	2017-05-22	Vogelwarte Sempach
RK_1285	Adult	f	2019-05-17	Life Eurokite
Laga_01_AUKO	Immature	unknown	2020-05-29	TBRaab Telemetry

The temporal resolution of the movement data varied depending on the research focus of the organization that tagged the birds. Most devices are not active during the night to save energy. Due to technical problems or empty batteries, the tracking devices may not send data for a certain period, especially in winter, or may fail completely. The movement data was aggregated to one location per individual per day, which has been done in other migratory connectivity studies to standardize the data (Phipps et al., 2019). Thus, the last location per individual per day was taken due to the expectation that in case of territorial behavior, the individual would be more likely to be located at its roost at the last daily GPS point and therefore helps identify the breeding location.

Most of the birds were tagged during the breeding season. However, some birds were tagged in the winter, especially in the main wintering region, Spain. Since this thesis focused on the birds' migration behavior in relation to their breeding sites, birds tagged in winter would have influenced the sampling strategy and caused a bias in the data. Consequently, birds equipped with tracking devices outside of the breeding season were excluded from the dataset.

The first birds were tagged in the spring of 2009 and the last data used was from February 2022 (*Table 3*). The initial data set consisted of 1'630 tracked birds. 610 red kites were excluded because their age was unknown, they were tagged during winter, or the sensor stopped transmitting before the first winter, either due to technical failures or because the animal was deceased. Thus, the remaining 1'020 individuals were used in this thesis. Roughly 80% of the red kites were tracked as nestlings. Thanks to the fact that so many different institutions contributed the tracking data, birds have been tagged over large parts of the breeding area (*Figure 3*).

Table 3: Overview of the movement data set.

Temporal timespan of tracking data	7. March 2009 to 28. February 2022
Daily location data	850'603
Total number of tagged individuals	1'630
Number of individuals with at least one full annual cycle	1'020
Number of annual cycles	
- Birds at first year	846
- Birds at second year	446
- Birds at third and later years	1'148
- Total	2'440

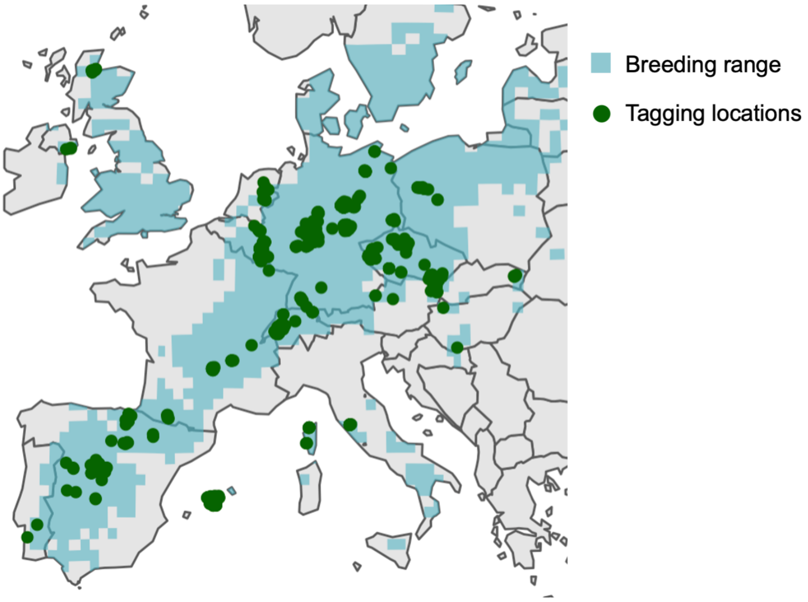

Figure 3: The spatial distribution of the red kites' tagging locations. A green dot represents an individual's tagging location, whereby only the locations are shown of birds that were used in the analysis. Because multiple birds were tagged at some places, the circles may overlap. The blue area represents the red kites' breeding range.

3.2. Abundance data

The European breeding bird atlas 2 (EBBA2) defined the species range and produced an estimate of breeding bird abundance based on country-specific estimates at a 50x50 km resolution (Keller et al., 2020). In this thesis, the raw numbers reported by the countries were used to calculate a more accurate breeding pair estimate. Each cell consisted of a cell id, the country, and the abundance class (A, B, C) corresponding to the minimal and maximal number of breeding pairs (1-9, 10-99, 100-999). In addition, some countries had reported the breeding populations more accurately, so a more specific minimum and maximum breeding pair number per cell was available. About one-third of all cells had more accurate breeding pair abundance estimates. Those without specific information showed a relatively large range of abundance, especially cells of class C, with a wide range from 100 to 999. If a grid cell represented territories of multiple countries, then the countries individually estimated the abundance of their sub-area.

To obtain a more accurate estimate of breeding pair abundance than just the abundance class, the following procedure was conducted. First, the abundance of cells with specific minimum and maximum values was computed by averaging the minimal and maximal abundance. Second, the abundance was calculated for cells of classes A and B without specific abundance estimates by averaging the minimal and maximal values of the abundance class (1-9, 10-99). And last, the abundance of the remaining cells (cells of class C with no specific abundance estimates) was calculated. Hereby, the abundance of the already estimated cells was summed up and subtracted from the total number of breeding pairs (35,000) and divided by the number of missing cells resulting in a single value representing the breeding pair abundance of class C cells without specific abundance data. Thus, the value was then assigned to the cells that were still undetermined. Last, if a grid cell had data from multiple countries, they were combined based on the cell ID.

Applying this procedure to the abundance data ensured that total abundances were distributed throughout the species' range and corresponded to the total number of 35,000 estimated breeding pairs. (*Figure 4*). Further, each cell got an abundance value representing breeding pair estimation as accurate as possible.

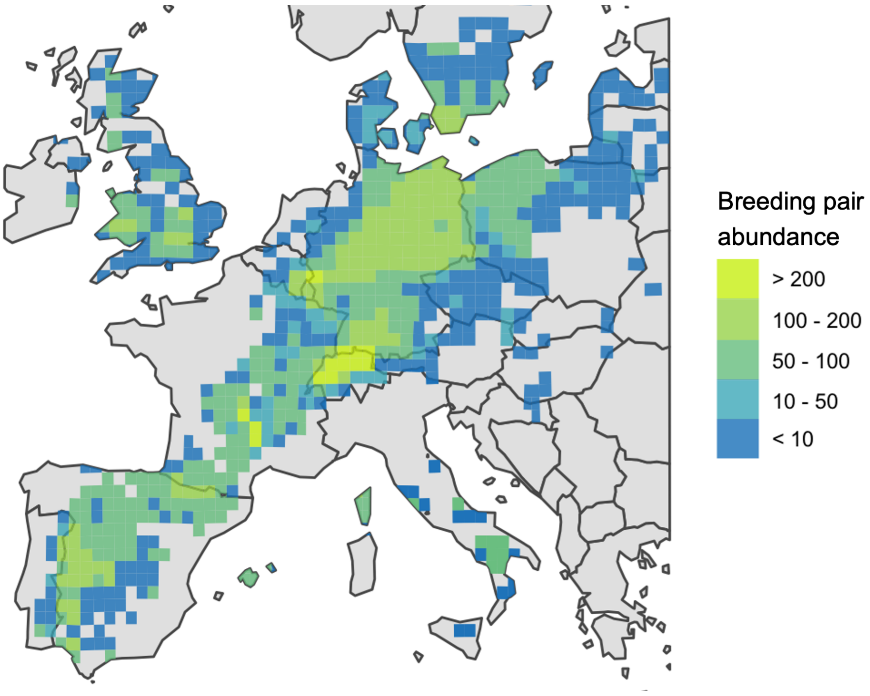

Figure 4: Estimated breeding pair abundance. High breeding pair abundance were found in Spain, France, Switzerland, Germany, the British Isles, Luxembourg, Belgium and Sweden.

4. Methods

4.1. Extraction of the annual breeding season and wintering locations

4.1.1. Splitting into annual cycles

The annual cycle of migrating red kites starts with the breeding phase, followed by fall migration and associated wintering, and ends after the spring migration. This thesis attempted to determine the migratory behavior of red kites based on breeding season and wintering locations per annual cycle. Consequently, the annual cycles were separated after the wintering period so that one annual cycle included both the breeding and wintering seasons. Since the earliest evidence of red kite oviposition was found in late February (Mougeot et al., 2011), tracking data for individuals were divided into separate annual cycles in mid-February. Thus, each annual cycle represented a bird at a particular age stage, so the corresponding bird age was assigned to each annual cycle. Red kites are usually accounted for as juveniles in their first year, immatures in their second year, and adults in their third or later year since they typically start to breed at the age of three (Aebischer & Scherler, 2021; Mougeot et al., 2011). In most cases, bird age at tagging was reported in age classes (juveniles, immatures, and adults) because the exact age of adult birds often could not be accurately determined. Thus, the birds' age of the respective annual cycles was also classified into these categories, even if the effective age would be precisely known, e.g., birds tagged as nestlings. However, combining all adult birds into one age class also solved the problem of insufficient data for old birds, as there were much fewer tracking data available for older birds. The average duration of tagging was 565 days per bird. The specific years (e.g., 2016, 2017) were not taken into account because, firstly, the difference between particular years was not the focus of this research. Secondly, without differentiating the years, more data was available to analyze the different age groups. Birds with no information about their age were excluded from the study since the primary goal of this thesis was to reveal age-structured migratory connectivity.

4.1.2. Detection of the breeding season and wintering locations

Next, the breeding season and wintering locations for each annual cycle should be derived. Multiple studies focused on extracting the nest sites based on telemetry data (Picardi et al., 2020; Schreven et al., 2021). However, this thesis did not intend to determine the nest location but rather the primary site of the individual during the breeding season since non-breeding adults and immature birds did not have nests. Thus, the term breeding season location was used in this context. However, the nest location and the extracted breeding season location should match spatially for breeding birds. Many migratory connectivity studies identified the summer and winter locations simply by the first and last point of the migration route of each individual (Phipps et al., 2019; Trierweiler et al., 2014). This approach was not feasible in this thesis because, first, not all red kites were migrating. Second, this method has a greater inaccuracy because the start and end were not always clearly determinable. Thus, a robust method was used to determine a bird's breeding season location even if GPS data were unavailable for some days.

As many individuals were tagged as nestlings, the extraction of the breeding season location was handled differently for nestlings than for older birds. For nestlings, all coordinates from the first four weeks after tagging were considered, and the central location was computed with the function *`get_centroid (spacey)`*.

For older animals, the ideal time window and, thus, the locations for computing the centroid were defined based on a minimal displacement method. Mougeot et al. (2011) looked at the egg laying date, incubation, and fledging period of different red kite populations. The earliest eggs were laid in late February, while the latest ones were laid in mid-April. Additionally, the incubation usually takes around 31 days with a variable fledging period of about 48 to 58 days (Mougeot et al., 2011). The timing of egg laying and fledging varied per population and individual. Using a large time window for the breeding season allowed the detection of both early and late arriving birds. Therefore, locations between the 1st of April and the 1st of July were considered for obtaining breeding sites. Further, this extended time frame accounted for immatures who were staying longer in the south and hindered not accidentally detecting wintering sites as breeding season locations.

Between the 1st of April and the 1st of July, a one-day moving window approach was used to generate the centroid of 4 weeks' location data. Then, the distances of these locations to the centroid were computed and averaged (*Figure 5*). Further, the centroid of the moving window with the smallest displacement was used as the breeding season location. The minimum displacement approach assumed that birds stayed close to their breeding site or territory during the breeding season and thus only showed slight displacement in the movement data. A four weeks window ensured getting enough data points, even if some days were missing due to GPS malfunctioning. This approach detected breeding season locations of red kites with high precision. The comparison between identified nests of the Swiss Ornithological Institute and breeding sites extracted by the algorithm showed a distance of 0.25 km ± 1.36 (see Appendix B). However, the accuracy of the breeding site could only be compared to breeding individuals whose nests were identified. All distances were computed with the function `distHaversine (geosphere)`.

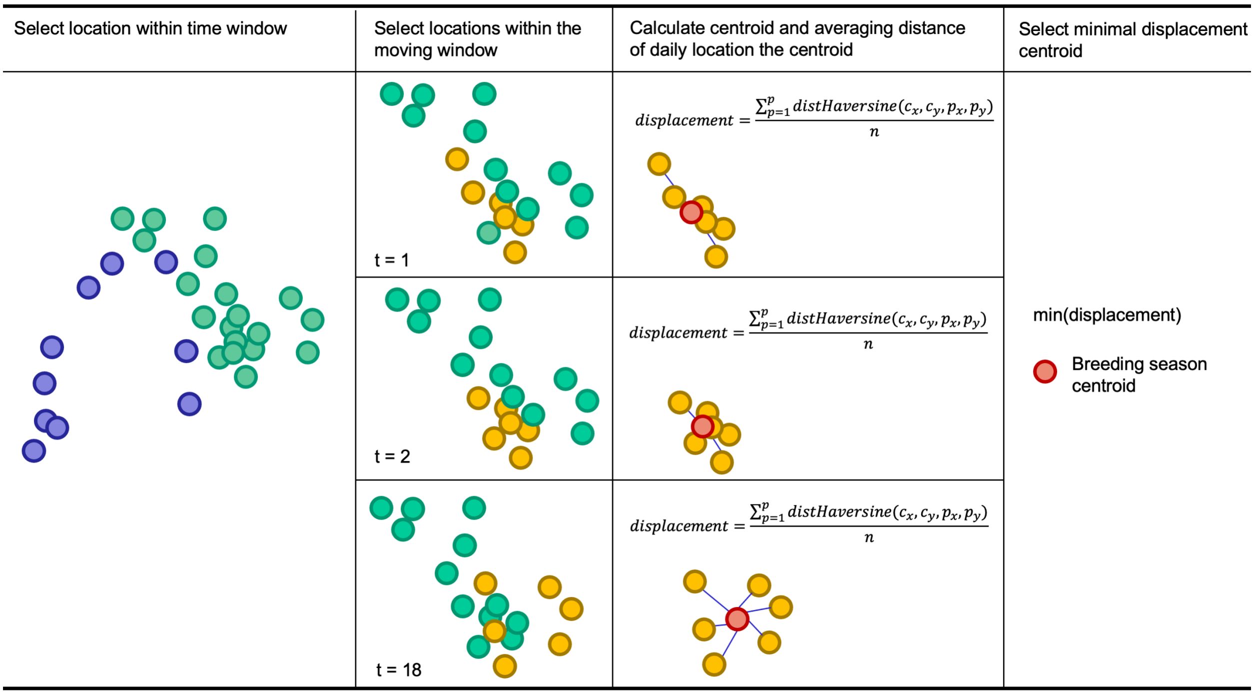

Figure 5: Extraction of the seasonal locations by a moving window and minimal displacement. First, the locations within the time window were selected (breeding respectively wintering season). Then, by iteratively going through the moving windows, the centroid of the locations belonging to the moving window was calculated and the average displacement to the centroid was obtained. Finally, the seasonal location was determined by finding the centroid of the moving window with the smallest displacement.

The same minimal displacement algorithm was used to extract the wintering sites of the annual cycles. The time window in which locations were looked at was defined based on a statistical analysis of the movement data, which showed that, on average, the movement of red kites was relatively stable between the 15th of December and the 24th of January (see Appendix A). Nehm (2020) determined the core winter period from December 8th to January 30th for red kites based in Switzerland. These dates were thus consistent with our definition by considering that locations that were looked at spanned two weeks in both directions from the moving window. Annual cycles that did not have at least one location during the breeding or wintering season were thus excluded due to incompletion.

4.2. Probability model of the migration strategies

4.2.1. Classification of the migration strategies

Based on the literature on red kites movement ecology, three broad migration strategies were differentiated: (1) year-round residency, (2) migration to western wintering grounds, and (3) migration to eastern wintering grounds. Most birds migrate along the western flyway to the Iberian Peninsula and France or stay resident all year round (Aebischer & Scherler, 2021; Mattsson et al., 2022). The western flyway is mainly used by the large northern breeding populations. However, some sparse populations northeast of the Alps use the eastern flyway around the Alps to reach Italy and the Balkans (Aebischer & Scherler, 2021; Maciorowski et al., 2019; Mattsson et al., 2022).

The distance between the breeding season and the wintering location was calculated for each individual, whereby many stayed within a radius of less than 200 km (*Figure 6*). Thus, a simple 200 km distance threshold was used to differentiate between residency and migration.

