Norwegian University
of Life Sciences

Master's Thesis 2021 60 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Area Uses and General Habitat Preferences of Ospreys

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Abstract

The area uses and general habitat preferences of ten ospreys from south-eastern Norway were studied in their home ranges, wintering areas, and during their migrations. The ospreys were tracked using GPS transmitters and their habitat preferences were analyzed using land cover maps based on satellite imagery. Habitat preferences were defined by the use of different habitat categories compared to the availability, and the distance to the different habitat categories compared to the expectation. Habitat preferences were compared between southward and northward migrations, between adult and juvenile ospreys during southward migrations, and between breeding years and non-breeding years for adults. The ospreys preferred forests in all seasons, they preferred open areas in their home ranges and during migration, and they preferred wetlands in their wintering areas. Water bodies were preferred in the ospreys' home ranges but were partly avoided during migration and in wintering areas. The ospreys used agricultural areas like the availability in all seasons, and preferred being closer to them in their home ranges and wintering areas. Bare land and urban areas were primarily avoided in all seasons, but some discrepancies were seen. Differences in the ospreys' habitat preferences were found between northward and southward migrations, possibly due to different migration strategies being used. Differences in habitat preferences between adults and juveniles were found, possibly due to the inexperience of juveniles. And differences were found in area uses and habitat preferences between breeding years and non-breeding years for adults, due to differences in behavior between years. The ospreys used the largest areas in their home ranges with a median size of 87.2 km^2 (95% minimum convex polygons). Their wintering areas had a median size of 57.4 km^2, and their stopover sites during migration had a median size of 2.5 km^2. Kernel core use areas of 50% and 95% were calculated for the different seasons as well, and areas were compared between adults and juveniles. This study has provided a general baseline in the knowledge of ospreys' area uses and habitat preferences, and the methodology shows promise in being able to study a migrating species' habitat preferences throughout the seasons using much less resources gathering data.

Acknowledgements

While I have studied ecology my interest in raptors has grown continuously, and I knew early on that my thesis would be on a raptor. My supervisor, Ronny Steen, held a class in vertebrae, where especially birds were in focus, during this class I understood that he was the one I should talk to about my thesis. When I finally talked to him about it, he already had a project in mind for me, because he knew I had a great interest in raptors, as well as a knack for computer programs, since I had been working in IT-support during my years at the university. When he first proposed the project to me, I thought it sounded very interesting, but I knew I wanted to do a lot of field work, so I was a bit skeptical. However, I was introduced to my other supervisor, Rune Aae, who is also the leader of a project which monitors, rings, and builds artificial nests for ospreys in south-eastern Norway. He invited me to come along ringing osprey chicks, and even collecting some chicks for translocation to Switzerland, and I was sold. The summer of climbing into osprey nests and ringing chicks was a great way to get to know the species, and I have no doubt I will continue working with ospreys. All the work in QGIS and RStudio has given me experience which will help me in many situations later. The whole experience of working with this project has been great, and I hope I will be able to continue working like this in the future.

Thank you, Ronny Steen (Norwegian University of Life Sciences), and Rune Aae (Østfold University College) for including me in this project and discussing my thoughts while working on this thesis.

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Ås, 31.05.2021

Contents

1. Introduction

The largest threat to biodiversity worldwide is change in land use, leading to the loss of habitat (IPBES, 2019). Conservation of a species ranges and habitats, is therefore the most obvious and important action we can do to ensure their survival. To be able to implement effective conservation measures one must properly understand a species ecology, where their area uses and habitat preferences are fundamental (Levin, 1995). A species area uses and habitat preferences are the sizes and locations of the areas they use, and which habitats are used versus what is available within these areas (Beyer et al., 2010). Beyer et al. (2010) defines habitats as:

"*Regions in environmental space that are composed of multiple dimensions, each representing a biotic or abiotic environmental variable; that is, any component or characteristic of the environment related directly (e.g. forage biomass and quality) or indirectly (e.g. elevation) to the use of a location by the animal*".

Here, I study the general habitat preferences of ospreys (*Pandion haliaetus*), where the habitat categories are aggregations of land cover classes which are classified from satellite images (e.g. Copernicus Land Monitoring Service).

The osprey is a cosmopolitan species, which means it can be found as a breeding species around most of the world, except for Antarctica and only as a non-breeding migrant in South America (BirdLife, 2019). The osprey has earlier been persecuted and was heavily affected by the use of DDT in agricultural practices (Bierregaard et al., 2014). Osprey populations have grown considerably since the 1970's-80's, and have been widely researched, while there is still a need to improve our understanding of their ecology (Bierregaard et al., 2014). Some populations of ospreys are long distance migrants, while some are short distance migrants, and some are even stationary (BirdLife, 2019). Studies on ospreys in northern latitudes (long distance migrants) have in the past been heavily focused on their breeding grounds, only banding provided data on their migration and wintering areas, which had its limitations (Hake et al., 2001). The first-generation satellite transmitters made it possible to study ospreys outside of the breeding season in much greater detail but were not adequately accurate to discern habitats used during migration and in wintering areas (Bierregaard et al., 2014). Further developments in satellite telemetry and

GPS technology have made it possible to study the movements and habitat uses of ospreys in detail throughout the year (Bierregaard et al., 2014). Today, detailed information about the whole world from satellite images are publicly available. Many maps have been made, containing different kinds of information extracted from satellite imagery, for example land cover maps. The methods of extracting information from satellite images have become sophisticated and are able to classify many different types of habitats. Therefore, it is now possible to study the area uses and habitat preferences of ospreys throughout the year, without having to collect habitat data manually.

1.1 Research questions and hypotheses

What are the sizes of the areas ospreys use in each season, and are the sizes different between seasons? The osprey is a widely studied species (Bierregaard et al., 2014; Saurola, 1997; Schmidt-Rothmund et al., 2014). However, few studies have calculated and provided the range sizes of ospreys, and I have not found any study that has compared these between all seasons. In this study, I will calculate and compare the range sizes of ospreys in their home ranges (breeding grounds), in their wintering areas, and during stopovers. Additionally, I will separate and compare the range sizes of adults and juveniles in all seasons.

Ospreys are heavily dependent on water bodies, as they prey almost exclusively on fish (BirdLife, 2019). Therefore, few studies have focused on ospreys' habitat preferences on land. Some studies have included surrounding habitats as explaining factors, but have not performed a use versus availability analysis to show preferences (e.g. Bai et al., 2009; Washburn et al., 2014). One study did perform a use versus availability analysis (Crawford & Long, 2017), but this study was done on only juvenile ospreys. Juvenile ospreys are inexperienced and unable to compensate for wind drift during migration (Thorup et al., 2003), meaning that their movement patterns and therefore area uses and habitat preferences could be heavily affected by other factors. These facts made it apparent that further research on the habitat preferences of ospreys would benefit our understanding of the species. Additionally, since ospreys are migratory birds, and have very different movement patterns throughout the year, one would expect that their habitat preferences would be different throughout the year as well. These thoughts led to my first research question: Do ospreys have any preferred habitats on land, and are these different between seasons? I expected to find that the ospreys would have preferred habitats on land due to the earlier studies findings of habitats used. And I expected to find that the ospreys' habitat preferences would be different between seasons due to the different behaviors in each season. From these questions and expectations, I formulated this hypothesis: Ospreys have preferred habitats on land, and these are different between seasons.