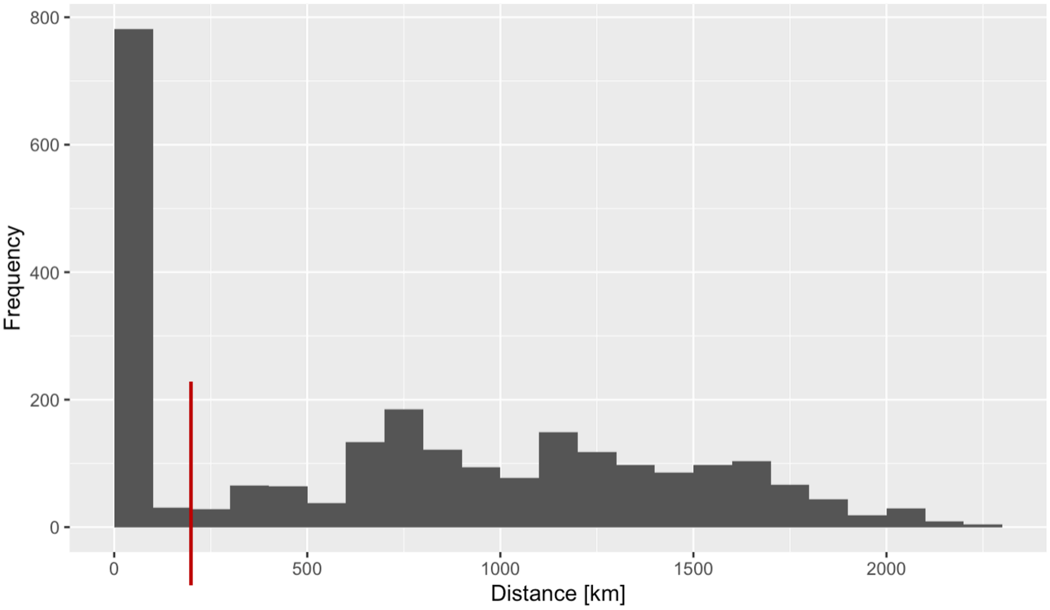

Figure 6: Histogram of the direct distance between the breeding season and wintering location of all annual cycles. A significant proportion of birds stayed within 100 kilometers, while only a few individuals had a distance difference from the breeding to the wintering site that was between 100 and 300 kilometers. The red line indicates the threshold of 200 kilometers used to detect annual cycles of resident birds.

As red kites migrate to different geographic areas for their overwintering, this thesis was differentiating between western and eastern wintering grounds. By distinguishing between these two migration strategies, it was possible to look at co-occurrence on the one hand and migratory divide on the other. Thus, the differentiation between the western and eastern migration was determined based on the overwintering location instead of looking at the flyway of the animals.

High mountains serve as a barrier to red kite migration. Hence, the main chain of the Alps was taken as a natural barrier distinguishing between the western and eastern areas of red kite migration. For other migrating bird species, a migratory divide was observed in eastern Germany and along the border of Austria, the Czech Republic, and Poland (Bobek et al., 2008; Delmore et al., 2020). Therefore, the eastern and western migration area was further drawn from the Austrian along the mountainous border of the Czech Republic and Germany up to the Baltic Sea. However, the exact definition of the northern border of the migratory areas did not influence the analysis as no migrant bird overwintered North of the Czech Republic. Thus, the migration strategy for non-resident annual cycles was determined according to the wintering site (*Figure 7*).

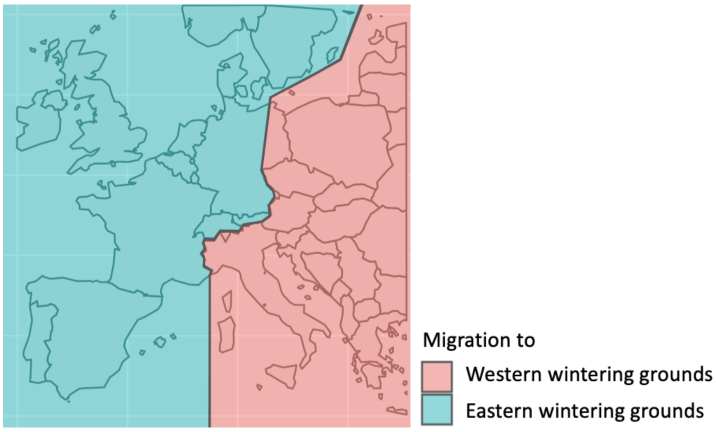

Figure 7: Illustration of the western and eastern wintering grounds. The border goes along the main chain of the Alps and from Austria further north along the mountainous border of the Czech Republic and Germany to the Baltic sea.

4.2.2. Modeling the migration strategies

The following minimum requirements had to be fulfilled by the modeling approach: a) the model had to predict the probabilities of all three migration strategies, b) the predictions had to be modeled over the species' global range, and c) the age had to be included as a spatially varying effect.

A multinomial logistic regression approach was used to predict the probability of a categorical dependent variable's possible outcomes from an set of variables. The multinomial distribution was used due to the fact that it provides a generalization of the binomial distribution, which is required for modeling categorical responses (Fahrmeir et al., 2013). Generalized additive model (GAM) models support multinomial regression models and additionally support modeling of nonlinear features (Hastie & Tibshirani, 1986). Bayesian additive models for location, extent, and shape (BAMLSS) are a probabilistic distribution extension of GAM, that capture location, extent, shape (and other aspects) of the response distribution (Umlauf et al., 2018). BAMLSS model allow to cope with complicated inference problems by supporting Markov chain Monte Carlo simulation (Umlauf et al., 2018). Due to the adaptive framework, BAMLSS models are used for modeling various problems, also in the spatial context, such as fire emergency response times with a survival mode or precipitation model (Umlauf et al., 2018).

To investigate how birds differed in their migration strategy as a function of age and breeding season location, a spatially explicit, hierarchical Bayesian approach was applied that accounts for a) spatial variation in sampling coverage to propagate spatial uncertainty of the parameter estimates and b) allowed the effect of the linear predictor (i.e., age of the bird) to vary in space. Specifically, the probability of a bird choosing among one of the three migration strategies (Resident, East, and West) was calculated by parametrizing a spatially explicit multinomial logit model within the BAMLSS framework (Umlauf et al., 2017) while c) taking into account repeated sampling of individuals. The resident strategy was used as the reference level.

Equation 1: BAMLSS multinomial logit model function with two smooth terms. The first smooth term is a spatially varying effect, and the second smooth term is a Markov random field of a neighborhood structure.

$$
\begin{aligned}
&f(Migration\ Strategy) \sim \\
&\quad s(summer.lat, summer.long, by = ageClass, \mathrm{bs} = c(ts, sos), k = 110)\ + \\
&\quad s(region_{id}, bs = c(\mathrm{mrf},\ \mathrm{ts}), xt = neighborhood, k = 3)
\end{aligned}
$$

To consider not only spatial scale in terms of distances but also to include neighboring structures of areas, two smooth terms were defined, one including a surface by latitude and longitude, and the other including the rough spatial neighborhood structure. Hence, the multinomial logit model function was created containing two smooth terms (*Equation 1*). The first smooth term was defined as a spatially varying effect, in which the age class can vary in space defined by latitude and longitude. Age classification includes juvenile, immature, and adult. The spatial variables are the latitudinal and longitudinal coordinates of the breeding season location. The first smooth term consists of 110 dimensions with two smoothing bases, `ts` and `sos`. The low-rank isotropic smoother `ts` was used to penalize the null space. In contrast, `sos` was used for its two-dimensional splines on a sphere specially designed for latitude and longitude data on large areas of the globe (e.g., the red kite global species' range).

A Markov random field (`mrf`) was applied as a second smooth term to model regional differences based on a neighborhood structure. Regions were specified based on hexagons projected across the breeding range. This approach allowed to model for geographic correlation among data points that were not solely based on geographic distance but rather on spatial clusters, such as islands. Hexagons that did not contain breeding season locations of at least two age classes were excluded. This resulted in 22 hexagons corresponding to 4 neighborhood complexes: the British Isles, the Balearian Islands, Italy, and the rest of Europe (see Appendix D). Thus, to each annual cycle, the hexagon in which it was located or was closest to was assigned, except for breeding season locations in the British Isles; these were always assigned to the British region. Again `ts` was used to allow penalization of the null space. Due to the small number of regions, the smooth term was defined with 3 dimensions.

The model was executed with the `opt_bbfit` optimizer, which estimates regression coefficients and smoothing variances batch-wise (Umlauf et al., 2017). Further, the General Markov Chain Monte Carlo sampler `sam_GMCMC` was used with the iteratively weighted least squares proposal function (Umlauf et al., 2017). Finally, the input data was weighted by the inverse number of breeding sites located within 200 km to counteract the over-representation of sites with many data points. Last, the individual's identifier was defined as a random intercept.

The model was performed on all annual cycles. The model was used to predict the migration strategy probabilities for all age classes over the entire breeding range. The input locations of the prediction were sampled from the breeding range in a 5 km raster. The model was set up to return all posterior predictions and the posteriors distribution was converted to probabilities to allow deriving own statistics from it (*Equation 2*). The average of the posterior distribution was used to model the probabilities of the three migration strategies per age group and location.

Equation 2: Conversion of the posterior distribution to posterior probabilities. P indicates the probabilities, while Q represents the posterior.

$$P_{East} \sim \frac{Q_{East}}{1 + Q_{East} + Q_{West}}$$

$$P_{East} \sim \frac{Q_{West}}{1 + Q_{East} + Q_{West}}$$

$$P_{Resident} \sim \frac{1}{1 + Q_{East} + Q_{West}}$$

Finally, the global number of red kites performing each migration strategy was calculated. Since the breeding pair abundance had a rather coarse cell size (50 km, see Section 3.2), the prediction was made at a higher spatial resolution (5 km), and therefore the abundance was downscaled proportionally. Only the probabilities of adult birds were used since the abundance data also referred solely to breeding pairs. Thus, the individual migration strategy probabilities were multiped with the breeding pair abundance so that each cell contained the number of breeding pairs per migration strategy at the specific location. Then, grid cells were summed up by the migration strategy resulting in a total number of breeding pairs per migration strategy. Additionally, the probabilities of the migration strategies per grid cell per age class were multiplied by the area of the grid cell and summed up to get a summary statistic of the three migration strategies with age.

Extracting the model uncertainty is a crucial aspect of analyzing the strengths and weaknesses of the model. The posterior probabilities were further analyzed to assess the predictive uncertainty of the model across the entire species range. Thus, the 95% credible interval was extracted from the posterior probabilities of the predictions for every age class and migration strategy individually. The uncertainty range was computed by subtracting the lower quantile from the upper. This results in nine uncertainty models about the species distribution range (three per age class and three per migration strategy).

The analysis of the age effect was made with two methods. First, the difference in the resident probability of adult and juvenile birds were calculated for every location in the breeding range. This indicates where and how much higher or lower the resident probability was for adult birds compared to juvenile birds. However, it did not indicate how certain the model was that an age effect existed. Thus, the posterior probabilities were analyzed to account for significant age effects. Therefore, if the 2.5% percentile of the posterior probability of adult birds was higher than the 97.5% percentile of juvenile birds for the resident strategy, a positive resident age effect was assumed. Conversely, if the 97.5% percentile of the posterior probability of adult birds was lower than the 2.5% percentile of young birds, a negative resident age effect was assumed. Thus, this posterior statistic enabled to determine areas where age had a real influence on the probability of an individual staying resident throughout the year.

Two methods were used to identify areas where the eastern and western migration strategies coexisted. First, for each location, the maximum probability per migration strategy was determined by taking the highest value of all age classes. Then the minimum shared probability was calculated by taking the smaller of the two probabilities (migration to eastern and western wintering grounds). The higher the minimum shared probability, the greater the probability that both migration strategies co-exist. A posterior statistic was applied to detect the co-occurrence of the two migration strategies while incorporating model uncertainty. If more than 97.5% of posteriors agreed that at a certain site both migration strategies had a probability of at least 2.5%, co-occurrence was assumed. Thus, only areas where the model predicted with high confidence the presence of both migration strategies were identified.

4.3. Migratory connectivity

Most studies calculated the strength of migratory connectivity using either the Mantel correlation coefficient (Ambrosini et al., 2009) or the population-specific transition probabilities (Cohen et al., 2018). Since both approaches have their strengths and weaknesses, they were computed separately and compared.

4.3.1. Mantel correlation coefficient

One way to determine the strength of migratory connectivity is by computing the Mantel correlation coefficient (r_M; Mantel, 1967) of individual pairwise distance matrices of breeding sites and wintering sites (Ambrosini et al., 2009). The extracted breeding season and wintering locations per individual per annual cycle (see chapter 4.1) were used to compute the mantel correlation coefficient. The mantel correlation coefficient and the 95% confidence interval by bootstrap were calculated using the `estMantel (MigConnectivity)`.

R_M was computed individually for juvenile, immature, and adult birds (limited to one annual cycle per individual) to extract the age effect on migratory connectivity. In addition, r_M was run once with the entire data set and once limited to one annual cycle per bird to eliminate potential bias from comparing an individual's behavior to themselves during another year. The limitation to one annual cycle per bird was done using random sampling.

4.3.2. Strength of migratory connectivity and population-specific transition probabilities

Another widely used method estimates the strength of migratory connectivity by considering the location and other sampling uncertainty based on population-specific transition probabilities (Cohen et al., 2018). The advantage of this method is that it incorporates the abundance of breeding pairs, and thus the influence of a non-representative sampling strategy can be minimized. However, individual birds must be assigned to regions, which could introduce additional errors. Furthermore, the population-specific transition probabilities also impose spatial constraints so that the calculation is no longer performed in continuous space.

Ideally, red kite breeding season locations would be distributed in such a way that they could be assigned to specific regions easily. However, because the data set consisted of many individuals, the regions were not clearly distinguishable everywhere. Eleven regions were created based on natural barriers such as high mountain ranges (the Alps and Pyrenees) and coastlines, and as an additional criterion at places where a divide was visible between the tagging locations (*Figure 8*). Many studies analyzed migratory connectivity for long-distance migrants, in which breeding regions were distinctive, and further breeding and wintering regions were not overlapping. However, red kites are known to be short-distance partial migrants. Thus, the defined breeding regions were also used as wintering regions. Hence, a resident bird should most likely have the same breeding area assigned as the wintering area.

The previously extracted breeding season and winter locations (see Section 4.1.2) were used to assign the annual cycles to the breeding and wintering regions. For each cycle, the breeding region was determined by spatially overlaying the breeding season location and the regions with the function *`st_nearest_feature (sf)`*. The same approach was performed for the wintering location and its wintering region. Thus, each annual cycle of an individual was assigned to a breeding and a wintering region.

Further, the preprocessed abundance data (see Section 3.2) was used to calculate the regional abundance by simply summing up all abundances within the region's area. The relative abundance was calculated by dividing the total abundance by the population-specific abundance.

To compute MC, a distance matrix of the regions was required. A simple centroid of region polygons was not ideal because the regions covered large areas and the centroid did not represent the distribution of the tracking dataset. Instead, each region's central location was determined by calculating the centroid based on the associated breeding season locations. Then, the distance matrix of the regions was computed with the centroid of the regional breeding season locations.

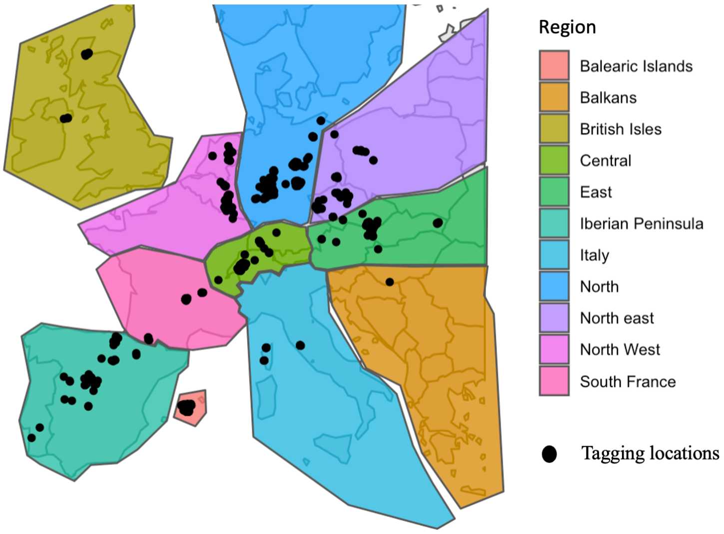

Figure 8: Regions used to separate the annual cycles into breeding and overwintering areas. The regions are shown as colored polygons, and the tagging location of each bird is shown as a black dot. Each region does represent a breeding population during the breeding season and an overwintering region during winter.

The function *`estTransition (migConnectivity)`* was used to calculate the transition probabilities and `estStrength` *`(migConnectivity)`* was used to calculate the strength of migratory connectivity based on the distance matrices of the breeding and wintering regions, the breeding and wintering regions, the breeding and wintering locations of the annual cycles, the assignment of each annual cycle to a breeding and wintering region and the relative abundance of the breeding regions. MC was computed individually for juvenile, immature, and adult birds (limited to one annual cycle per individual) to extract the age effect on migratory connectivity. In addition, MC was calculated once with the entire data set and once limited to one annual cycle per bird. To account for the influence of the random sampling, the calculations were computed ten times and the mean MC and its confidence interval were calculated from all ten iterations.

4.3.3. Population spread

Finch et al. (2017) describe the population spread as a relative geographical spread of a population on non-breeding grounds. The population spread was calculated by averaging the distances between the non-breeding areas of different birds within the same population (Finch et al., 2017; Sarà et al., 2019). However, these papers analyzed long-distant migrants with distinctive populations with a small spatial range of fewer than 100 kilometers. Because the red kite is a short-distance migrant, and tracking data were distributed almost continuously across space, and the regions represented large areas, and consisted of varying sample sizes, the method was extended to increase expressiveness. The average distance of all wintering locations between individuals in a breeding population was calculated, as well as the average distance of breeding season locations between individuals. The relative population spread was computed by normalizing the average overwintering distances with the average breeding season distance to make a more meaningful statement.

5. Results

5.1. Migration strategies

All annual cycles of individuals that had GPS data at least during the breeding and wintering season were considered. Of all 2440 bird cycles, 813 were residents, and 1626 were migrants (*Table 4*). Further, of the 1626 annual cycles of migrants, 1524 belonged to migration to western wintering grounds, while only 103 bird cycles belonged to a migration to the eastern wintering grounds. Among young birds, more than 75% migrated to the western wintering grounds, whereas among adult birds almost half remained resident. Thus, summary statistics proposed a change from juveniles migrating to western wintering grounds to resident adults.

Table 4: Summary of the annual cycles by age and migration strategy. The first number describes the percentage of annual cycles by migration strategy and age, and the second value shows the number of annual cycles.

Age	Migration to western wintering grounds	Migration to eastern wintering grounds	Resident	Total
Juvenile	26.6% (650)	2.2% (53)	5.9% (143)	34.7% (846)
Immature	11.9% (291)	0.7% (16)	5.7% (139)	18.3% (446)
Adult	23.9% (583)	1.4% (34)	21.8% (531)	47.0% (1148)
Total	62.5% (1524)	4.2% (103)	33.3% (813)	100.0% (2440)

A third of all individuals with multiple annual cycles changed their migration strategy over the years (*Table 5*). This means that individuals' migration strategies are not predetermined at birth to be maintained throughout the lifespan. Thus, there was a change in migration strategies during a bird's lifetime, suggesting evidence of a potential age effect. Only a few birds who were residents in the first year after tagging changed their migration strategy (12.4%), while many birds who migrated in their first year changed to residents in a subsequent year (37.8%). Besides, birds that migrated to the western wintering grounds never changed their strategy to the eastern wintering grounds. Conversely, some birds changed their strategy such that, after migrating to eastern areas in the first year, they migrated to western areas in a subsequent year. Furthermore, no bird was observed to conduct all three migration strategies during the tracking period. However, these results were strongly biased by the sampling strategy and thus by the breeding season location of the individuals. The following sections present the age-dependent migration strategies in more detail.

Table 5: Migration strategies of individuals with multiple annual cycles. The first two rows show the migration strategy distribution during the first year after tagging. Rows 3 to 5 show the distribution of the migration strategy of individuals during the subsequent years. If an individual exercised a different strategy in at least one year compared to the first year, it is assigned to that strategy. The same strategy was assigned only if there was no change in subsequent years. 568 individuals had tracking data during multiple years with an average of 3.5 annual cycles per bird.

Migration strategy of individuals at the first year after tagging		Migration strategy of individuals in subsequent years			
		Residents	West	East	Change of strategy
Residents	57	106 (87.6%)	12 (9.9%)	3 (2.5%)	15 (12.4%)
West	355	145 (35.3%)	266 (64.7%)	0 (0.0%)	145 (35.3%)
East	36	21 (58.3%)	3 (8.3%)	12 (33.3%)	24 (66.6%)

5.1.1. Probabilities of migration strategies

The probabilities of migration strategies varied per age class and spatially across the species' range (*Figure 9*). Populations with individuals being full-year residents at all ages were found in Italy, the British Isles, and in Mediterranean Islands. Apart from the British Isles, individuals that stayed at higher latitudes during the breeding season migrated more likely than southern individuals. In general, the probability of birds remaining resident increased with age, while the probability of migrating to western or eastern wintering grounds decreased. Only individuals from eastern breeding populations migrated to eastern winter areas.

Alternatively, probabilities were plotted along a cross-section from southwest to northeast per age class to show how the probabilities of the three migration strategies changed with location and how they differed with age (*Figure 10*). The probability of residency was rather small for juvenile birds throughout the cross-section. Migration to western wintering grounds was the dominating migration strategy from southwest Europe up to central Europe. However, eastwards of the Czech Republic, individuals tended to migrate to the eastern wintering grounds. Thus, a cline of migration strategy was observed along the longitudinal breeding range (see Section 5.1.4). The general pattern stayed similar for different ages. The older the birds were, the higher the probability of residency. However, the influence of age was not equally pronounced at all locations.

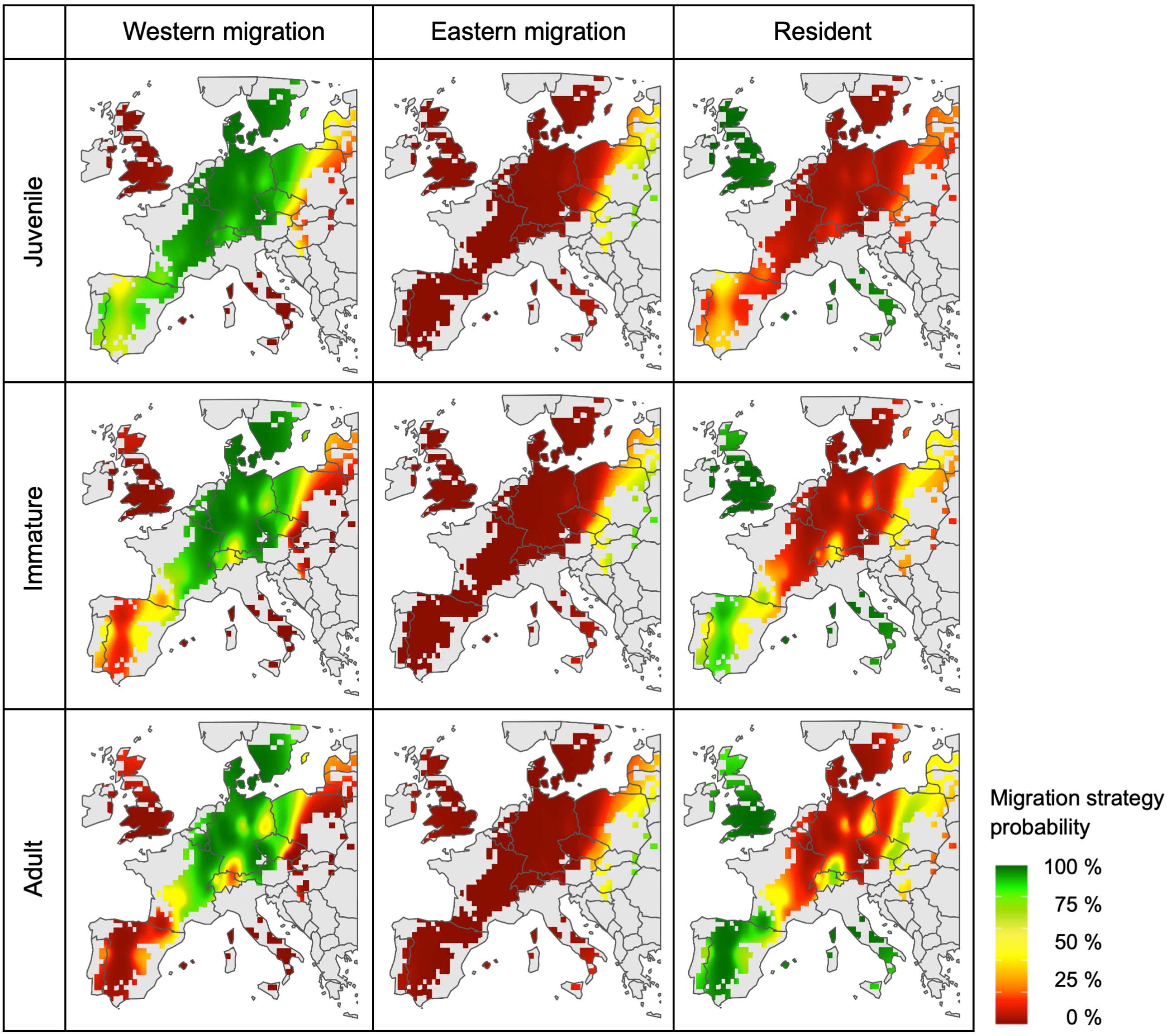

Figure 9: Probability of the migration strategies by age groups throughout the breeding range. The migration strategies are represented as columns and the age groups as rows. Each map shows the probability with which an

individual of a given age applies the associated migration strategy with respect to where it stays during the breeding season. Green values indicate high and red values represent low probabilities. Example: The upper left map shows the probability of a juvenile bird migrating to the western wintering grounds depending on the breeding season location. A juvenile bird that stays in Denmark during the breeding season migrates to the western wintering grounds with a probability of almost 100%.

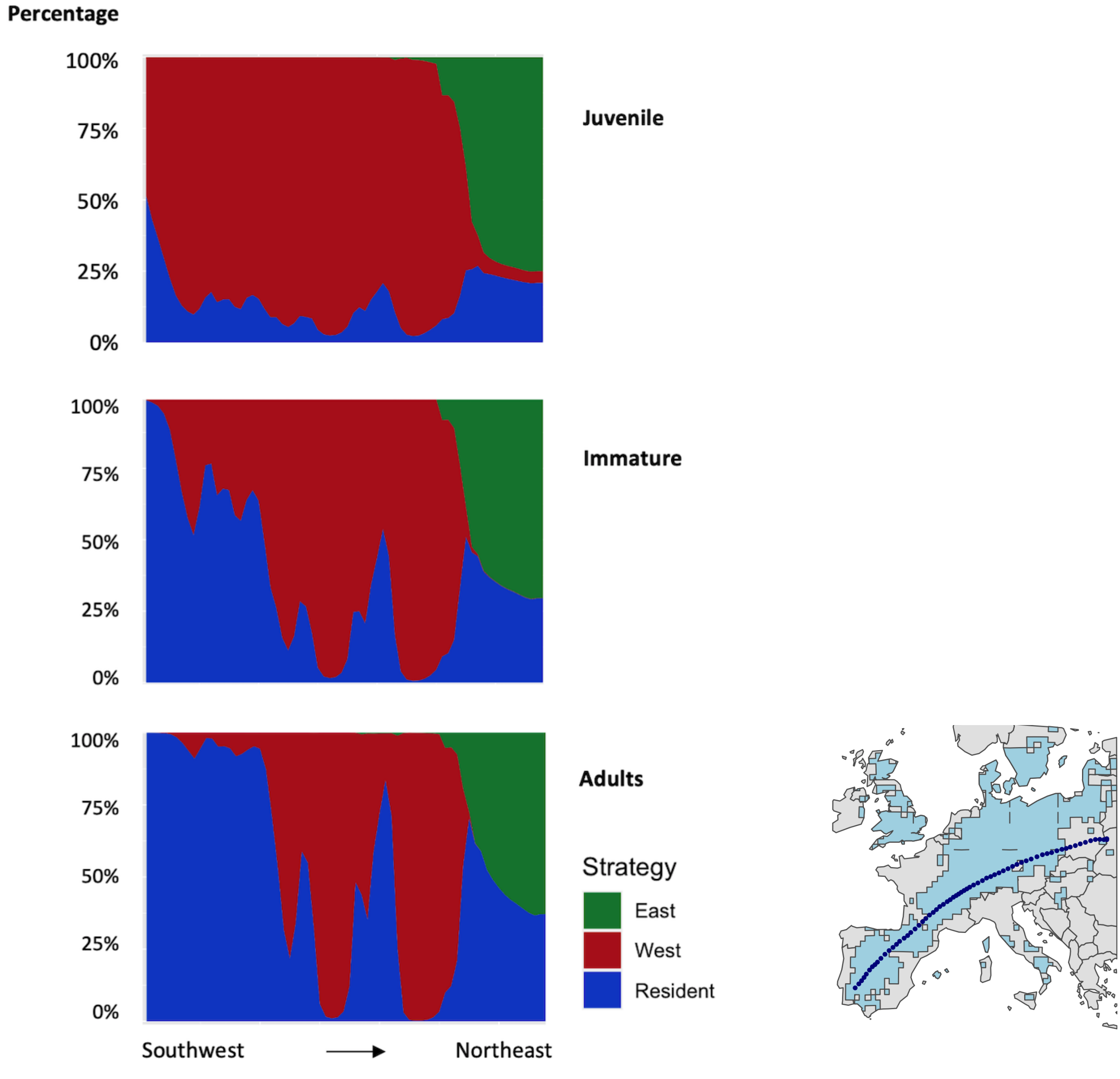

Figure 10: Probabilities of the migration strategies by age group from southwestern to northeastern Europe. Each age group has a separate chart showing the probabilities of the migration strategies along a cross-section. The probabilities of migration to western wintering grounds are colored in red; migration to eastern wintering grounds in green; and residents in blue. A clear shift from western to eastern migration was observed in all three age classes, while the probability of residents increased with age.

Most breeding pairs either migrated to western wintering grounds or remained residents (*Table 6*). Almost half of the breeding pairs (44.3%) were expected to stay resident all year round, while more than half of the breeding pairs migrated to western wintering grounds (54.4%). Due to the low abundance in eastern Europe, only a small portion of adults migrated to the Eastern wintering grounds (1.3%). With increasing age, the area percentage of western migration strongly decreased (-23.3%), while a substantial increase in residency was observed (+24.0%).

Table 6: Summary statistics of the red kite migration strategies. The estimated number of breeding pairs per migration strategy is shown in the first part. The second part shows the area in percentage per migration strategy for each age class.

Animal-ID	Migration to Western wintering grounds	Migration to Eastern wintering grounds§	Resident
Breeding pairs	19’050 54.4%	443 1.3%	15’507 44.3%
Area			
Juvenile	71.7%	6.0%	22.2%
Immature	57.5%	6.2%	36.4%
Adult	48.4%	5.5%	46.2%

5.1.2. Model uncertainty

Model uncertainty varied spatially with respect to both migration strategy and age class (*Figure 11*). While most areas showed low uncertainties for juvenile birds, higher uncertainties were found in southern Spain and the Baltics. High model uncertainties often occurred in areas with a sparse red kite tracking coverage (e.g., southern Spain, southern Italy, and the Baltics) and especially in places peripheral to the breeding area (see Appendix C). The model prediction of adult birds exhibited a more complex uncertainty pattern, probably due to less dominant migration strategies and higher intra-population variability.