The southward autumn migrations and the northward spring migrations of ospreys are different in spatial and temporal aspects (Alerstam et al., 2006). The southward migrations of ospreys are typically longer in time, includes longer stopovers, and the timing of the migrations are more flexible compared to their northward migrations (Alerstam et al., 2006; Strandberg & Alerstam, 2007). The reasons for these differences are that an earlier arrival to the breeding grounds in spring is advantageous in territory claiming (Kokko, 1999), environmental conditions not being suitable further north for an early spring migration, differences in energy deposits before each migration, and different expected fueling/foraging opportunities along the migration paths (Alerstam et al., 2006). Even though total migration time is shorter during northward migrations, daily travel distances and travel speed are similar between both migrations (Monti et al., 2018a). This is due to different migration strategies being used, where the days spent at stopovers during southward migrations make the total migration time longer (Alerstam et al., 2006; Monti et al., 2018a; Strandberg & Alerstam, 2007). The two different migration strategies are the stopover strategy and the fly-and-forage strategy. The stopover strategy means that the bird in question stops in one location for several days during migration, often several times during the entire migration, to stock up on energy reserves before continuing the migration. While the fly-and-forage strategy means that the bird in question scouts for foraging opportunities during flight, and has many short foraging stops, without staying in one location for several days. Ospreys do not simply use only the stopover strategy on the way south and only the fly-and-forage strategy on the way north but combine the two during both migrations. However, ospreys seem to use the stopover strategy more on the way south (Alerstam et al., 2006; Strandberg & Alerstam, 2007). These differences in behavior during migrations raised the question: Do ospreys have different habitat preferences during southward and northward migrations? I expected to find that the ospreys would have different preferences between their southward and northward migrations due to the differences in behavior between the migrations. From this question and expectation, I formulated this hypothesis: Ospreys have different habitat preferences between their southward and northward migrations.

Do adult and juvenile ospreys have different habitat preferences during their southward migration? Adult ospreys have high route fidelity during migrations, and often use the same stopover sites between years (Alerstam et al., 2006; Vardanis et al., 2016). North-European ospreys migrate on a broad front across Europe, the Mediterranean, and northern Africa, while maintaining this high individual route fidelity (Vardanis et al., 2016). This shows that ospreys choose routes and navigate based on past experiences (Alerstam et al., 2006; Hake et al., 2001). As previously mentioned, juvenile ospreys are inexperienced and unable to compensate for wind drift during migration, which could affect their area uses and habitat preferences as well. Therefore, an analysis of habitat preferences during the southward migration of adult and juvenile ospreys could reveal differences. Therefore, I expected to find that the adult and juvenile ospreys would have different habitat preferences during their southward migration, or that the juveniles would not have any at all. From this question and expectation, I formulated this hypothesis: Adult and juvenile ospreys have different habitat preferences during their southward migration.

Ospreys are not always successful in breeding, sometimes due to one of the pair arriving to the breeding grounds late in spring (Strandberg et al., 2010), and sometimes due to the one or both individuals trying to mate with other individuals in other nests, leading to unsuccessful copulation in their own nest (pers. obs.). During these non-breeding years, the individuals could show different movement patterns as they are not bound to the nest in the same way, which could reveal different habitat preferences as well. During breeding years in their home range, the male must hunt more to feed the female and the chicks (Poole, 1985), and both the male and the female must defend their nest to protect their young (Bai et al., 2009; Clancy, 2006). Presumably expending more energy during the entire breeding season, which could affect their movement patterns during their migration southward as well. This raised the questions: Do adult ospreys show different movement patterns in their home ranges and during their migration southward between breeding years and non-breeding years? And do they have different habitat preferences in their home ranges and during their migration southward between breeding years and non-breeding years? I was not able to find a previous study exploring differences in behavior between breeding and non-breeding years, but one study found that late arrival to the breeding grounds due to difficulties during migration led to lower breeding success (Strandberg et al., 2010), showing that energy expenditure in one season could affect the other seasons. Another study found that surrounding habitats affected breeding success (Bai et al., 2009), meaning that breeding or not breeding could affect uses of different habitats as well. And Candler and Kennedy (1995) showed that ospreys used different migration strategies between years, which is linked to the amount of energy deposition prior to migrations. Therefore, I expected to find that the adult ospreys would have different area uses and habitat preferences in their home ranges between breeding years and non-breeding years. While more research is needed on differences in temporal and spatial aspects during southward migration between breeding and non-breeding years. Therefore, I limited the study and only expected to find that the adult ospreys would have different habitat preferences during their southward migration between breeding and non-breeding years. From these questions and expectations, I formulated these hypotheses: Adult ospreys have different movement patterns in their home ranges between breeding years and non-breeding years. Adult ospreys have different habitat preferences in their home ranges and during their migration southward between breeding years and non-breeding years.

2. Methods and data

2.1 Study species

The osprey is a medium-large sized raptor that preys almost exclusively on fish (BirdLife, 2019). Ospreys throughout the world are usually perceived as one species and are divided into four different subspecies (Monti et al., 2015). The population that breeds in Scandinavia and migrates to Africa south of Sahara is part of the nominate subspecies (*Pandion haliaetus haliaetus*), hereafter called osprey. The Norwegian ospreys arrive in their breeding grounds in spring, and the chicks are fully grown by the end of July (Nordbakke, 1994). The female leaves as soon as the juveniles are able to fly, while the male stays until the juveniles show they can hunt on their own or migrates south, and they all migrate individually to Africa south of Sahara (Kjellen et al., 2001). More southern populations of osprey can migrate shorter distances and winter north of Sahara (Monti et al., 2018b). The juveniles often stay at least one summer in southern latitudes before returning to their native areas to claim a territory and find a partner (Österlöf, 1977).

Ospreys are found in forests, wetlands, and most different kinds of water bodies where the ospreys can forage (BirdLife, 2019). Their nesting sites are primarily in forests, in large trees with a good view of the surroundings, preferably close to fishing waters, but in areas with human disturbance the nest can be several kilometers from water bodies (Saurola, 1997). Some exceptions are seen in local populations that nest in cliffs or on power line pylons in the middle of open fields (Saurola, 1997). The ideal natural nesting sites for ospreys are small islands covered by big trees in lakes (Saurola, 1997).

Figure 1: An adult osprey returning to the nest with a fish, finding ornithologists climbing the nest tree.

2.2 Study area

The study area stretched from south-eastern Norway, through all of Europe and northern Africa, to the south of Sahara (figure 2). The very large study area contained most different types of habitats, but for this study these were aggregated into different habitat categories based on land cover categories in the maps used, a table containing the aggregated habitat categories is shown in the next sub-chapter.

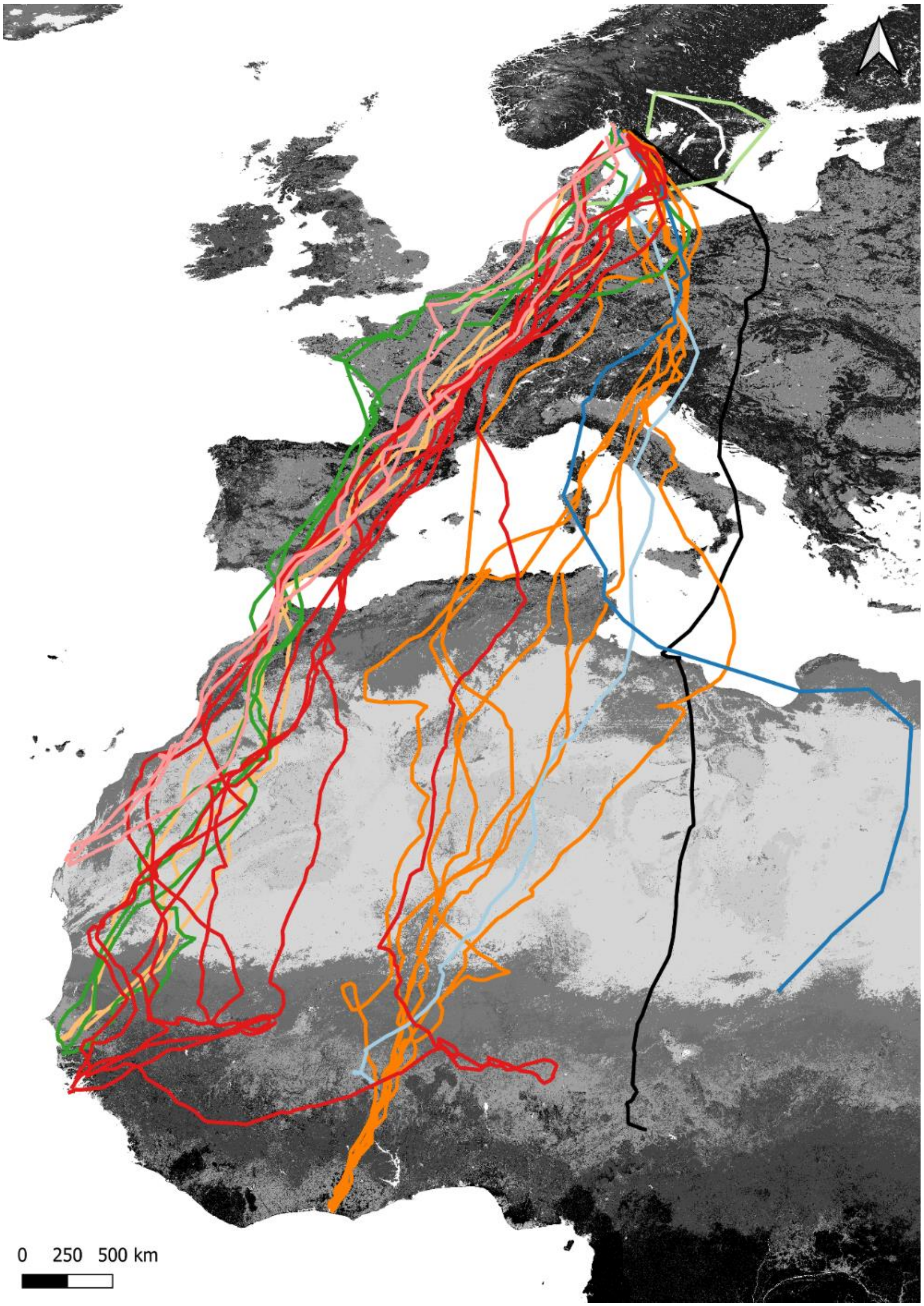

Figure 2: Study area from south-eastern Norway to Africa south of Sahara, with all migrations made by the studied individuals.

2.3 Data collection

The GPS data was collected from ten individuals fitted with an Argos GPS transmitter (www.argos-system.org). Six adults and four juveniles were fitted. The individuals were fitted with transmitters between 2011 and 2019. The adults collected data continuously for up to five years, while all juveniles either died or the transmitter stopped working during their first migration southward. One marked individual is still transmitting, Mrs. Huseby, while Mr. Huseby was found dead in May 2021.

The ospreys were captured and marked following standard methods of fitting birds with GPS technology (e.g. Alerstam et al., 2006; Hake et al., 2001). Adults were captured while on the nest with claptraps, and the juveniles were fitted at the nest before they had learned to fly but were fully grown. The transmitter used was a small backpack, powered by solar panels. The weight of the backpacks never exceeded 2.5% of the bodyweight of the birds.

The transmitters from each individual uploaded data at set intervals to the Argos satellites. The data was then sent to Argos' server, where the data could be downloaded directly by the owner. This means that the bulk of the data was collected automatically, while the collection of data for the variables was done through QGIS 3.14.16 (www.qgis.org). A challenge presented itself when trying to find maps that included data from the whole world, as the file sizes would either be incredibly large, or the maps would be in a very low resolution. The best map was selected based on coverage, resolution, and size. The map used for the analysis was "Land cover (GLCNMO) – Global version" and was developed by the Geospatial information Authority of Japan, Chiba University and collaborating organizations. For home ranges that were exclusively in Norway, a high-resolution land cover map was available, which was called "Arealressurskart AR5" and was developed by Geovekst.

After having received the GPS data from the fitted individuals, the data was controlled manually, and different variables were computed in QGIS. The standard QGIS function "sample raster values" was used to collect which habitat category a point was in. To collect a point's distance to a habitat category, proximity maps to the different habitat categories were generated, also a standard QGIS function, and the points were sampled in the same way. Computing of the distance variables in the high-resolution map in Norway, was done using the plugin for QGIS "NNjoin".

Using standard QGIS functions, random points were generated within the Minimum Convex Polygons (100%) of each individual's home range and wintering area, for all years. The random points represented the availability of the different habitats (Beyer et al., 2010). The number of random points within an area was the same as the number of observed points.

The available habitat for migration was set as a buffer of ca. 100 km around the flight path. This was because the large and general habitat categories made it so that all observed points and random points were in the same habitat, if the minimum convex polygons of stopover sites were used as available habitat. Therefore, an analysis of preference was done on the entire migration. Approximately 100 km was set as a buffer for the migration as a conservative distance the ospreys would be able to fly in a day. Average daily travel distances were calculated (ignoring days spent at stopovers), showing that adults had an average just under 200 km and juveniles just above 200 km. But as these distances were traveled southward or northward (direction of migration), and it is unlikely they would fly this distance eastward or westward, the distance was split in half for the buffer. The reason the buffer was not exactly 100 km, was because the buffer could only be generated in the corresponding map units to the map used in the analysis. The map was a world map, using the WGS84 coordinate system. Therefore, the buffer set at one degree, did not correspond to the same length in km at northern latitudes as around equator. One degree longitude is 111 km at equator, and 56 km at 60 degrees latitude. This gave the buffer a "cone" shape, being narrower in the north and wider in the south.

Seasons were defined by the individual's movement. Home ranges and wintering areas included the points from the day after arrival to the day before departure. Migrations included the first and last points on a clear migration path in and out of the home ranges and wintering areas. Stopovers included points in areas that were clearly different from migration where the individual stayed for more than 24 hours. (e.g. Crawford & Long, 2017; Hake et al., 2001; Monti et al., 2018b)

Land cover categories from both maps were aggregated into seven different habitat categories based on the land cover categories used in the maps (table 1).

Table 1: Aggregation of different land cover categories from the two different maps used in the habitat preference analysis.