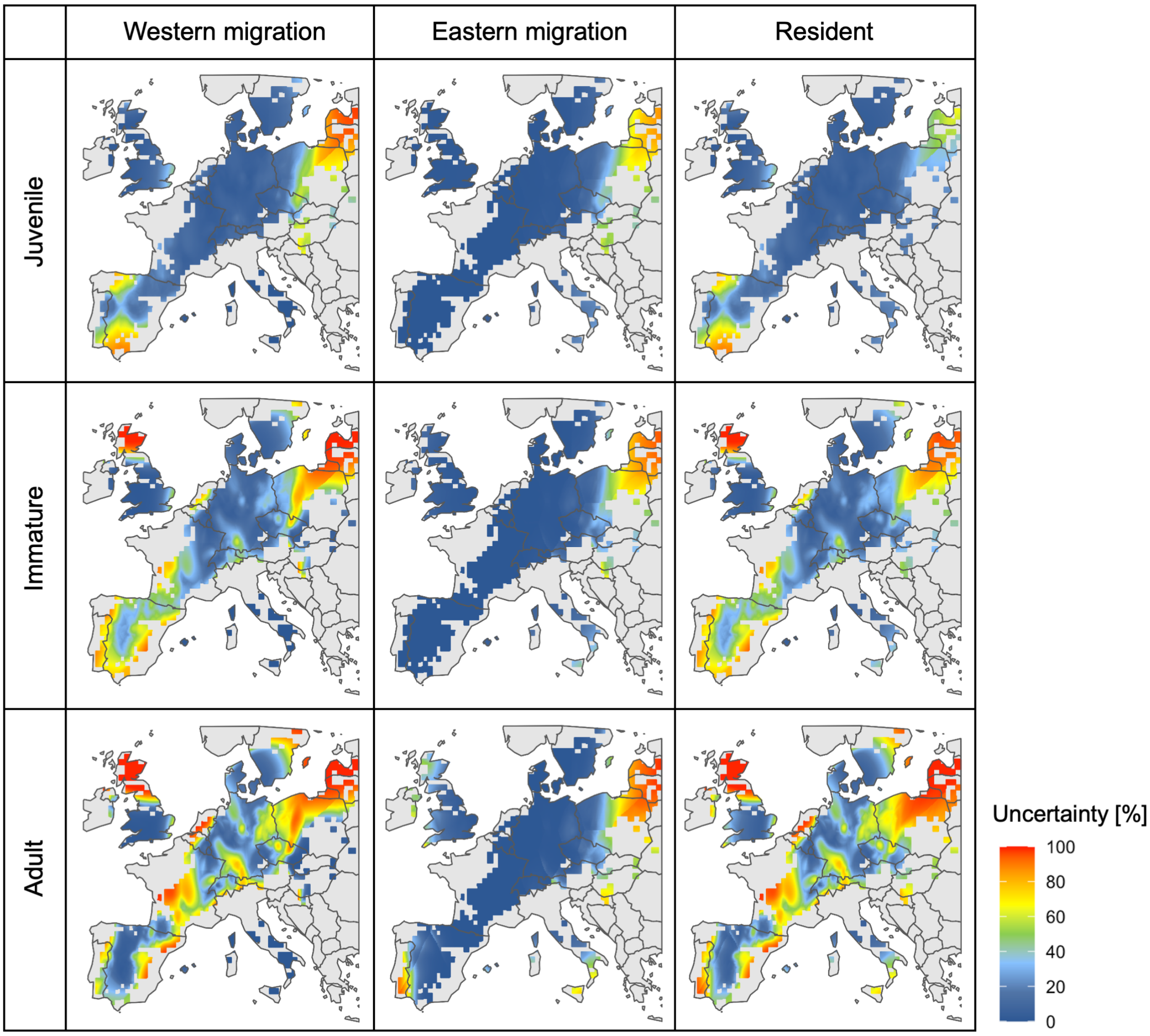

Figure 11: Model uncertainty by migration strategies and age groups. The model uncertainty corresponds to the 95% credible interval of the posterior distribution. Blue areas indicate a low uncertainty, while yellow to red areas show a large uncertainty. The Baltic states show the largest uncertainty due to non-existing tracking data.

5.1.3. Age-dependent probability of resident birds

The absolute difference in resident probability between adult and juvenile birds revealed that the prevalence of age-dependent partial migration varied strongly across the species range (*Figure 12A*). Some areas showed strong positive values, indicating an increased residency probability with age. Roughly half of the global species' range showed an age-dependent effect on the migration strategy meaning a higher absolute probability difference of residency between juvenile and adult birds than 10%. Most observed probability differences showed an increased probability of residency with age, except for the negative age effect in Scotland. The negative values in Scotland proposed a decrease in residency with age. However, due to model uncertainties, an age effect was not simply confirmed at all sites with high probability differences.

To account for model uncertainty, posterior statistics were applied to determine whether an age effect was present at specific locations (*Figure 12B*). Thus, an age effect was confirmed in 41% of the red kites' breeding range. Moreover, by combining both analyses, no negative age effect of residency was identified. Therefore, at breeding season locations with confirmed age effects, adults were expected to stay resident throughout the year with higher probabilities than juveniles. Age-dependent migration strategies were identified from southern Spain up to central France, around Switzerland, in eastern Germany, and from Croatia up to Poland. The most considerable age effects were found in the Iberian Peninsula.

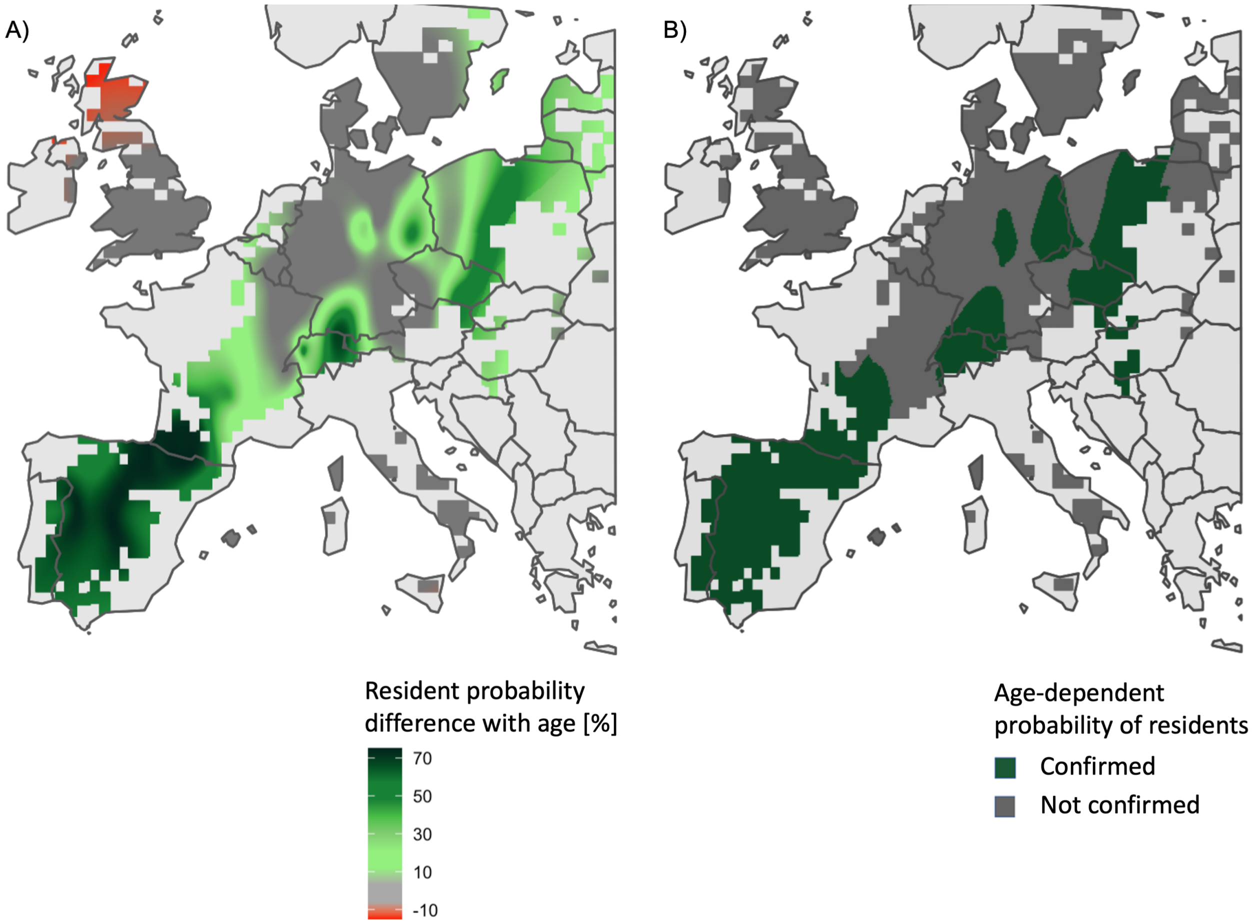

Figure 12: Age-dependent change in resident probability. ***(A)*** *Absolute difference in resident probability of adult and juvenile birds. Positive numbers indicate an increase in resident probability with age, while negative numbers indicate a decrease.* ***(B)*** *Confirmed age-dependent resident probabilities computed by posterior statistics. Green areas indicate a confirmed age effect, while in grey areas an age effect was not confirmed.*

5.1.4. Co-occurrence of western and eastern migration

While most individuals migrate to the southwest, some migrate to the southeast. Where precisely this migration divide occurs and in which areas both migration strategies coexist was not yet determined. Individuals that migrated to eastern wintering grounds may change their migration strategy in subsequent years to migration to western wintering grounds (see Section 5.1). Hence, it seemed likely that there were breeding populations in which individuals migrated both to the western and eastern wintering grounds. According to the minimal shared probability, co-occurrence of the western and eastern migration was found in the whole eastern species range (*Figure 13A*). High co-occurrence values were found on a thin curved band from Croatia up to the Baltic countries.

Posterior statistics enabled to account for uncertainties so that co-occurrence is presented only at confirmed breeding season locations (*Figure 13B*). Both assessments agreed that the two migration strategies co-occurred from Croatia through western Hungary, the Austrian-Slovakian border through the Czech Republic and Poland, and the Baltic countries. Migration to western and eastern wintering grounds occurred concurrently for individuals on about 10% of the breeding range. Further, the co-occurrence of the migration to eastern and western wintering grounds simultaneously represented the migratory divide. Since west of the co-occurrence, no migration to eastern winter areas occurred, while east of the co-occurrence, no migration to western winter areas occurred.

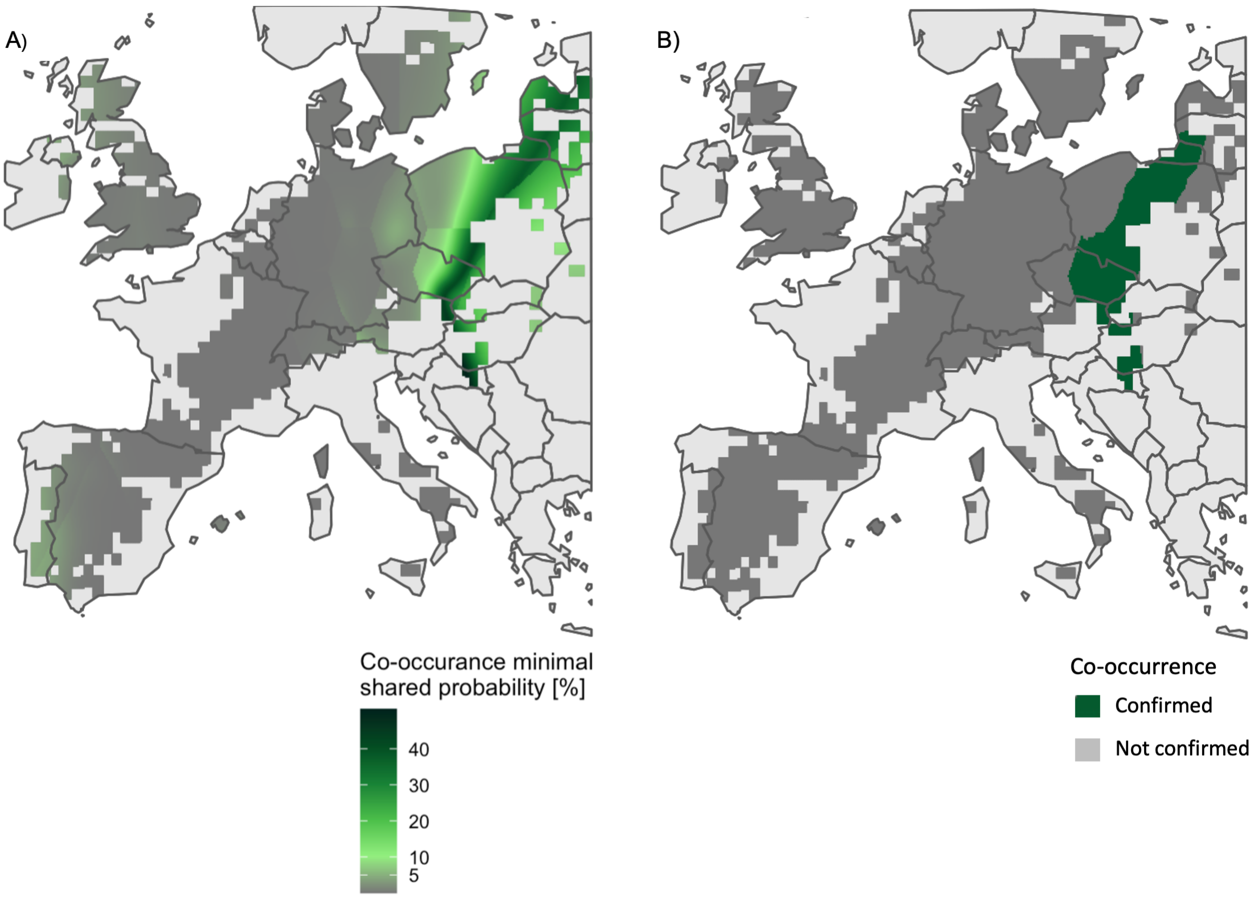

*Figure 13: Co-occurrence of the two migration strategies: Migration to western wintering grounds and migration to eastern wintering grounds. **(A)** The minimal shared probability of the western and eastern migration strategy is illustrated in green if it exceeds 2.5%. In grey areas, at least one of the two strategies has a smaller probability than 2.5%. **(B)** Co-occurrence agreement based on the posterior distribution. Green areas indicate confirmed co-occurrence, while in grey-colored areas, co-occurrence was not confirmed.*

5.1.5. Migration distance

Furthermore, statistics on the direct migration distance of migrating red kites were computed. The average direct migration distance was 1100 km and the maximum distance was 2300 km. The migration distance of individuals significantly differed between the breeding populations (*Figure 14A*). The pairwise Kruskal Wallis test showed significant differences in the average migration distance between all populations except between the Central and Eastern populations. Migrating individuals of northern populations migrated over larger distances, while individuals of southern populations migrated the shortest distances. Further, birds migrating to western wintering grounds covered a longer direct distance than birds migrating to eastern wintering grounds (average migration distance to: eastern wintering grounds = 742 km; western wintering grounds = 1127 km; *Figure 14B*). However, pairwise comparison between age groups showed no significant difference in the direct migration distance of different age groups (average migration distance: juveniles = 1126 km, immatures = 1019 km, adults = 1117 km; *Figure 14C*).

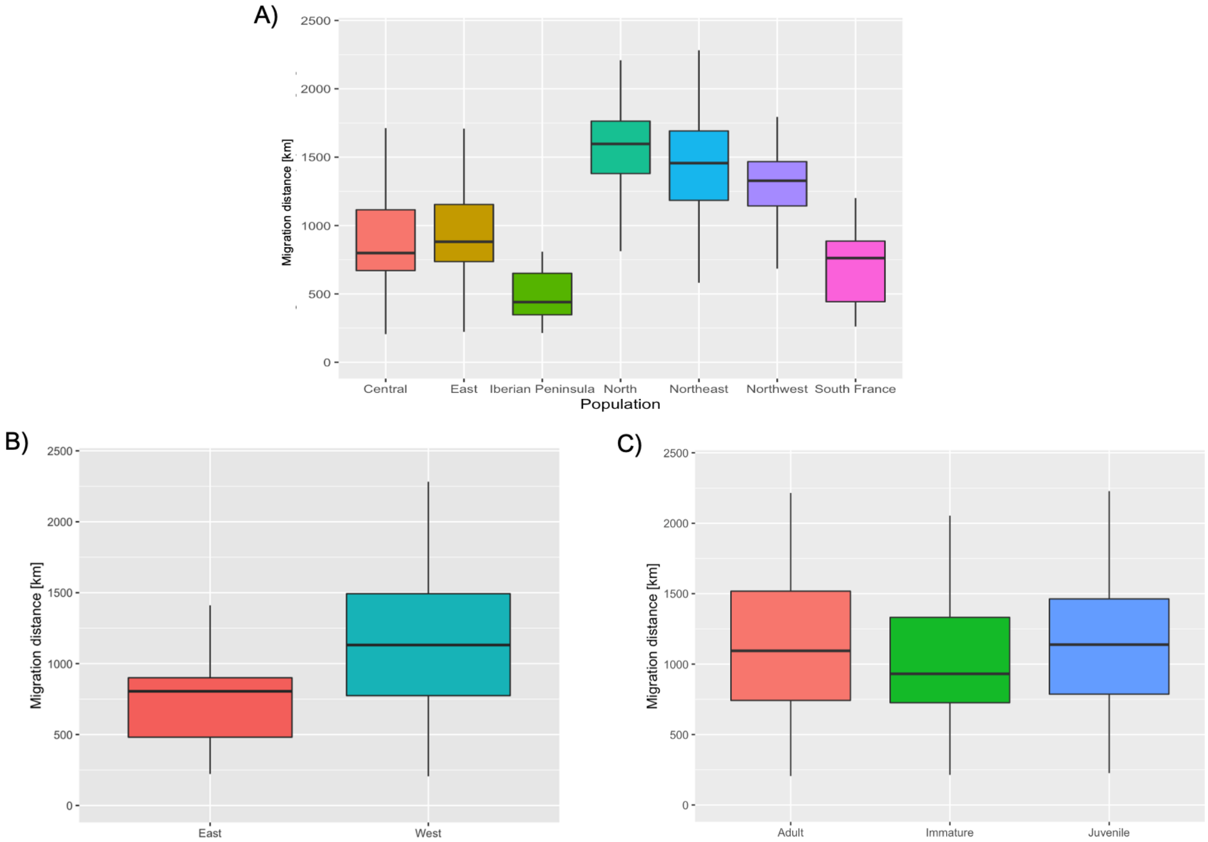

Figure 14: Boxplots showing median and interquartile range of the direct migration distance by breeding population, migration strategy, and age class. The direct migration distance between the breeding season and wintering location was calculated for each annual cycle of a migrating red kite. ***(A)*** *Direct migration distance by breeding population.* ***(B)*** *Direct migration distance by migration strategy.* ***(C)*** *Direct migration distance by age class.*

5.2. Migration connectivity

5.2.1. Transition probabilities of individuals between regions

The transition probabilities of individuals between regions varied considerably (*Table 7*). Some populations overwintered entirely or with a very high probability in the same region as they stayed during the breeding season (e.g., the populations of the Balearic Islands, British Isles, Iberian Peninsula, and Italy). Other populations, such as those in the North and North West, showed a high probability of overwintering in the Iberian Peninsula. In contrast, many regions showed a large inter-population variety of overwintering behavior (e.g., Central, South France, the Balkan, North East, and East). The eastern breeding population showed the most versatile transition probabilities with linkage to six other regions; four of these were higher than 7 %. Almost exclusively, all birds that migrated to another region overwintered either in the southwest (the Iberian Peninsula and southern France) or in the southeast (Italy and the Balkans). By far, the highest transition probabilities are seen in the wintering region of the Iberian Peninsula as individuals of many populations migrate there. Interestingly, the eastern and northeastern populations were the only two populations with a higher transition probability to southern France than to the Iberian Peninsula. Possibly, individuals that were far east during the breeding season and thus had a long migration route ahead of them may have chosen to winter less southwards to save energy. Northern regions were not used as wintering areas except by resident birds, as no transition from other regions to these areas was noted, which means that whenever birds migrated, they migrated to more southerly regions.