Habitat category	GLCNMO	AR5
Forest	Broadleaf evergreen forest	Forest
	Broadleaf deciduous forest	
	Needleleaf evergreen forest	
	Needleleaf deciduous forest	
	Mixed forest	
Open	Tree open	Open solid ground
	Shrub	
	Herbaceous	
	Herbaceous with sparse tree/shrub	
	Sparse vegetation	
Agriculture	Cropland	Plowed cropland
	Paddy field	Cleared cropland
	Cropland/other vegetation mosaic	Pasture
Wetland	Mangrove	Marsh
	Wetland	

Bare land	Bare area, consolidated (gravel, rock) Bare area, unconsolidated (sand) Snow/ice	Glacier
Urban	Urban	Developed land Roads, railways etc.
Water bodies	Water bodies	Freshwater Ocean

2.4 Statistical analysis

Large amounts of data were analyzed, 60114 observations, half of which were random points. A generalized linear mixed effects model (GLMM) was fitted to the data, using the “lme4” package in RStudio 1.3.1073 (www.rstudio.com). This means that the model included fixed effects and random effects, which – if used correctly – eliminates the problems with autocorrelation in data (Bolker et al., 2009). The data was separated into the different seasons: home range, migration, and winter. The GLMM was fitted to the variables:

- Response: Point type (binomial, with two outcomes: observed and random points, where observed = 1 and random = 0)
- Predictors (fixed effects): Habitat category (which habitat category a point was in) and distance to the different habitat categories (a points distance to the closest of each habitat category)
- Random effects: individual and year

Two different GLMM’s were fitted where the first included habitat category as predictor and the second included distance to the different habitat categories as predictors. Additionally, in the individuals’ home ranges, distance to nest was included as a fixed effect, in both GLMM’s.

Distances to different habitat categories and to the nest were normalized, meaning that all distances were recalculated to be on the scale 0-1. What this did was eliminate larger effects on the response variable from predictor variables with larger values (Lakshmanan, 2019).

The model including habitat category as the predictor showed the use vs. availability (observed vs. random points) of different habitat categories compared to the use vs. availability of agricultural areas, which was set as the intercept (simply due to “Agriculture” starting with an “A”). A positive or negative estimate of the intercept meant that agricultural areas were used more or less than the availability, and a higher positive estimate of another habitat category meant that the use vs. availability was higher than in agricultural areas. The probabilities of a given point being an osprey in different habitat categories were then predicted and plotted using the package “ggeffects” in RStudio. A habitat preference or avoidance was seen if the predicted probability was significantly higher or lower than the expectation. The expectation was that a habitat was used like the availability (same number of observed points in a habitat category as random points), which would show a probability of 50%. The difference was significant if the entire confidence interval (95%) was over or under the expectation. (Beyer et al., 2010)

The model including distances to the different habitat categories as the predictors showed the observed vs. expected (random points) distances to the closest of each habitat category. A negative estimate of the distance to a habitat category meant that the ospreys were closer to a habitat category than expected. The probabilities of a given point being an osprey was then predicted and plotted at different normalized distances to each habitat category, also using the “ggeffects” package. A preference of being closer to or further away from a habitat category was seen if the predicted probability was significantly different from the expectation. The expectation was that the ospreys would be found at the same distances to the different habitat categories as the random points, which would show a probability of 50% at all distances to the habitat category. The difference was significant if the entire confidence interval (95%) was over or under the expectation at different distances to the habitat category. (Beyer et al., 2010)

The same analysis was performed on the different subsets: southward migrations, northward migrations, southward migrations for juveniles, southward migrations for adults, home ranges for adults in breeding years, home ranges for adults in non-breeding years, southward migrations for adults in breeding years, and southward migrations for adults in non-breeding years.

Minimum convex polygons and kernel core use areas were calculated using the “AdehabitatHR” package in RStudio. The smoothing factor for kernel core use areas was chosen using the “reference bandwidth” method, since the kernels of each individual were often very fragmented, meaning that the “least squares cross validation” method could not provide an accurate smoothing factor for each individual. (Paterson, 2018)

3. Results

Minimum convex polygons (MCP) and kernel core use areas were calculated for all individuals, in their home ranges, wintering grounds, and in stopover areas during migration. Habitat preferences were found in all seasons, both in use of habitat categories and distance to habitat categories. Differences in preferences were found between all seasons, between southward and northward migrations, between adults and juveniles during southward migration, and between breeding and non-breeding years for adults in their home ranges. While only small differences were found during southward migration between breeding years and non-breeding years.

Results for each season are presented with MCP sizes and kernel core use areas for all individuals, for adults, and for juveniles. Habitat preferences in each season are for all individuals and a comparison of habitat preferences between adults and juveniles are presented in its own sub-chapter.

Maps showing each individual's home ranges, migrations with stopovers, and wintering areas, for all years, are presented in Appendix 1.

3.1 Home range

Minimum convex polygons (95%) for all individuals had a median size of 87.20 km^2, ranging from 0.02 to 1179.76 km^2. For only adults, the median size was 95.94 km^2, and the range was the same as for all individuals. Juveniles' home ranges had a median size of 1.93 km^2 and ranged from 0.02 to 46.51 km^2.

Kernel core use areas (95%) for all individuals had a median size of 110.23 km^2, ranging from 0.05 to 629.92 km^2. For only adults, the median size was 126.58 km^2 and the range was 0.48 to 629.92 km^2. For only juveniles, the median size was 4.42 km^2 and the range was 0.05 to 85.04 km^2.

Kernel core use areas (50%) for all individuals had a median size of 8.90 km^2 and ranged from 0.01 to 91.77 km^2. For only adults, the median size was 11.26 km^2 and the range was 0.05 to 91.77 km^2. For only juveniles, the median size was 0.26 km^2 and the range was 0.01 to 4.63 km^2.

In their home ranges, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests, open areas, and water bodies, while they were less in urban areas (table 2). The model was adjusted for distance to nest, meaning that the distance to the nest was considered when calculating estimates for the use of the different habitat categories. Close to the nest, the probability of a given point being an osprey was higher than the expectation in forests, open areas, and water bodies, it was lower in urban areas, and it was not significantly different from the expectation in agricultural areas (figure 3). Meaning that close to the nest, the ospreys preferred being in forests, open areas, and water bodies, they avoided being in urban areas, and agricultural areas were used like the availability. While further from the nest, it would seem the ospreys avoided every habitat category, but this was simply an effect of the ospreys' preference of being closer to the nest. The relationship between the uses of the different habitat categories was the same further away from the nest.

Table 2: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas in the ospreys' home ranges (N=21438, groups: individual, 10; year, 9). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	-0.05	0.16	0.746
Forest	0.51	0.11	<0.001***
Open	0.65	0.13	<0.001***
Urban	-4.73	1.00	<0.001***
Water bodies	0.74	0.11	<0.001***
Distance to nest	-2.79	0.10	<0.001***

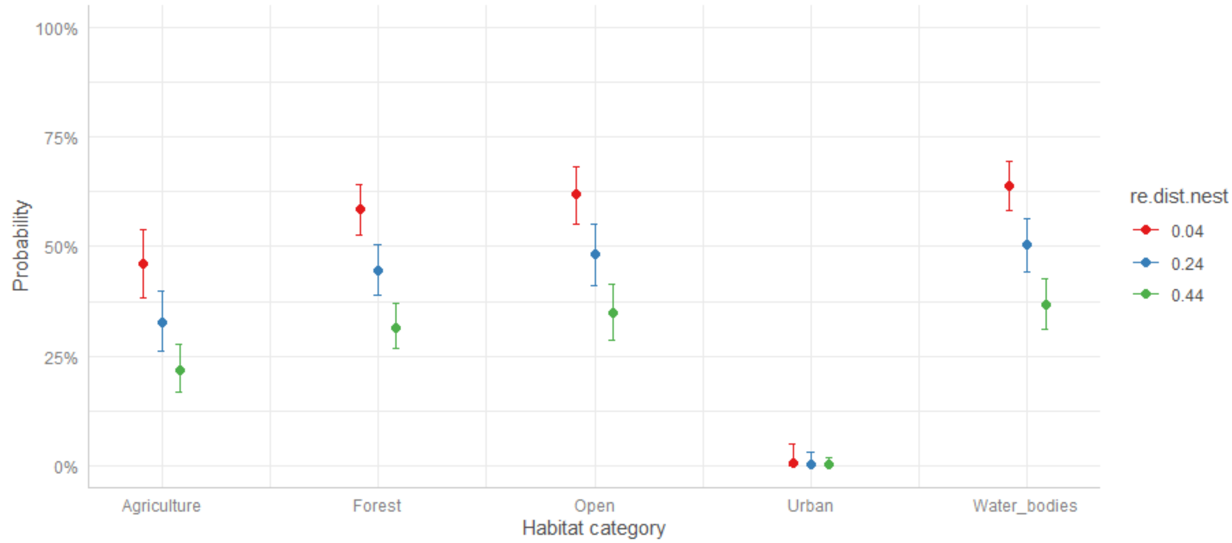

Figure 3: Predicted probabilities of a given point being an osprey in the different habitat categories in the ospreys' home ranges, at different normalized distances to the nest (chosen automatically). Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

In their home ranges, the ospreys were closer to forests, open areas, water bodies, and agricultural areas, while they were further away from urban areas, compared to the expectation (table 3). The probability of a given point being an osprey was higher than the expectation closer to forests, open areas, water bodies, and agricultural areas, while it was lower closer to urban areas (figure 4). Meaning that in the ospreys' home ranges, they preferred being closer to forests, open areas, water bodies, and agricultural areas, and they preferred being further away from urban areas.

Table 3: Parameter estimates for distance to different habitat categories in home ranges (N=21438, groups: individual, 10; year, 9). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.73	0.43	0.091
Distance to water bodies	-2.89	0.12	<0.001***
Distance to urban	5.65	0.17	<0.001***
Distance to forest	-9.80	0.43	<0.001***
Distance to open	-6.42	0.17	<0.001***
Distance to agriculture	-0.36	0.08	<0.001***
Distance to nest	-3.19	0.12	<0.001***

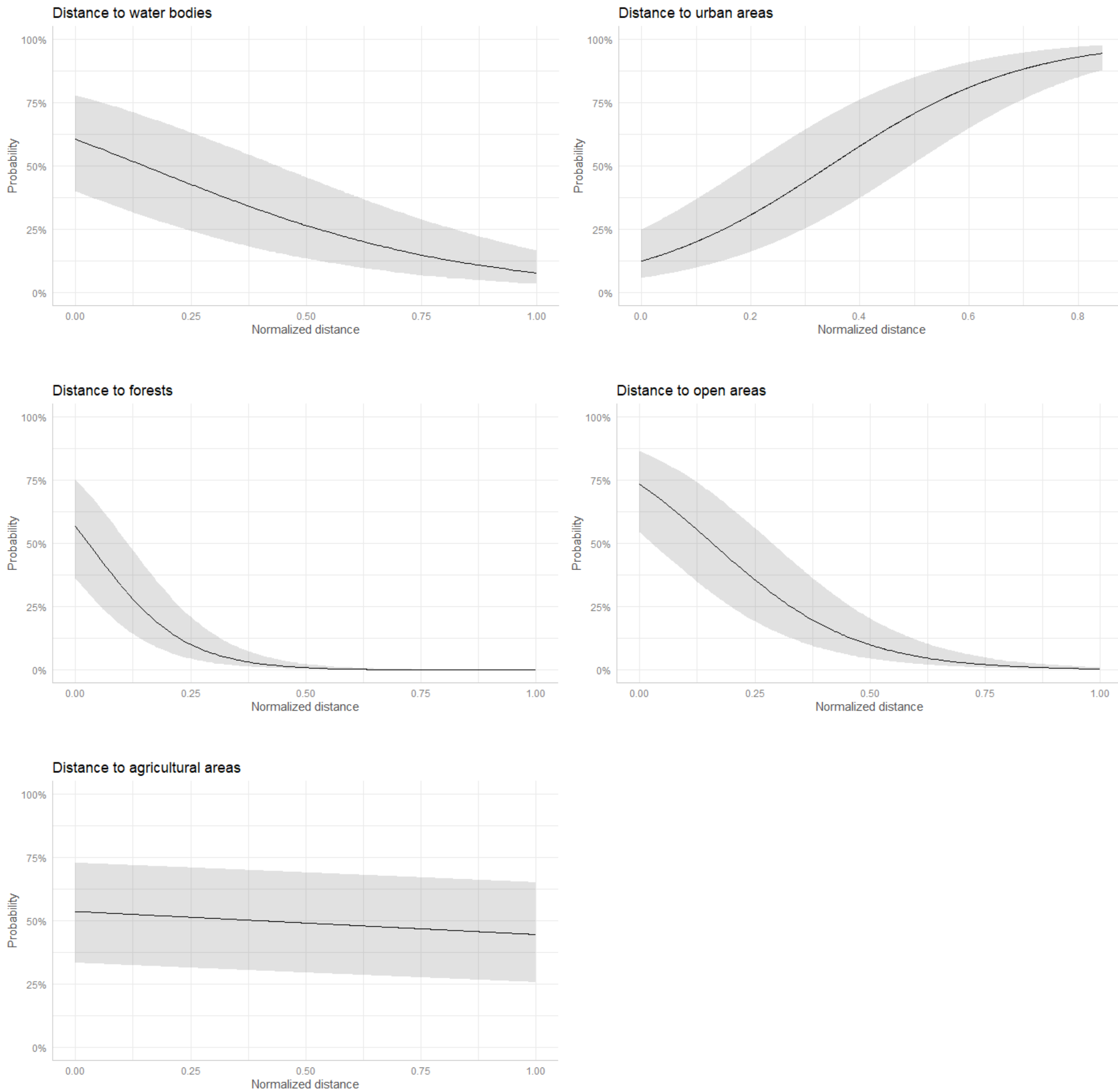

Figure 4: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories in the ospreys' home ranges. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.1.1 Home range with higher resolution map

When analyzing with the high-resolution map, the ospreys with home ranges exclusively in Norway, used agricultural areas less than the availability. Compared to the use vs. availability of agricultural areas, the use was higher in forests, open areas, water bodies, and wetlands, and it was lower in urban areas (table 4). Close to the nest, the probability of a given point being an osprey was higher than the expectation in forests and open areas, it was lower in agricultural areas, urban areas, and water bodies, and it was not significantly different from the expectation in wetlands (figure 5). Meaning that when analyzed with the detailed map, in their home ranges, the ospreys preferred being in forests and open areas, they avoided being in agricultural areas, urban areas, and water bodies, and they used wetlands like the availability.