The simplified map shows the transition probabilities of individuals between regions, with the lines indicating a transition of individuals from one breeding area to another wintering area (*Figure 15*). The British Isles and the Balearic Islands population were separated from the other populations, as there was no transition to or from these areas. The most significant exchange of individuals occurred in the Iberian Peninsula, as a large proportion of individuals from different populations overwintered there.

Table 7: Estimated probabilities that red kites from each breeding site overwintered in the overwintering sites. Areas represent both breeding and wintering areas, with year-round resident birds showing the same area in the two seasons. If the probability is greater than 0.05, it is highlighted with green, whereby the greener, the higher the probability. The last row shows the cumulative transition probability of the overwintering region. Regions are highlighted in blue if they have a positive transition, red if they have a negative transition, and in gray if transition is constant.

	Wintering region										
Breeding region	Balearic Islands	Iberian Peninsula	Central	Italy	South France	Balkans	North West	North	North East	East	British Isles
Balearic Islands	1	0	0	0	0	0	0	0	0	0	0
Iberian Peninsula	0	0.98	0.02	0	0	0	0	0	0	0	0
Central	0	0.50	0.23	0	0.27	0	0	0	0	0	0
Italy	0	0	0	0.97	0.03	0	0	0	0	0	0
South France	0	0.58	0.03	0	0.39	0	0	0	0	0	0
Balkans	0	0	0	0	0	1	0	0	0	0	0
Northwest	0	0.84	0	0	0.10	0	0.06	0	0	0	0
North	0	0.77	0.01	0	0.17	0	0.01	0.05	0	0	0
Northeast	0	0.41	0.04	0.01	0.48	0.01	0	0	0.04	0.02	0
East	0	0	0.02	0.27	0.11	0.08	0	0	0	0.51	0
British Isles	0	0	0	0	0	0	0	0	0	0	1
Cumulative overwintering	1	4.08	0.35	1.25	1.55	1.09	0.07	0.05	0.05	0.53	1

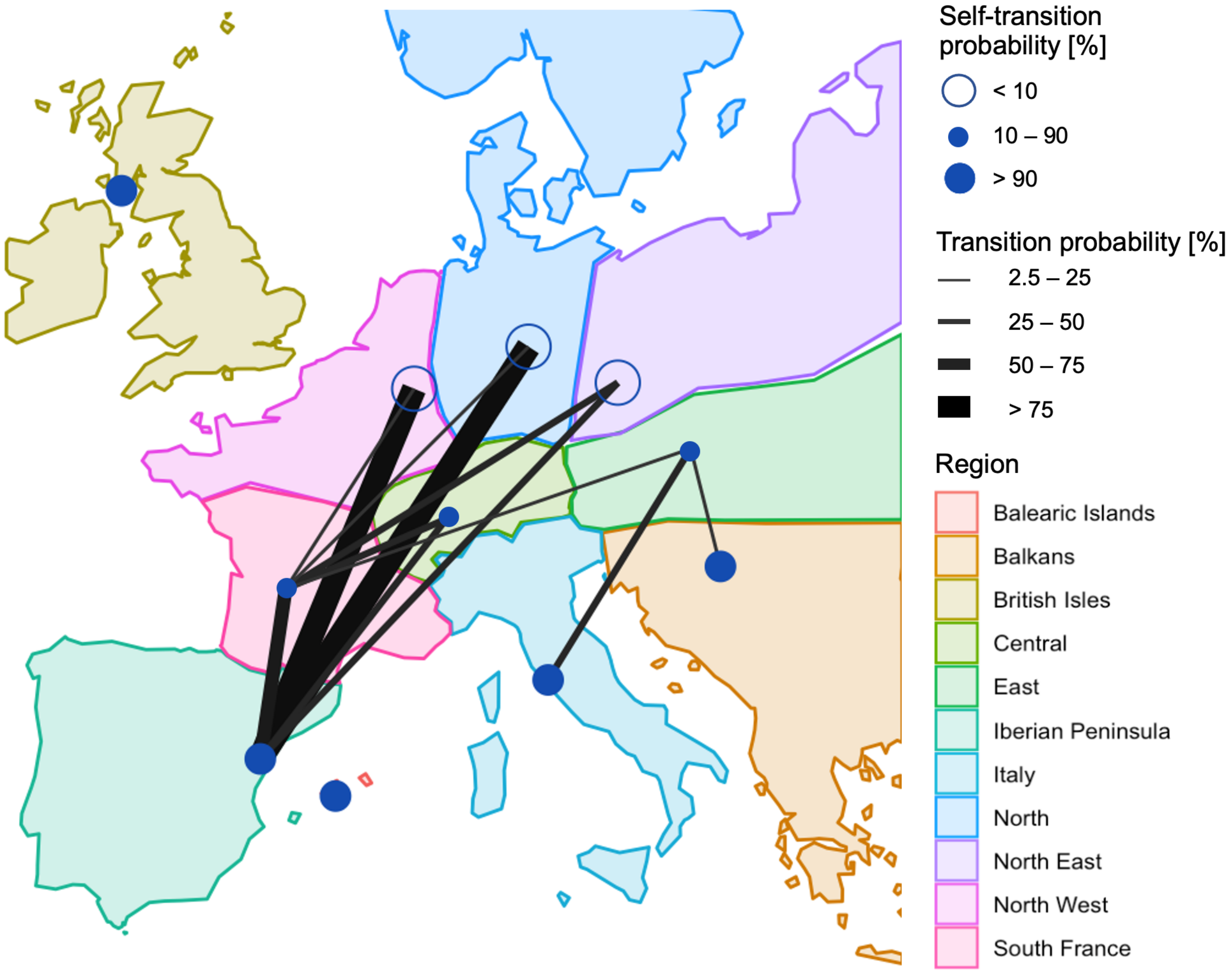

Figure 15: Transition probabilities of individuals between regions from breeding season to overwintering. Blue-filled circles show the percentage of individuals staying in the same region for overwintering, whereas a larger circle indicates a higher probability. In contrast, an unfilled circle indicates a probability of less than 10%. The dark lines show the transition from the breeding area to overwintering. The thicker the line, the higher the transition probability. Transition probabilities smaller than 2.5 % were ignored to maintain the readability of the graphic.

5.2.2. Strength of migratory connectivity

The strength of migratory connectivity was analyzed with different methods for all age classes, whereas the strength of migratory connectivity of the whole dataset was 0.263 on average (*Table 8*). In both methods, juveniles showed significantly higher migratory connectivity values than older age classes (juvenile connectivity = 0.336; adult connectivity = 0.253; *Table 8*, *Figure 16*). Thus, this decrease in strength of migratory connectivity with age suggested that young individuals who were close by during breeding season tended to stay closer to each other during overwintering than older birds. Therefore, the migration strategies of close individuals were getting more diverse with age.

Table 8: Comparison of the strength of migratory connectivity of the different methods (MC and r_M) by age groups. The first row shows the mean, while the values in brackets indicate the 95% credible intervals.

Age Group	MC	r_m	Mean
Juveniles	0.331 (0.318 - 0.344)	0.340 (0.293 - 0.390)	0.336 (0.306 - 0.367)
Immatures	0.279 (0.252 - 0.304)	0.282 (0.231 - 0.338)	0.281 (0.242 - 0.321)
Adults	0.266 (0.249 - 0.286)	0.240 (0.176 - 0.291)	0.253 (0.213 - 0.289)
All ages	0.276 (0.266 - 0.286)	0.249 (0.223 - 0.281)	0.263 (0.245 - 0.284)
All ages (One cycle per individual)	0.288 (0.272 – 0.301)	0.238 (0.200 -0.278)	0.263 (0.236 - 0.290)

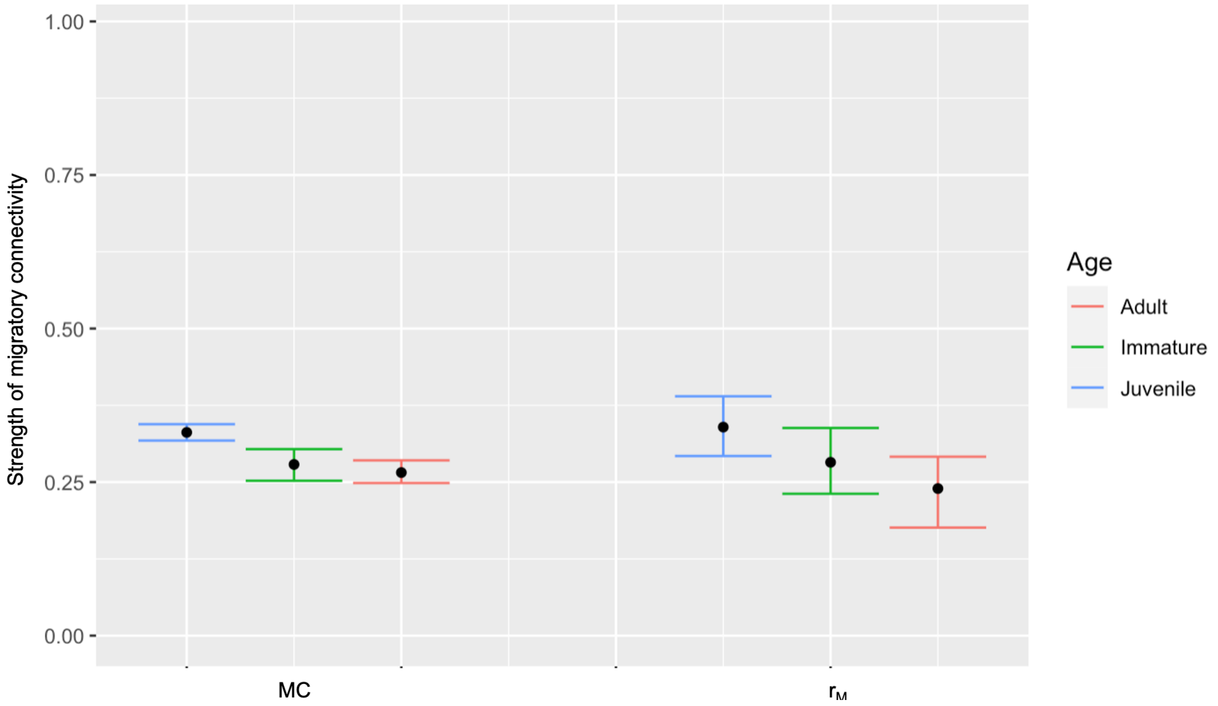

Figure 16: Age-structured migratory connectivity computed by MC and r_M. The black dots represent the mean values and the colored error bars show the 95% credible intervals of the age-structed migratory connectivity.

5.2.3. Population spread

The population spread of individuals within a population indicated significant differences between different breeding populations (*Figure 17*). Values close to 0 km suggest that there was no spreading of individuals in overwintering, which was mainly found in resident-dominated populations such as the Balearic Islands, British Isles, South, and the Iberian Peninsula. Although the average spread was close to zero, the Iberian population showed large distance variances compared to other resident-dominated populations, suggesting some migrating individuals within the population. All other populations showed a population spread during the overwintering season as the pairwise distance increased compared to the breeding season. The highest variability occurred in the eastern population, likely due to the diverse migration strategies of individuals who can stay resident throughout the year, and migrate to western or eastern overwintering sites. All populations with a high spread showed big variances, even into negative values, which means some individuals got closer to each other in the overwintering compared to the breeding season.

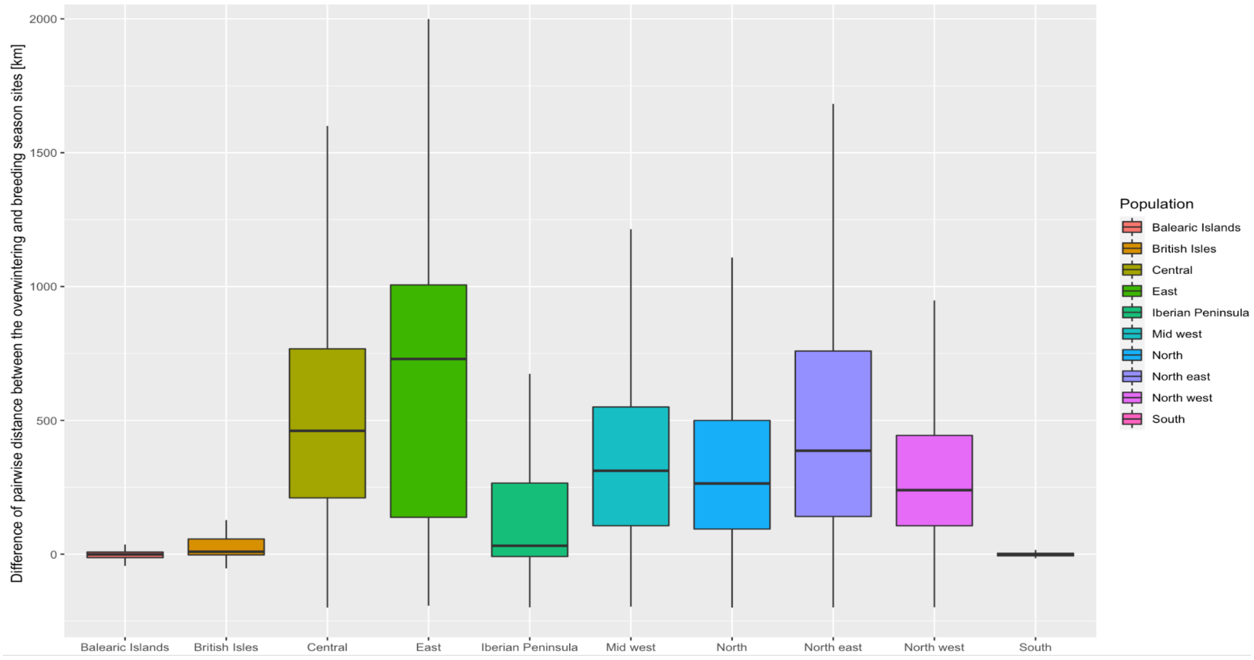

Figure 17: Boxplot of the population spread calculated by the difference between the pairwise distance of individuals of the breeding and the overwintering location by the breeding population. Large positive values indicate that individuals within a population were spreading out during overwintering, values around 0 suggest no relative difference between the individuals during different seasons, while negative values are associated with individuals who stayed closer together during overwintering in comparison to the breeding season.

6. Discussion

In this chapter, the results presented in the previous chapter are discussed in detail, and the research questions are answered. As this thesis focused on the methodological aspect, the findings need to be elaborated in greater depth by an ornithologist to finally assess the impact on the ecology of the red kite.

6.1. RQ - 1: Migration strategies by age and breeding season location

The first research question focused on the effect of breeding season location and age on different migration strategies in a continuous space. Three migration strategies were distinguished: year-round residents, migration to western wintering grounds, and migration to eastern wintering grounds.