Table 4: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas in home ranges with the detailed map (N=7520, groups: individual, 5; year, 3). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	-1.20	0.43	0.005**
Forest	2.59	0.12	<0.001***
Open	2.32	0.15	<0.001***
Urban	-1.80	0.43	<0.001***
Water bodies	0.37	0.13	0.005**
Wetland	1.46	0.37	<0.001***
Distance to nest	-3.61	0.15	<0.001***

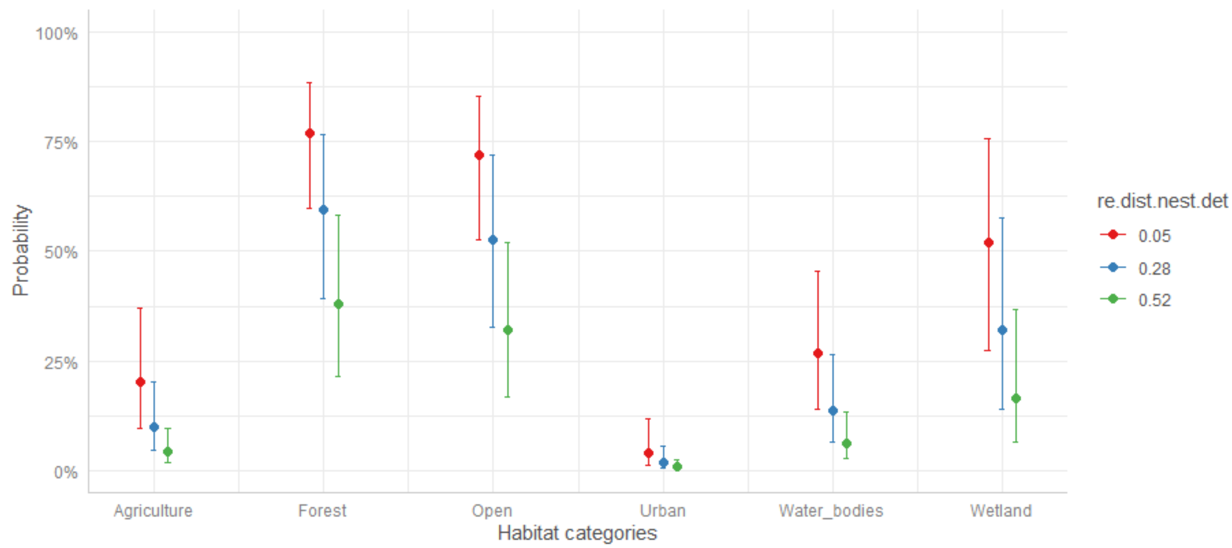

Figure 5: Predicted probabilities of a given point being an osprey in different habitat categories in the ospreys' home ranges (with the detailed map), at different normalized distances to the nest (chosen automatically). Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

The analysis of distance to different land cover categories on the detailed map showed that the ospreys were closer to forests, open areas, urban areas, agricultural areas, while they were further away from wetlands, compared to the expectation. The ospreys were not significantly closer to water bodies compared to the expectation (table 5). The probability of a given point being an osprey was higher than the expectation closer to forests, open areas, urban areas, and agricultural areas, and it was lower closer to wetlands. The probability was not significantly different than the expectation at different distances to water bodies (figure 6). Meaning that when analyzed with the detailed map, in their home ranges, the ospreys preferred being closer to forests, open areas, urban areas, and agricultural areas, they preferred being further away from wetlands, and the distance to water bodies was like the expectation.

Table 5: Parameter estimates for distance to different habitat categories in home ranges with the detailed map (N=7520, groups: individual, 5; year, 3). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	1.62	0.42	<0.001***
Distance to water bodies	-0.32	0.17	0.059
Distance to urban	-3.83	0.32	<0.001***
Distance to forest	-10.85	0.71	<0.001***
Distance to open	-7.83	0.54	<0.001***
Distance to agriculture	-1.49	0.24	<0.001***
Distance to wetland	1.18	0.18	<0.001***
Distance to nest	-4.33	0.16	<0.001***

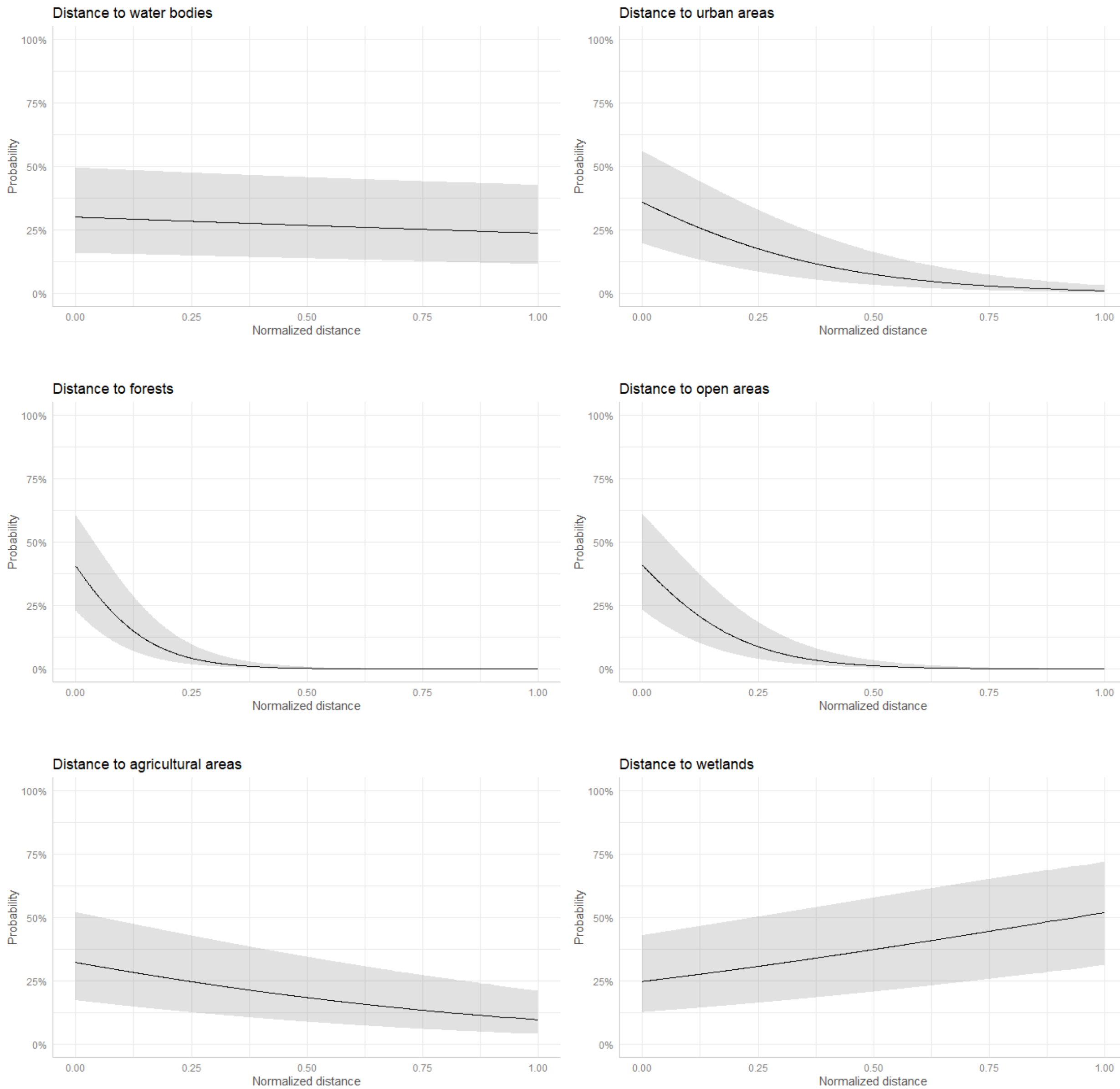

Figure 6: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories in the ospreys' home ranges (with the detailed map). The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.2 Migration

The analysis of habitat preferences was done on the ospreys' entire migrations. However, minimum convex polygons and kernel core use area sizes for stopover sites are included. Only two juveniles had any stopovers during their migrations, with four stopovers in total, compared to 51 stopovers made by adults. Therefore, the sizes of juveniles' stopover sites should be interpreted carefully.

Minimum convex polygons (95%) for all stopover sites had a median size of 2.50 km^2 and ranged from 0.05 to 97.42 km^2. For only adults, the median size and range was the same as for all individuals. For only juveniles, the median size was 2.65 km^2 and the range was 0.47 to 6.13 km^2.

Kernel core use areas (95%) for all individuals had a median size of 12.21 km^2 and ranged from 0.19 to 658.02 km^2. For only adults, the median size was 12.19 km^2 and the range was 0.19 to 658.02 km^2. For only juveniles, the median size was 19.03 km^2 and the range was 3.67 to 31.22 km^2.

Kernel core use areas (50%) for all individuals had a median size of 2.21 km^2 and ranged from 0.03 to 101.08 km^2. For only adults, the median size was 2.06 km^2 and the range was 0.03 to 101.08 km^2. For only juveniles, the median size was 3.85 km^2 and the range was 0.92 to 4.76 km^2.

During their migration, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests, wetlands, and open areas, while they were less in water bodies, urban areas, and bare land (table 6). The probability of a given point being an osprey was higher than the expectation in forests and open areas, lower in bare land, urban areas, and water bodies, and not significantly different than the expectation in agricultural areas and wetlands (figure 7). Meaning that during their migrations, the ospreys preferred being in forests and open areas, they avoided being in bare land, urban areas, and water bodies, and used agricultural areas and wetlands like the availability.

Table 6: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas during migrations (N=17208, groups: individual, 10; year, 9). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.00	0.04	0.898
Bare land	-0.48	0.05	<0.001***
Forest	0.88	0.05	<0.001***
Open	0.09	0.04	0.029*
Urban	-0.77	0.22	<0.001***
Water bodies	-1.22	0.07	<0.001***
Wetland	0.50	0.29	0.080

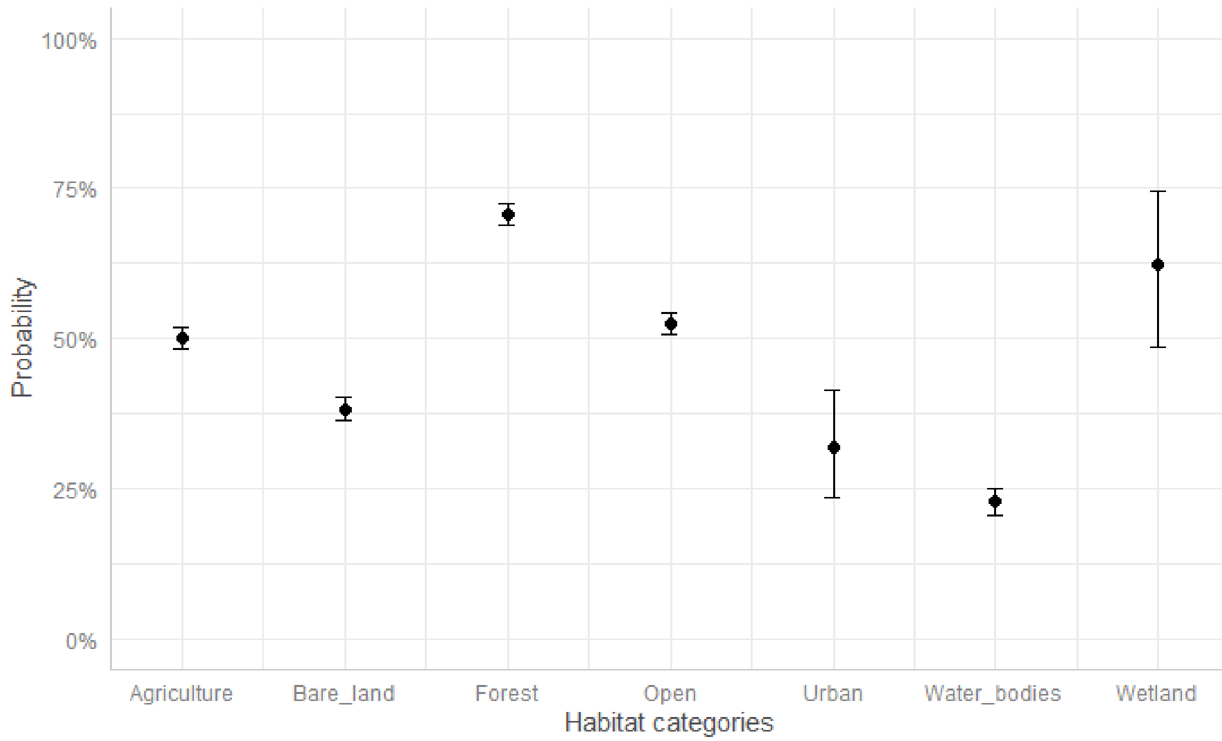

Figure 7: Predicted probabilities of a given point being an osprey in the different habitat categories during the ospreys' migrations. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

During their migration, the ospreys were closer to open areas, urban areas, forests, water bodies, and agricultural areas, while they were further away from bare land, compared to the expectation. Distance to wetland was not significantly different than the expectation (table 7). The probability of a given point being an osprey was higher than the expectation closer to open areas, urban areas, forests, and water bodies, lower closer to bare land, and not significantly different than the expectation at different distances to agricultural areas and wetlands (figure 8). Meaning that during their migration, the ospreys preferred being closer to open areas, urban areas, forests, and water bodies, they preferred being further away from bare land, and their distances to agricultural areas and wetlands were like the expectations.

Table 7: Parameter estimates for distance to different habitat categories during migrations (N=17208, groups: individual, 10; year, 9). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.20	0.07	0.002**
Distance to water bodies	-0.37	0.11	<0.001***
Distance to urban	-1.08	0.14	<0.001***
Distance to forest	-0.55	0.13	<0.001***
Distance to open	-13.53	0.82	<0.001***
Distance to agriculture	-0.32	0.17	0.066
Distance to wetland	0.01	0.14	0.950
Distance to bare land	0.95	0.08	<0.001***