The results of this thesis revealed that the migration strategy of red kites differs spatially over the species' global range. Individuals at some breeding sites almost exclusively use the same strategy. In contrast, individuals at other breeding sites use a wide range of migration strategies, suggesting a large inter-population and intra-population variability of migration strategies. Moreover, individuals may even change their migration strategy over the course of their lives. Island Populations, e.g., the British Isles and the Balearic Islands, showed a very low variability of migration strategies as all individuals were residents throughout the year. Furthermore, at some northern European breeding sites, all the individuals migrate to the western wintering grounds. A location-specific large-scale effect was found where red kites that spend their breeding season at northern latitudes are more likely to migrate than southern individuals. The red kite population in the British Isles is an exception, as individuals are resident throughout the year despite the high latitude of the breeding site. Not only the migration strategy but also the direct migration distance varies spatially across the breeding range. Since most birds migrate to the Iberian Peninsula, birds that stay in northern breeding grounds have to travel long distances to reach southern wintering grounds. Migration strategies of adult birds were calculated for the total breeding population. Over 54% of the breeding pairs migrate to western wintering areas, while over 44% stay resident throughout the year, and just over 1% migrate to eastern wintering areas. The eastern wintering areas are only used by eastern breeding populations, which have a low abundance. Thus only a tiny part of the total population migrates to the eastern wintering areas.

To better evaluate the model predictions, an uncertainty analysis was performed. While the model is relatively good at predicting migration strategy at some locations, other regions are highly uncertain. The high level of uncertainty is primarily due to two reasons. First, some areas have no or only a few annual cycles and thus do not have sufficient tracking data to make meaningful predictions. Second, the phenomena is a highly complex small and large-scale pattern of a variable in space, which makes it difficult for a model to make reliable predictions for all cases. Although the models' uncertainty can reach high values, this information is beneficial in interpreting the results.

Moreover, a migratory divide was identified roughly along the border between Austria and Slovakia northward through Poland. Individuals residing west of this imaginary border tend to migrate with high probability to the southwestern breeding grounds in the Iberian Peninsula and southern France. Individuals staying easterly of this border tend to migrate to Italy and the Balkan. The migration strategy of red kites is strongly influenced by the longitude of the breeding season location, as migration to eastern wintering grounds occurs only in eastern populations. However, there is an intermediate range where individuals can migrate westward and eastward, so both strategies co-exist. Yet, the area of the migratory divide is very sparsely populated, especially in Poland, and there is too little tracking data available to precisely extract the migratory divide. Thus, there is potential to study the extent of the co-occurrence of both migration strategies and the location of the migratory divide by gathering more tracking data in the area highlighted in this thesis. Evidence was found that the migration distance is much shorter for individuals migrating to the southeast. Energy efficiency serves as a general explanation for bird migration at various scales, from individual behavior to global patterns (Somveille et al., 2021). Individuals may migrate to the eastern winter grounds when the migration distance is much shorter compared to the western wintering grounds. Hence, suggesting that the higher amount of energy needed for the migration to western wintering grounds is compensated with better overwintering areas. Future research may investigate the ecological reasons and factors that lead to the migration divide in the first place. This will give new insights into an essential aspect of the red kites movement ecology.

Age influence was examined across the breeding range to investigate if, how, and where age impacts migration strategies. The major age effect found in this work was an increase in the residency rate of older birds. This means that younger birds tend to migrate with a higher likelihood, and as the birds get older, the possibility of staying resident increases. Age-related differential migration of the red kite has been revealed, which even results in a partial migration caused by age. However, this phenomenon does not occur everywhere to the same extent, nor are all places affected by this phenomenon. Roughly one-third of the species' global range showed a significant age effect. The main changes in the birds' migration strategy with age were observed in Spain, southern France, Switzerland, and parts of Germany, Poland, and Austria. The age effect does not only appear on a coarse scale, e.g., on a north-south gradient but also shows more complex structures, such as a significant age effect in Switzerland. Interestingly, the direct migration distance of migrating individuals did not differ significantly by age. Hence, age only affects the probability of migration, but when a red kite migrates, the distance is independent of age.

In general, age-dependent migration behavior is not uncommon, and migration may differ in timing, route, or distance; and in extreme cases, one of the age groups is not migrating while others do (Wille & Klaassen, 2022). Sometimes partial migration manifests in different migration strategies stratified by age, often occurring in marine animals (Wille & Klaassen, 2022). However, a partial migration, where juveniles migrate, and adults stay resident, is uncommon for birds. A passerine bird's partial migration appeared to be due to structural size and immune function rather than age dependence (Hegemann et al., 2015). Since this behavior occurs in the red kite and not in other bird species, it is essential to find the causes.

The dominance hypothesis might explain the strong age effect and the resulting partial migration of red kites. The dominance hypothesis describes competition for food, in which dominant (typically older) individuals outcompete subordinates for scarce food resources during the winter months; hence, dominants are able to stay residents all year round, while subordinates migrate to areas where food competition is less intense (Boyle, 2008; Ketterson & Nolan, 1976). One ecological reason which could potentially lead to a residency with age is population density. Population densities of the red kite are very high in both Switzerland and eastern Germany (Knaus et al., 2018), where increasing residency with age has been revealed. One possible explanation is the early arrival theory, which assumes that birds that arrive earlier at the breeding site can acquire better territories and thus have advantages in mating (Kokko, 1999). Hence, if breeding birds stay resident all year round, they have a guaranteed territory and possibly benefit from reproduction.

Anthropogenic feeding may be another reason for the observed age effect. In some regions (e.g., Switzerland), feeding of red kites is quite common, and the feeding rate was exceptionally high during winter (Cereghetti et al., 2019). A large food availability just before the fall migration could influence the migratory behavior of individuals and thus lead to more residency. Particularly because changes in food availability significantly impact the ecology and dynamics of bird populations (Newton, 1998; Robb et al., 2008), with many bird species particularly affected by the presence of anthropogenic food (Jones & James Reynolds, 2008). However, the question of whether and why anthropogenic feeding primarily influences the migratory behavior of adult birds would have to be explained first. This master thesis has shown that birds become more resident with increasing age, but the ecological explanation has not yet been identified. As a result, the following research gaps exist: Why do migrating juvenile birds become year-round resident adults in certain red kite populations, and what factors determine this transition?

This thesis demonstrated a novel approach to modeling the diverse migration behavior of bird species in continuous space over the whole species global range, including age as an additional factor. The complex space-time pattern was modeled by a multinomial BAMLSS model based on the breeding season location and bird age.

6.2. RQ - 2: Age-structured migratory connectivity

The second research question looks at red kites' age-specific migratory connectivity between breeding season and wintering locations. The migratory connectivity analysis of this chapter is exceptionally due to 1. the almost continuous tracking data over the species' global range, 2. the sheer number of tracked individuals of one species, 3. the age-structured component of the migratory connectivity, and 4. the first analysis of migratory connectivity for the species of red kites. Hereby, as observed in the previous chapter, red kites can change their migration strategies with age. Thus, age-related differential migration is expected to impact the migratory connectivity of red kites.

Most studies in the field of migratory connectivity looked at individuals' breeding and wintering sites. Then, migratory connectivity was calculated using the Mantel correlation coefficient (r_M) or MC (Ambrosini et al., 2009; Cohen et al., 2018). In this work, both methods were used to compute the strength of migratory connectivity and both approaches were compared. MC incorporates species abundance, which also allows addressing the sampling strategy bias, yet results in no longer considering the breeding and wintering sites continuously in space. Thus, if the strength of migration connectivity of the two methods differs substantially, either a sampling strategy bias (for r_M) or region classification (for MC) would be the trigger. The strength of migratory connectivity is quite constituent for both methods for all subset computations, with a value of 0.276, respectively 0.249 for MC and r_M for the entire dataset. Thus, these values indicate low migratory connectivity, with most likely a high inter-population mixing (Finch et al., 2017). While low connectivity can facilitate rapid range shifts, but it may not be a good strategy when overall habitat availability is limited, such as by climate change. (Finch et al., 2017). For a species with a large spread and low connectivity, changes in the availability or quality of non-breeding habitats have a diffuse but far-reaching effect on breeding populations of a species (Finch et al., 2017; Taylor & Norris, 2010).

To contextualize the weak migration connectivity of the red kite, it can be compared to the migration connectivity of other bird species. The Egyptian vulture, another widespread raptor species, showed a very strong migratory connectivity (Phipps et al., 2019). However, high connectivity is unusual for species with large overwintering spread (Finch et al., 2017). Also, the European population of the lesser kestrel showed a strong migratory connectivity (Sarà et al., 2019). In contrast, most of the 28 long-distance migratory land-bird species had a low connectivity (Finch et al., 2017). However, direct comparisons to other species are difficult, as the red kite is an exception among the bird species evaluated so far; firstly, it migrates only over short distances; secondly, connectivity has not yet been determined for a species with partial migration. The strength of the migratory connectivity is underestimated when the sampling strategy is spatially limited to a subarea; furthermore, a small sample size of less than 100 leads to substantial changes (Vickers et al., 2021). Because this study used an extensive dataset (n > 1000) that is well distributed across the breeding range, the sampling strategy is likely to have little effect on the connectivity.

So far, the impact of differential migration on the strength of migratory connectivity has not been demonstrated in any species, probably because an extensive movement data set with different demographic characteristics must be available for this. Here, for the first time, the influence of differential migration on connectivity was determined with different age groups (juveniles, immatures, and adults). Juvenile birds show the strongest connectivity, which decreases with increasing age. Both methods (r_M and MC) agree that the strength of migratory connectivity is significantly higher for juveniles than adults. Thus, an age effect on migratory connectivity could be confirmed for red kites. The migratory connectivity of immature birds was between the values of juvenile and adult birds, whereby migratory connectivity of red kites can be assumed to decrease with the age of the birds. Thus, the unraveled age-structured migratory connectivity proposes that differential migration is likely to affect the connectivity of species. The higher migratory connectivity of juvenile birds suggests that they are potentially more endangered if the quality of essential wintering sites decreases as individuals conduct a more similar overwintering strategy. As seen in the results, the Iberian Peninsula is the main wintering site, particularly important for young birds. Thus, if the quality of the Iberian wintering grounds declines, younger birds will suffer greater consequences due to higher mixing. On the other hand, deterioration of wintering habitats in, e.g., northern latitudes, has a more substantial effect on adult birds, as they have lower connectivity and a higher tendency to residency. However, to have a thriving red kite population, both adult and young birds need to be protected appropriately. Many monitoring programs focus on adult breeding birds, but this thesis demonstrates that juvenile birds have a different migration behavior and stronger migratory connectivity. These monitoring programs may be suboptimal, as changes in juvenile mortality have a delayed effect on the breeding population.

Furthermore, the population-specific transition probabilities of the individuals were extracted. The transition probabilities complement the results of the first research question by summarizing breeding areas at the regional level and providing a more refined decomposition of migratory movements to the wintering grounds. Thus, the migration to western wintering areas is classified more precisely, showing, for example, whether the birds winter more often in the Iberian Peninsula or southern France. Large-scale patterns become apparent, such as individuals of the northern populations migrating to great parts to the Iberian Peninsula and partly to southern France. Thus, high mortality rates in these wintering areas would also affect many breeding populations. Poisoning is the main reason for the high mortality of red kites (Knott et al., 2009; Mattsson et al., 2022), therefore, effective poison prevention measures at this wintering site would have a positive effect on many breeding populations.

Individuals of the eastern population additionally migrate to Italy and the Balkans. Southern and island populations generally stay in their region and do not migrate to another area. While in research question 1, a Spanish juvenile migrating 400 kilometers south from northern Spain would be identified as migrating to the western breeding ground, in this transition probability approach, it would remain in the same region. Hence, the breeding and wintering areas would have to be divided into finer sections to capture the small migrations. Furthermore, it was demonstrated that the British Isles and the Balearic Islands populations are decoupled from the others. Neither do animals migrate from these two regions to others, nor do individuals from other regions overwinter in these areas. Detecting these enclosed populations reveals insights into the genetic inheritance and disease transmission. Enclosed subpopulations lead to limited gene flow among subpopulations, and thus local adaptation and potential for speciation are expected (Marra et al., 2006).

Last, substantial inter-population differences were observed. Almost no population spread occurs in resident-dominated populations (Balearic Islands, British Isles, Italy, and the Iberian Peninsula) due to the limited movement of individual birds between seasons. However, the Iberian population has a relatively large variation in population spread, indicating some inter-seasonal movements. The higher variation is explained in the previous sections by the short migrations of predominantly young birds. On the other hand, a high population spread occurs in populations with high migration probabilities. The highest population spread appeared in the eastern population, likely due to the diverse migration strategies of individuals who can stay resident throughout the year or migrate to western or eastern overwintering sites. The population spread provides additional insightful information about the overwintering behavior of different populations. Populations with a smaller population spread are more susceptible to changes in their overwintering grounds because large parts of the populations are affected.

7. Conclusion

7.1. Contributions

This thesis has built on the work of countless ornithologists and organizations who have independently tagged red kites with a tracking device, which allowed the creation of this unprecedented dataset in size and distribution of one bird species. Based on this data set, the migration behavior of red kites was studied in great detail.

A novel approach to model the migratory behavior of birds continuously over the entire species range was presented. Moreover, the different migration strategies were investigated by breeding season location and bird age, providing a deep insight into red kite migration ecology. The migration behavior of red kites varies across the breeding season location and with the bird's age. Migration strategies differ between populations as well as within populations. While in some populations, all individuals follow the same migration strategy, there are populations where individuals exhibit different strategies. In southern and island populations, many red kites stay resident throughout the year, while most birds of northern populations are migrating to wintering grounds. A migration divide between migration to western and eastern winter ranges could be identified, whereby along a narrow band, both migration strategies co-exist. Depending on location, red kite migration behavior may be influenced by age. Here it was discovered that an age-induced differential migration exists, in which young birds migrate more frequently and old birds remain resident more frequently.

By combining the tracking data, migratory connectivity could be inferred not only over the entire range but also on an age-specific basis. For the first time, the strength of migratory connectivity was calculated for the red kit, resulting in a low strength of migratory connectivity. However, age-structured migratory connectivity was revealed, whereas the strength decreased with age. Thus, leading to consequences for the population dynamics and the optimal conservation of the species. Most migrating individuals of various populations overwinter in the Iberian Peninsula. The relatively large mixture in the main wintering area promotes, e.g., disease transmission, especially for younger birds, as they mix stronger.

The results of this work help improve the understanding of the movement behavior of red kites and thus helps to enhance the protection of the species and make it more efficient.

7.2. Limitations

Due to the scope of the topic and limited resources, certain limitations apply to this thesis. First, tracking data were limited in certain areas (e.g., Sweden, Baltic countries, Ukraine). Even though, except for Sweden, breeding populations are very small, this still affects the results of this thesis. Therefore, in addition to the probabilities of the migration strategies, the uncertainties of the model were calculated. Knowledge of uncertainty was incorporated into specific methods, but the exact behavior in these locations remains uncertain and is, therefore, a limitation of this thesis. Further, Bayesian regression models allow a variety of ways to set up the model, though not all have been explored. Thus, the model may still be improved further.

In addition, some calculations are based on breeding pair abundance data, which shows substantial disparities depending on the location. The final calculation of the number of birds following a given migration strategy and the measure of the strength of migratory connectivity using the MC method was subject to uncertainties regarding abundance. In the next step, the uncertainty of the breeding pair abundance should be included in the calculations to estimate its influence better. Further, if more accurate breeding numbers are available, the evaluations could be recalculated to get more accurate results.

Another limitation of this master thesis is that migratory connectivity was calculated on the individual's location during breeding season and overwintering. Analyzing the migratory connectivity on a finer temporal scale would bring new insight into the red kites movement ecology. Further, subsequent years were examined independently of each other. The return link from the wintering area to the breeding area was not investigated, and thus, dispersal phenomena were disregarded.

Moreover, the main focus of this thesis was the revealing the age-structured migratory connectivity. However, more research is needed to identify the ecological reasons for the observed phenomena.

7.3. Future research

The field of migratory connectivity is being heavily studied today and still offers room for new methods. Especially, finding appropriate measures for a full annual migratory connectivity with a fine temporal resolution has much potential for future research. In the field of migratory connectivity, there is still much potential for methodological research.

The mechanism for the different migratory behaviors needs to be studied in more detail in red kite research. However, this is a vast topic and therefore allows focused studies per subtopic. Hereby, the ecological reasoning behind the increase in residency with age remains to be found. The cause of why individuals of some populations show an age effect in their migration strategies while others do not has yet to be resolved. Thus, another research gap is, studying whether individuals from central European populations are more frequently becoming residents with age if they are breeding in an area with a dense red kite population. In addition, the impact of the age effect of migration strategies on population dynamics should be investigated. Moreover, the migratory divide and the co-occurrence of migration to eastern and western wintering grounds could be studied more in-depth by selectively tagging individuals at breeding sites of particular interest, highlighted in this study. Also, the ecological reason for the migratory divide has not yet been determined.

The current LIFE EUROKITE project is studying red kite mortality in many breeding and wintering areas, including using studies red kite mortality in many breeding and wintering areas, including tracking data. (LIFE EUROKITE, 2021). In this context, knowledge of where, when, and why red kites die can be combined with the knowledge of red kite migratory connectivity obtained in this thesis to identify the effects of increased local mortality on different breeding populations. Which ultimately approaches the great goal of conservation of the species.

8. Literature

Aebischer, A. (2009). Distribution and recent population changes of the Red Kite in the Western Palaearctic — results of a recent comprehensive inquiry. *Red Kite International Symposium, October 17th & 18th 2009*, 12–14.

Aebischer, A., & Scherler, P. (2021). *Der Rotmilan: Ein Greifvogel im Aufwind*. Haupt Verlag. Bern, Switzerland.

Ambrosini, R., Møller, A. P., & Saino, N. (2009). A quantitative measure of migratory connectivity. *Journal of Theoretical Biology*, *257*(2), 203–211. https://doi.org/10.1016/j.jtbi.2008.11.019

Bauer, S., Lisovski, S., & Hahn, S. (2016). Timing is crucial for consequences of migratory connectivity. *Oikos*, *125*(5), 605–612. https://doi.org/10.1111/oik.02706

BirdLife International. (2022). *Species factsheet: Milvus milvus*. http://www.birdlife.org

Bobek, M., Hampl, R., Peške, L., Pojer, F., Šimek, J., & Bureš, S. (2008). African Odyssey project - Satellite tracking of black storks Ciconia nigra breeding at a migratory divide. *Journal of Avian Biology*, *39*(5), 500–506. https://doi.org/10.1111/j.0908-8857.2008.04285.x

Boyle, W. A. (2008). Partial migration in birds: Tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology*, *77*(6), 1122–1128. https://doi.org/10.1111/j.1365-2656.2008.01451.x

Briedis, M., & Bauer, S. (2018). Migratory connectivity in the context of differential migration. *Biology Letters*, *14*(12). https://doi.org/10.1098/rsbl.2018.0679

Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Krist, M., Liechti, F., Lisovski, S., Meier, C. M., Procházka, P., & Hahn, S. (2020). Broad-scale patterns of the Afro-Palaearctic landbird migration. *Global Ecology and Biogeography*, *29*(4), 722–735. https://doi.org/10.1111/geb.13063

Brum-Bastos, V., Łoś, M., Long, J. A., Nelson, T., & Demšar, U. (2022). Context-aware movement analysis in ecology: a systematic review. *International Journal of Geographical Information Science*, *36*(2), 405–427. https://doi.org/10.1080/13658816.2021.1962528

Cereghetti, E., Scherler, P., Fattebert, J., & Grüebler, M. U. (2019). Quantification of anthropogenic food subsidies to an avian facultative scavenger in urban and rural habitats. *Landscape and Urban Planning*, *190*. https://doi.org/10.1016/j.landurbplan.2019.103606

Cohen, E. B., Hostetler, J. A., Hallworth, M. T., Rushing, C. S., Sillett, T. S., & Marra, P. P. (2018). Quantifying the strength of migratory connectivity. *Methods in Ecology and Evolution*, *9*(3), 513–524. https://doi.org/10.1111/2041-210X.12916

Cristol, D. A., Baker, M. B., & Carbone, C. (1999). Differential migration revisited. In V. Nolan, E. D. Ketterson, & C. F. Thompson (Eds.), *Current Ornithology,* 15, 33–88. Springer. Boston, MA. https://doi.org/10.1007/978-1-4757-4901-4_2

Delmore, K. E., Van Doren, B. M., Conway, G. J., Curk, T., Garrido-Garduño, T., Germain, R. R., Hasselmann, T., Hiemer, D., Van Der Jeugd, H. P., Justen, H., Lugo Ramos, J. S., Maggini, I., Meyer, B. S., Phillips, R. J., Remisiewicz, M., Roberts, G. C. M., Sheldon, B. C., Vogl, W., & Liedvogel, M. (2020). Individual variability and versatility in an eco-evolutionary model of avian migration. *Proceedings of the Royal Society B*, *287*(1938). https://doi.org/10.1098/rspb.2020.1339

Dodge, S., Weibel, R., & Lautenschütz, A. K. (2008). Towards a taxonomy of movement patterns. *Information Visualization*, *7*(3–4), 240–252. https://doi.org/10.1057/palgrave.ivs.9500182

Evans, I. M., Summers, R. W., O'toole, L., Orr-Ewing, D. C., Evans, R., Snell, N., & Smith, J. (1999). Evaluating the success of translocating red kites milvus milvus to the uk. *Bird Study*, *46*(2), 129–144. https://doi.org/10.1080/00063659909461125

Fahrmeir, L., Kneib, T., Lang, S., & Marx, B. (2013). Regression: Models, methods and applications. In *Regression: Models, Methods and Applications*. Springer-Verlag. Berlin. https://doi.org/10.1007/978-3-642-34333-9/COVER

Finch, T., Butler, S. J., Franco, A. M. A., & Cresswell, W. (2017). Low migratory connectivity is common in long-distance migrant birds. *Journal of Animal Ecology*, *86*(3), 662–673. https://doi.org/10.1111/1365-2656.12635

Franklin, K. A., Nicoll, M. A. C., Butler, S. J., Norris, K., Ratcliffe, N., Nakagawa, S., & Gill, J. A. (2022). Individual repeatability of avian migration phenology: A systematic review and meta-analysis. *Journal of Animal Ecology*, *91*(7), 1416–1430. https://doi.org/10.1111/1365-2656.13697

Fudickar, A. M., Jahn, A. E., & Ketterson, E. D. (2021). Animal Migration: An overview of one of nature's great spectacles. *Annual Review of Ecology, Evolution, and Systematics*, *52*, 479–497. https://doi.org/10.1146/annurev-ecolsys-012021-031035

García-Macía, J., De La Puente, J., Bermejo-Bermejo, A., Raab, R., & Urios, V. (2022). High variability and dual strategy in the wintering Red Kites (Milvus Milvus). *Diversity*, *14*(2). https://doi.org/10.3390/d14020117

García-Macía, J., Vidal-Mateo, J., De La Puente, J., Bermejo, A., Raab, R., & Urios, V. (2022). Seasonal differences in migration strategies of Red Kites (Milvus milvus) wintering in Spain. *Journal of Ornithology*, *163*(1), 27–36. https://doi.org/10.1007/s10336-021-01918-5

Hastie, T., & Tibshirani, R. (1986). Generalized additive models. *Statistical Science*, *1*(3), 297–310. https://doi.org/10.1214/ss/1177013604

Hegemann, A., Marra, P. P., & Tieleman, B. I. (2015). Causes and consequences of partial migration in a passerine bird. *American Naturalist*, *186*(4), 531–546.

Heredia, B., Alonso, J. C., & Hiraldo, F. (1991). Space and habitat use by Red Kites Milvus milvus during winter in the Guadalquivir marshes: a comparison between resident and wintering populations. *Ibis*, *133*(4), 374–381. https://doi.org/10.1111/j.1474-919X.1991.tb04585.x

Jones, D. N., & James Reynolds, S. (2008). Feeding birds in our towns and cities: A global research opportunity. *Journal of Avian Biology*, *39*(3), 265–271. https://doi.org/10.1111/j.0908-8857.2008.04271.x

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240). https://doi.org/10.1126/science.aaa2478

Keller, V., Herrando, S., Vorisek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvanova, A., Kalyakin, M., Bauer, H., & Foppen, R. (2020). European Breeding Bird Atlas 2: Distribution, Abundance and Change. In *European Breeding Bird Atlas 2. Distribution, Abundance and Change*.

Ketterson, E. D., & Nolan, V. (1976). Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed Juncos (Junco Hyemalis Hyemalis). *Ecology*, *57*(4), 679–693. https://doi.org/10.2307/1936182

Knaus, P., Antoniazza, S., Samual, W., Guélat, J., Strebel, N., Sattler, T., & Kéry, M. (2018). *Schweizer Brutvogelatlas 2013–2016. Verbreitung und Bestandsentwicklung der Vögel in der Schweiz und im Fürstentum Liechtenstein*. Schweizerische Vogelwarte. Sempach, Schweiz.

Knight, S. M., Bradley, D. W., Clark, R. G., Gow, E. A., Bélisle, M., Berzins, L. L., Blake, T., Bridge, E. S., Burke, L., Dawson, R. D., Dunn, P. O., Garant, D., Holroyd, G. L., Hussell, D. J. T., Lansdorp, O., Laughlin, A. J., Leonard, M. L., Pelletier, F., Shutler, D., … Norris, D. R. (2018). Constructing and evaluating a continent-wide migratory songbird network across the annual cycle. *Ecological Monographs*, *88*(3), 445–460. https://doi.org/10.1002/ecm.1298

Knott, J., Newbery, P., & Barov, B. (2009). Action plan for the red kite Milvus milvus in the European Union. *BirdLife International, European Union, Brussels, Belgium*, 1–55.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*(5), 940–950.

Kramer, G. R., Andersen, D. E., Buehler, D. A., Wood, P. B., Peterson, S. M., Lehman, J. A., Aldinger, K. R., Bulluck, L. P., Harding, S., Jones, J. A., Loegering, J. P., Smalling, C., Vallender, R., & Streby, H. M. (2018). Population trends in Vermivora warblers are linked to strong migratory connectivity.

Proceedings of the National Academy of Sciences, *115*(14). https://doi.org/10.1073/pnas.1718985115

LIFE EUROKITE. (2021). *Winter count of the red kite roosting sites in whole europe*. Mitteleuropäische Gesellschaft zur Erhaltung der Greifvögel (MEGEG), Zurndorf, Austria.

Literák, I., Horal, D., Raab, R., Matušík, H., Vyhnal, S., Rymešová, D., Spakovszky, P., Skartsi, T., Poirazidis, K., Zakkak, S., Tomik, A., & Skyrpan, M. (2019). Sympatric wintering of Red Kites and Black Kites in south-east Europe. *Acta Zoologica Academiae Scientiarum Hungaricae*, *65*(4), 381–398. https://doi.org/10.17109/AZH.65.4.381.2019

Literák, I., Raab, R., Škrábal, J., Vyhnal, S., Dostál, M., Matušík, H., Makoň, K., Maderič, B., & Spakovszky, P. (2022). Dispersal and philopatry in Central European Red Kites Milvus milvus. *Journal of Ornithology*, *163*, 469–479. https://doi.org/10.1007/s10336-021-01950-5

Literák, I., Raab, R., Vyhnal, S., Spakovszky, P., & Steindl, J. (2018). Occurrence of Red Kites Milvus milvus in Serbia based on birds tracked by telemetry devices. *Acrocephalus*, *39*(176–177), 27–32. https://doi.org/10.1515/acro-2018-0002

Maciorowski, G., Kosicki, J., Polakowski, M., Urbańska, M., Zduniak, P., & Tryjanowski, P. (2019). Autumn migration of immature red kites milvus milvus from a central European population. *Acta Ornithologica*, *54*(1), 45–50. https://doi.org/10.3161/00016454AO2019.54.1.004

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*(2), 209–220.

Marra, P., Cohen, E., Harrison, A.-L., Studds, C., & Webster, M. (2019). Migratory connectivity. In *Encyclopedia of Animal Behavior*, 643–654. https://doi.org/10.1016/B978-0-12-809633-8.20761-9

Marra, P., Cohen, E., Loss, S., Rutter, J., & Tonra, C. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, *11*(8). https://doi.org/10.1098/rsbl.2015.0552

Marra, P., Norris, R., Haig, S., Webster, M., & Andrew Royle, J. (2006). Migratory connectivity. In K. R. Crooks & M. Sanjayan (Eds.), *Connectivity conservation*, 157–183. Cambridge University Press. London.

Mateo-Tomás, P., Olea, P. P., Mínguez, E., Mateo, R., & Viñuela, J. (2020). Direct evidence of poison-driven widespread population decline in a wild vertebrate. *Proceedings of the National Academy of Sciences*, *117*(28), 16418–16423. https://doi.org/10.1073/pnas.1922355117

Mattsson, B. J., Mateo-Tomás, P., Aebischer, A., Rösner, S., Kunz, F., Schöll, E. M., Åkesson, S., De Rosa, D., Orr-Ewing, D., Bodega, D. de la, Ferrer, M., Gelpke, C., Katzenberger, J., Maciorowski, G., Mammen, U., Kolbe, M., Millon, A., Mionnet, A., Puente, J. de la, … Viñuela, J. (2022). Enhancing monitoring and transboundary collaboration for conserving migratory species under global change: The priority case of the red kite. *Journal of Environmental Management*, *317*(115345), 1–17. https://doi.org/10.1016/j.jenvman.2022.115345

Mougeot, F., Garcia, J. T., & Viñuela, J. (2011). Breeding biology, behaviour, diet and conservation of the red kite (Milvus milvus), with particular emphasis on Mediterranean populations. In I. Zuberogoitia & J. E. Martínez (Eds.), *Ecology and conservation of European dwelling forest raptors and owls*, 190–204. Editorial Diputación Foral de Vizcaya. Bilbao, Spain.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

Nehm, K. (2020). *The overwintering movement behaviour of the Red Kite (Milvus milvus) in Switzerland*. Albert-Ludwigs-University Freiburg. Freiburg.

Newton, I. (1998). *Population limitation in birds*. Academic Press. London. https://doi.org/10.2307/4089355

Newton, I. (2007). The migration ecology of birds. In *The Migration Ecology of Birds*. Academic Press. https://doi.org/10.1016/B978-0-12-517367-4.X5000-1

Panter, C. T., Literák, I., Raab, R., Tolhurst, B. A., & White, R. L. (2022). Age, landscape, and arrival date explain ranging behavior of wintering red kites in southwest Europe. *Journal of Wildlife Management*, *86*(1). https://doi.org/10.1002/jwmg.22147

Panter, C. T., Xirouchakis, S., Danko, Matušík, H., Podzemný, P., Ovčiariková, S., & Literák, I. (2020). Kites (Milvus spp.) wintering on Crete. *European Zoological Journal*, *87*(1), 591–596. https://doi.org/10.1080/24750263.2020.1821801

Pfeiffer, T. (2009). Untersuchungen zur Altersstruktur von Brutvögeln beim Rotmilan (Milvus milvus). *Populationsökologie Greifvogel- Und Eulenarten*, *6*, 197–210.

Phipps, W. L., López-López, P., Buechley, E. R., Oppel, S., Álvarez, E., Arkumarev, V., Bekmansurov, R., Berger-Tal, O., Bermejo, A., Bounas, A., Alanís, I. C., de la Puente, J., Dobrev, V., Duriez, O., Efrat, R., Fréchet, G., García, J., Galán, M., García-Ripollés, C., … Vallverdú, N. (2019). Spatial and temporal variability in migration of a soaring raptor across three continents. *Frontiers in Ecology and Evolution*, *7*(323). https://doi.org/10.3389/fevo.2019.00323

Picardi, S., Smith, B. J., Boone, M. E., Frederick, P. C., Cecere, J. G., Rubolini, D., Serra, L., Pirrello, S., Borkhataria, R. R., & Basille, M. (2020). Analysis of movement recursions to detect reproductive events and estimate their fate in central place foragers. *Movement Ecology*, *8*(24). https://doi.org/10.1186/s40462-020-00201-1

Robb, G. N., McDonald, R. A., Chamberlain, D. E., & Bearhop, S. (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, *6*(9), 476–484. https://doi.org/10.1890/060152

Rushing, C. S., Andrew Royle, J., Ziolkowski, D. J., & Pardieck, K. L. (2020). Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. *Proceedings of the National Academy of Sciences*, *117*(23), 12897–12903.

Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, *131*(1), 93–105. https://doi.org/10.1016/j.biocon.2006.02.008

Sarà, M., Bondì, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., de la Puente, J., Evangelidis, A., Frassanito, A., Fulco, E., Giglio, G., Gradev, G., Griggio, M., López-Ricaurte, L., Kordopatis, P., Marin, S., Martínez, J., Mascara, R., Mellone, U., … Rubolini, D. (2019). Broad-front migration leads to strong migratory connectivity in the lesser kestrel (Falco naumanni). *Journal of Biogeography*, *46*(12), 2663–2677. https://doi.org/10.1111/jbi.13713

Scherler, P. (2020). *Drivers of departure and prospecting in dispersing juvenile Red Kites (Milvus milvus)*. University of Zurich.

Schreven, K. H. T., Stolz, C., Madsen, J., & Nolet, B. A. (2021). Nesting attempts and success of Arctic-breeding geese can be derived with high precision from accelerometry and GPS-tracking. *Animal Biotelemetry*, *9*(25), 1–13. https://doi.org/10.1186/s40317-021-00249-9

Somveille, M., Bay, R. A., Smith, T. B., Marra, P. P., & Ruegg, K. C. (2021). A general theory of avian migratory connectivity. *Ecology Letters*, *24*(9), 1848–1858. https://doi.org/10.1111/ele.13817

Spatz, T., Katzenberger, J., Friess, N., Gelpke, C., Gottschalk, E., Hormann, M., Koschkar, S., Pfeiffer, T., Stübing, S., Sudfeldt, C., Rösner, S., Schabo, D. G., & Farwig, N. (2022). Sex, landscape diversity and primary productivity shape the seasonal space use of a migratory European raptor. *Journal of Avian Biology*, *e02925*. https://doi.org/10.1111/JAV.02925

Stevens, M., Murn, C., & Hennessey, R. (2020). Population change of Red Kites Milvus milvus in Central Southern England between 2011 and 2016 derived from line transect surveys and multiple covariate distance sampling. *Acta Ornithologica*, *54*(2), 243–254. https://doi.org/10.3161/00016454AO2019.54.2.010

Taylor, C. M., & Norris, D. R. (2010). Population dynamics in migratory networks. *Theoretical Ecology*, *3*, 65–73. https://doi.org/10.1007/s12080-009-0054-4

Trierweiler, C., Klaassen, R. H. G., Drent, R. H., Exo, K.-M., Komdeur, J., Bairlein, F., & Koks, B. J. (2014). Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society B*, *281*(1778), 1–9. https://doi.org/10.1098/RSPB.2013.2897

Umlauf, N., Klein, N., & Zeileis, A. (2018). BAMLSS: Bayesian Additive Models for Location, Scale, and Shape (and Beyond). *Journal of Computational and Graphical Statistics*, *27*(3), 612–627. https://doi.org/10.1080/10618600.2017.1407325

Umlauf, N., Klein, N., Zeileis, A., & Thorsten, S. (2017). *bamlss: Bayesian Additive Models for Location Scale and Shape (and Beyond), R Package*. https://doi.org/10.1080/10618600.2017.1407325

van Bemmelen, R. S. A., Kolbeinsson, Y., Ramos, R., Gilg, O., Alves, J. A., Smith, M., Schekkerman, H., Lehikoinen, A., Petersen, I. K., Þórisson, B., Sokolov, A. A., Välimäki, K., van der Meer, T., David Okill, J., Bolton, M., Moe, B., Hanssen, S. A., Bollache, L., Petersen, A., … Tulp, I. (2019). A migratory divide among red-necked phalaropes in the Western Palearctic reveals contrasting migration and wintering movement strategies. *Frontiers in Ecology and Evolution*, *7*(86). https://doi.org/10.3389/fevo.2019.00086

Vickers, S. H., Franco, A. M. A., & Gilroy, J. J. (2021). Sensitivity of migratory connectivity estimates to spatial sampling design. *Movement Ecology*, *9*(16), 1–12. https://doi.org/10.1186/s40462-021-00254-w

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395. https://doi.org/10.1038/416389a

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution*, *17*(2), 76–83. https://doi.org/10.1016/S0169-5347(01)02380-1

Wille, M., & Klaassen, M. (2022). Should I stay, should I go, or something in between? The potential for parasite-mediated and age-related differential migration strategies. *Evolutionary Ecology*, 1–14. https://doi.org/10.1007/s10682-022-10190-9

R packages

bamlss, 1.1-7

dplyr, 1.0.6

geosphere, 1.5-10

geodist, 0.0.7

ggplot2, 3.3.5

grDevices, 4.1.0

migConnectivity, 0.4.1

mgcv, 1.8-35

move, 4.0.6

sf, 1.0-1

spdep, 1.1-8

spacey, 0.1.1

rgeos, 0.5-5

Appendix A

Identifying the main overwintering period

A minimum displacement approach was used to determine the main overwintering period. The same method was used in section 4.1.2 to extract the breeding season and wintering location. For each bird, the daily displacement was generated using a one-day moving window in which all GPS data points within 14 days were used to compute the centroid. Then, the average deviation of the 29 locations to the centroid was calculated. The individual bird displacements were then combined by averaging on the day of the year. The average displacement of all birds from late autumn to early spring showed high displacement values in November and early December due to the ongoing migration of individuals. From mid of December to mid of January, the displacement reached a low level, meaning most birds stayed stationary during this time period (349th to the 24th day of the year). Hence, the low level corresponded to the main wintering period of red kites, and this period was used for the overwintering site extraction.

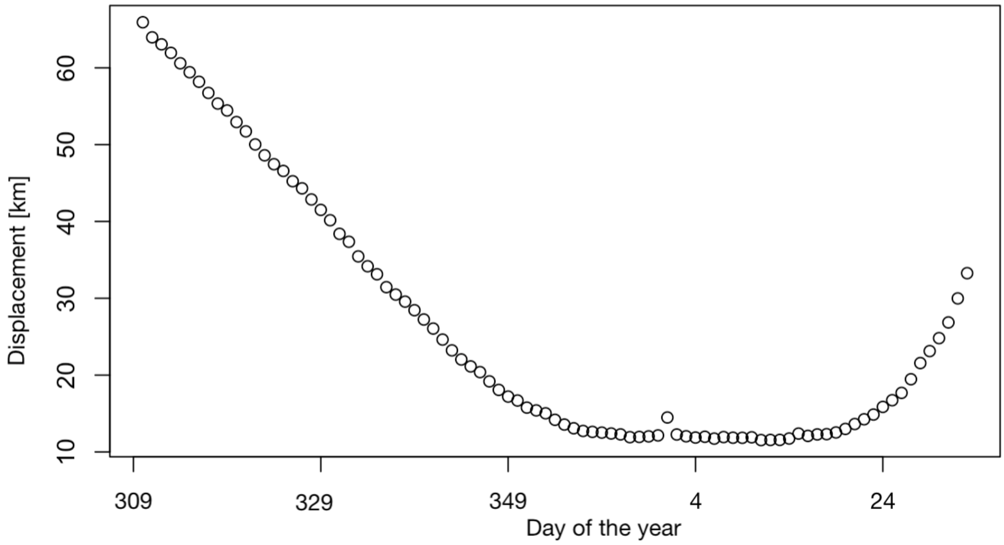

Figure 18: Mean displacement of all tracked red kites between late autumn and early spring. High values indicate large movements of individuals, e.g., ongoing migration. Low values occur when a large proportion of birds do not move over a large extent for several days and hence can be associated with the main wintering period.

Appendix B

Validation of the breeding season location

Validation was performed to ensure the quality of the breeding season location extraction. Hereby, the extracted breeding season locations were compared to a reference data set. Researchers of the Swiss Ornithological Institute went to the field to observe the tracked red kites and searched for their nests. Three hundred sixty-four identified bird nests corresponded to tracked individuals of a specific year. Thus, the distance between the observed nests and the solely data-based breeding season locations extraction approach were compared individually (*Figure 19*). Of these bird nests, 248 corresponded to year-round resident birds. For resident birds, the breeding season location detection worked with very high precision since all birds showed a distance difference below 1.5 kilometers except one nest having a difference of 3 kilometers. For migrating red kites, 116 nest locations were found. Most of the extracted breeding season locations differed from the nest by fewer than 1 kilometer. However, a few nests have a distance difference of up to 20 kilometers. For the context of our work, the accuracy is more than sufficient since any analyses are performed on a large scale in the European continent. The validation revealed that the extraction of breeding sites was performed precisely, at least for breeding adults. The breeding season location was not verified for immature and non-breeding adult birds as they did not build nests.

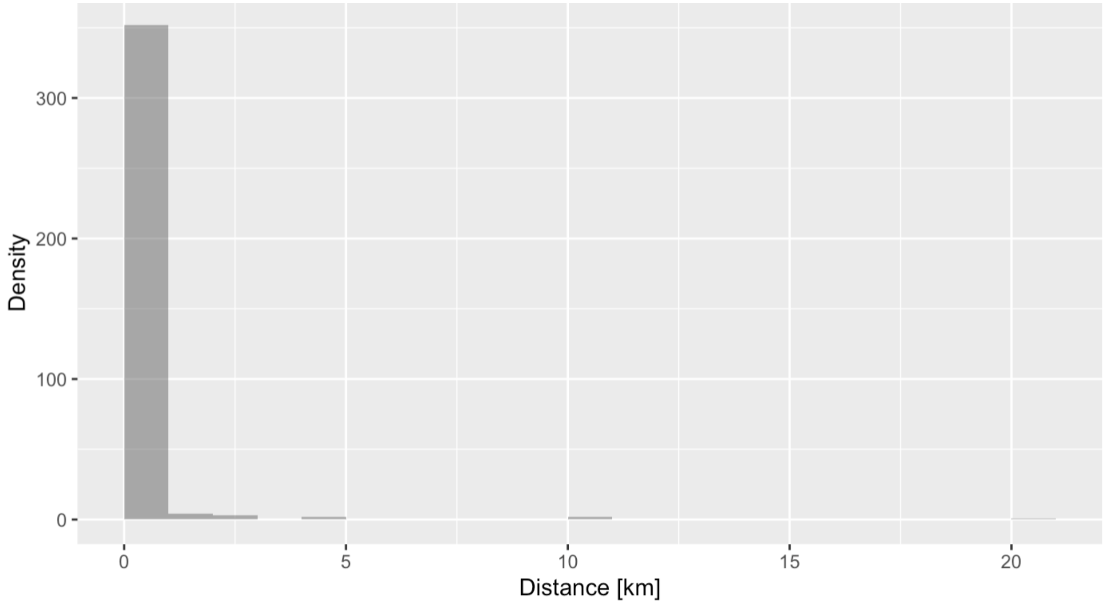

Figure 19: Frequency of the distance difference between observed nests and the extracted breeding season locations for red kites in Switzerland. The majority of the extracted breeding season locations were closer than 1 kilometer to the actual nest.

Appendix C

Breeding season location density

The breeding season location of all annual cycles were used to compute the tracking data breeding location density over the breeding range. Thus, for the whole breeding area, the number of breeding season locations within 200 km was determined (*Figure 20*). In Switzerland, as well as in large parts of Germany and the Czechian Republic a very large number of extracted breeding season locations was found. Yet, very low to absent breeding season sites were found in border regions of the breeding range (e.g., Southern Italy, Sweden, England and the Baltic Countries). The number of nearby breeding sites provides an indication of where the calculations of this thesis were inaccurate due to insufficient data.

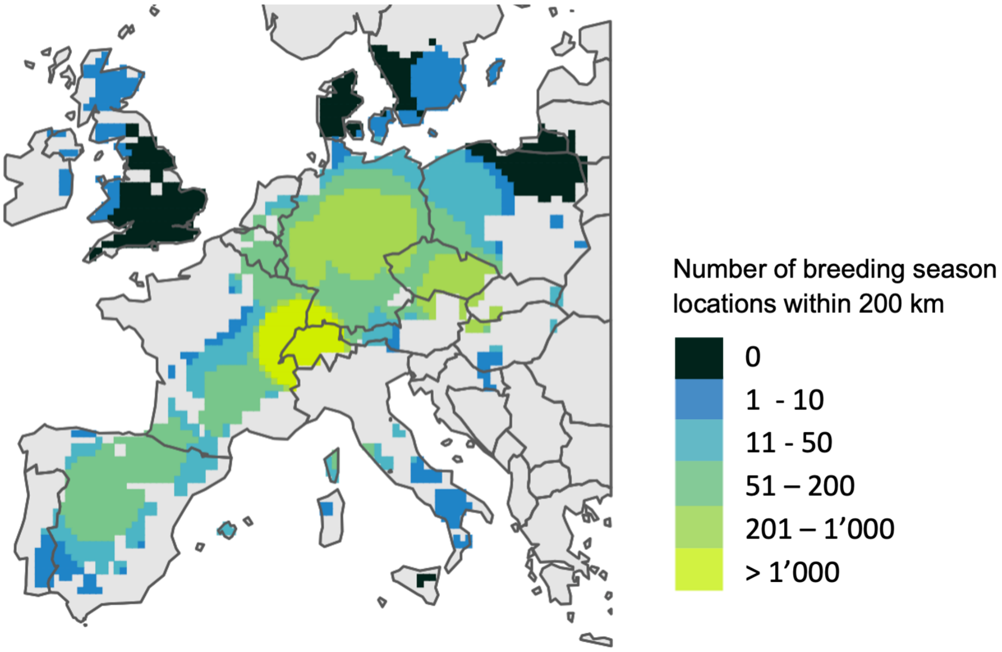

Figure 20: Number of breeding season locations within 200 km over the breeding range. The brighter the color the more data is available.

Appendix D

Generating a hexagonal neighborhood complex

The following procedure describes the process of the hexagonal neighborhood layer, which was used as a smooth term in the BAMLSS model. First, a convex hull of all breeding season locations was created (with the function `chull (grDevices)`. Then, a small buffer was applied with the function `gBuffer (rgeos)` to the convex hull so that the convex hull covers all locations. With `st_make_grid (sf),` a hexagonal grid was created with the size of 11 and 10 in longitudinal respectively latitudinal directions. Further, the hexagonal grid was converted to hexagonal polygons, and polygons that did not contain any breeding season locations were removed. However, because some hexagons contained only single annual cycles and thus did not represent the behavior of several years, hexagons containing annual cycles with only one age class were omitted. The function `poly2nb (spdep)` was used to calculate the neighborhood of the hexagons. This resulted in 22 hexagons corresponding to 4 neighborhood complexes: the British Isles, the Balearian Islands, Italy, and the rest of Europe (*Figure 21A*).

One more time, the breeding season locations were assigned to hexagons, this time, each breeding season location was assigned to the closest hexagon. Thus, the neighborhood complex and the reference to the hexagons of each breeding season location were passed to the BAMLSS model in the Markov Random Field.

On the other hand, each location needed an assigned hexagon for predicting the probabilities of the migration strategies. Thus, for each location, the nearest hexagon was determined and assigned, except for locations on the British Isles which were never assigned by distance but always to the British Hexagon. The assignment of the breeding range locations to the hexagonal neighborhood is shown in *Figure 21B*.

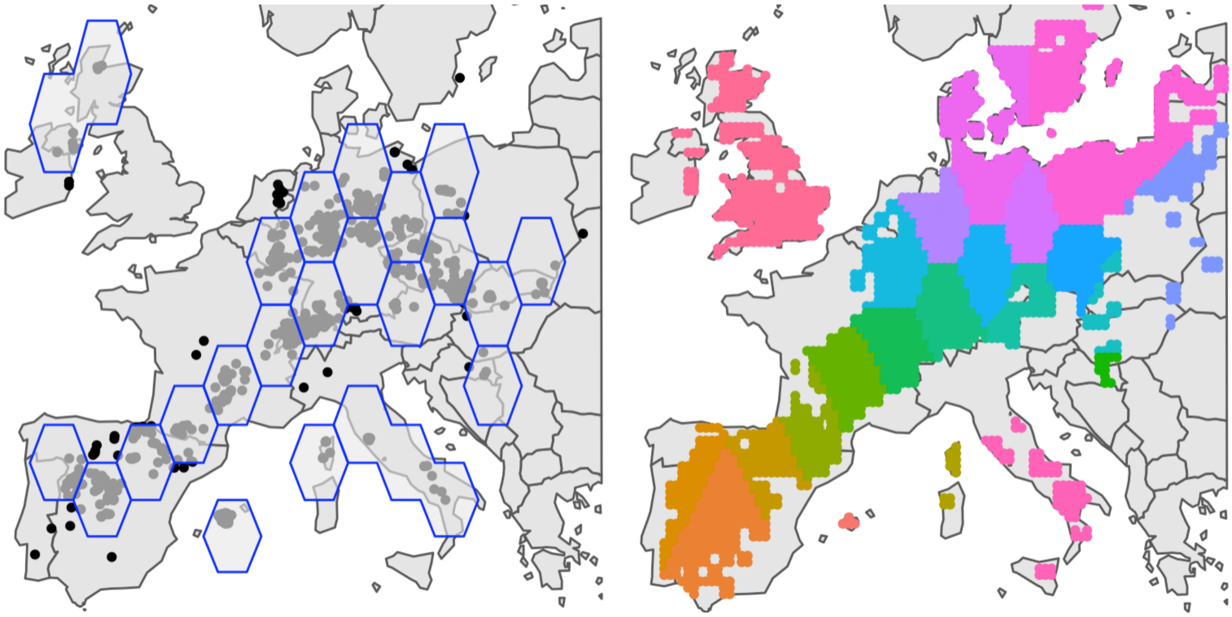

Figure 21: Hexagonal neighborhood complex used as a Markov Random Field smoother. ***(A)*** *Hexagons distributed over the breeding range in blue and breeding season locations are shown as a black dot.* ***(B)*** *Assignment of all locations of the breeding range to one of the hexagons of the neighborhood complex.*

Declaration of Authorship

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.

Date	Signature of the author
Lenzburg, 30.09.2022	M. Niederberger