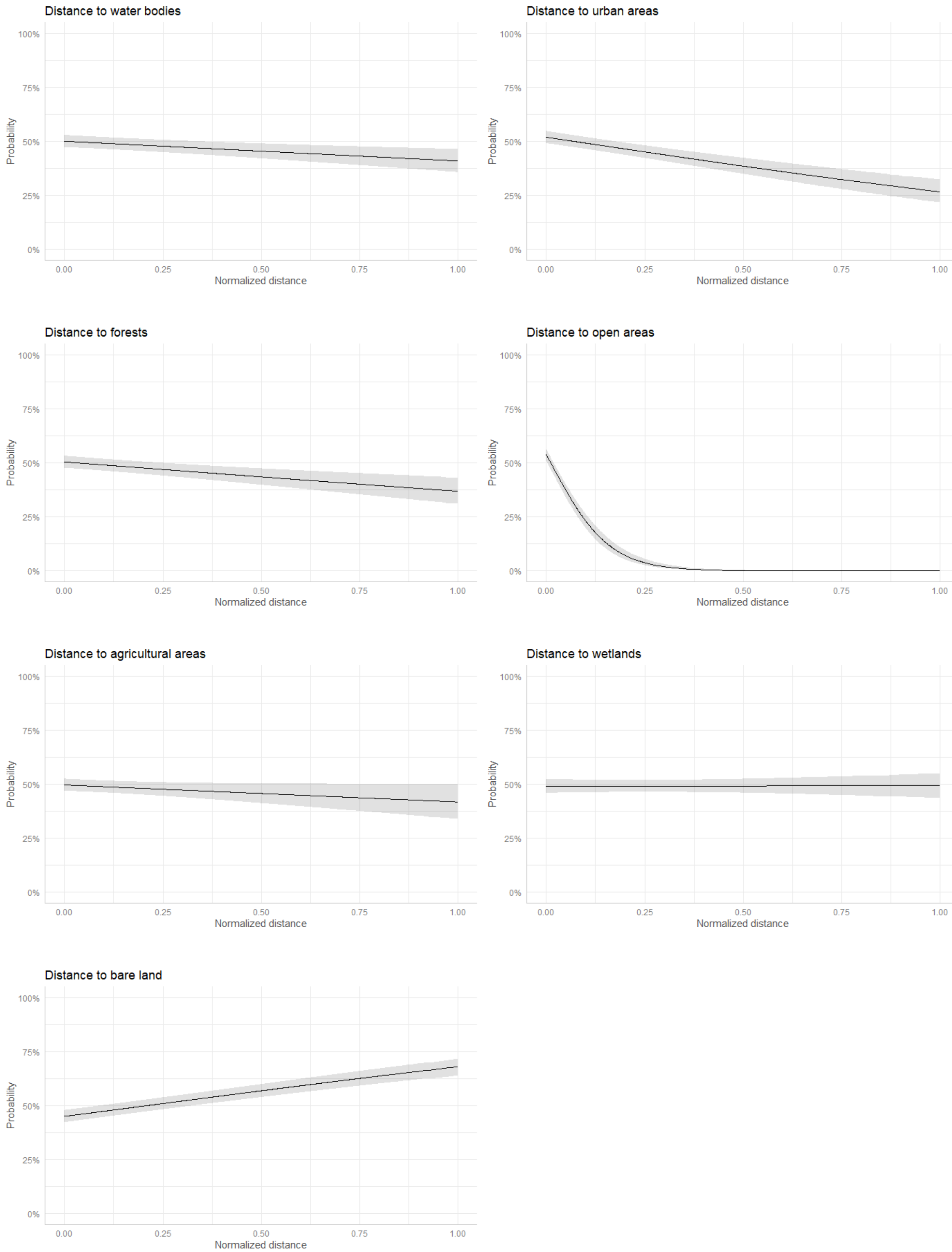

Figure 8: Predicted probabilities of a given point being an osprey at different normalized distances from the different habitat categories during the ospreys' migrations. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.3 Wintering area

No juveniles made it past their first migration southwards, either because of death or transmitter failure. Therefore, wintering areas sizes and habitat preferences were from adults only. Minimum convex polygons (95%) for all adults in their wintering areas had a median size of 57.43 km^2 and ranged from 3.76 to 812.24 km^2. Kernel core use areas (95%) had a median size of 90.05 km^2 and ranged from 0.01 to 9576.86 km^2. Kernel core use areas (50%) had a median size of 10.10 km^2 and ranged from 0.02 to 1911.00 km^2.

In their wintering areas, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests and wetlands, while they were less in bare land and water bodies. Open areas were also used like the availability (table 8). The probability of a given point being an osprey was higher than the expectation in forests and wetlands, lower in bare land and water bodies, and not significantly different than the expectation in agricultural areas and open areas (figure 9). Meaning that in their wintering areas, the ospreys preferred being in forests and wetlands, they avoided being in bare land and water bodies, and they used agricultural areas and open areas like the availability.

Table 8: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas in wintering areas (N=21250, groups: year, 7; individual, 5). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.15	0.16	0.327
Bare land	-2.74	0.21	<0.001***
Forest	0.85	0.05	<0.001***
Open	0.05	0.04	0.225
Water bodies	-1.58	0.06	<0.001***
Wetland	0.41	0.07	<0.001***

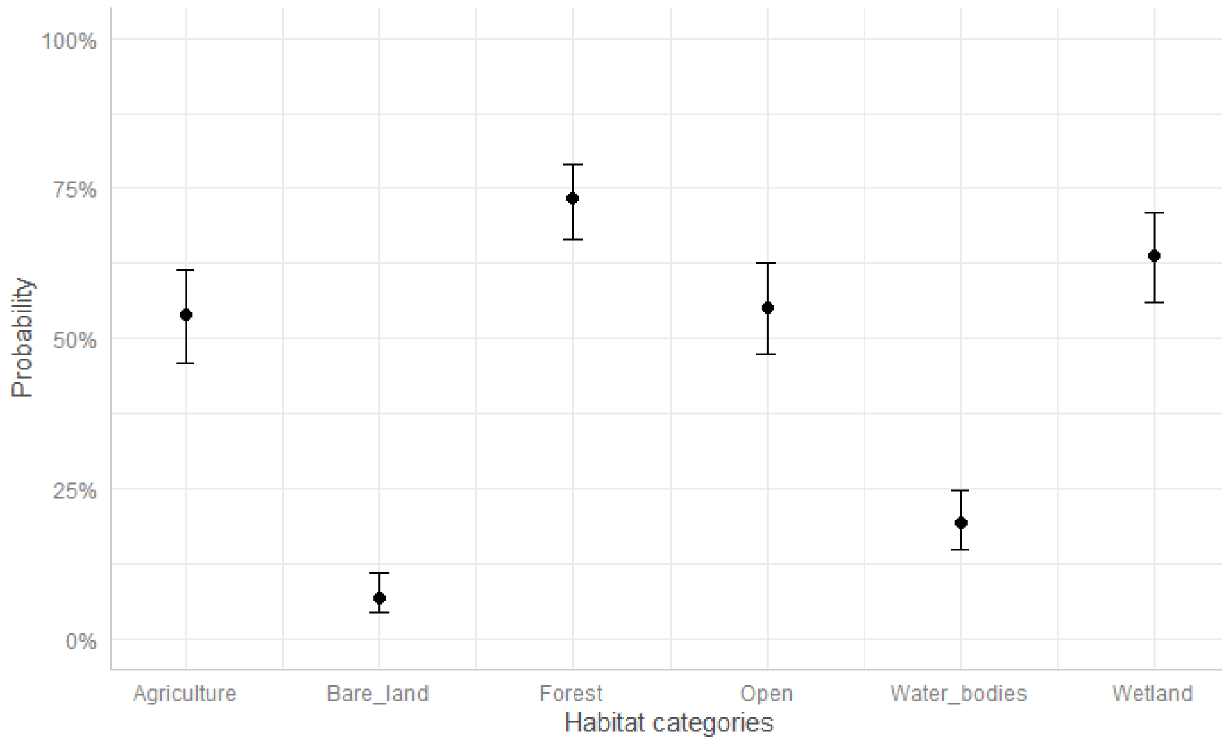

Figure 9: Predicted probabilities of a given point being an osprey in the different habitat categories in the ospreys' wintering areas. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

In their wintering areas, the ospreys were closer to water bodies, agricultural areas, open areas, wetlands, and bare land, while they were further away from forests, compared to the expectation (table 9). The probability of a given point being an osprey was higher than the expectation closer to water bodies, agricultural areas, open areas, wetlands, and bare land, and lower closer to forests (figure 10). Meaning that in their wintering areas, the ospreys preferred being closer to water bodies, agricultural areas, open areas, wetlands, and bare land, while they preferred being further away from forests.

Table 9: Parameter estimates for distance to different habitat categories in wintering areas (N=21250, groups: year, 7; individual, 5). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	1.47	0.38	<0.001***
Distance to water bodies	-4.60	0.22	<0.001***
Distance to forest	4.66	0.23	<0.001***
Distance to open	-3.83	0.21	<0.001***
Distance to agriculture	-4.31	0.20	<0.001***
Distance to wetland	-2.94	0.62	<0.001***
Distance to bare land	-2.76	0.15	<0.001***

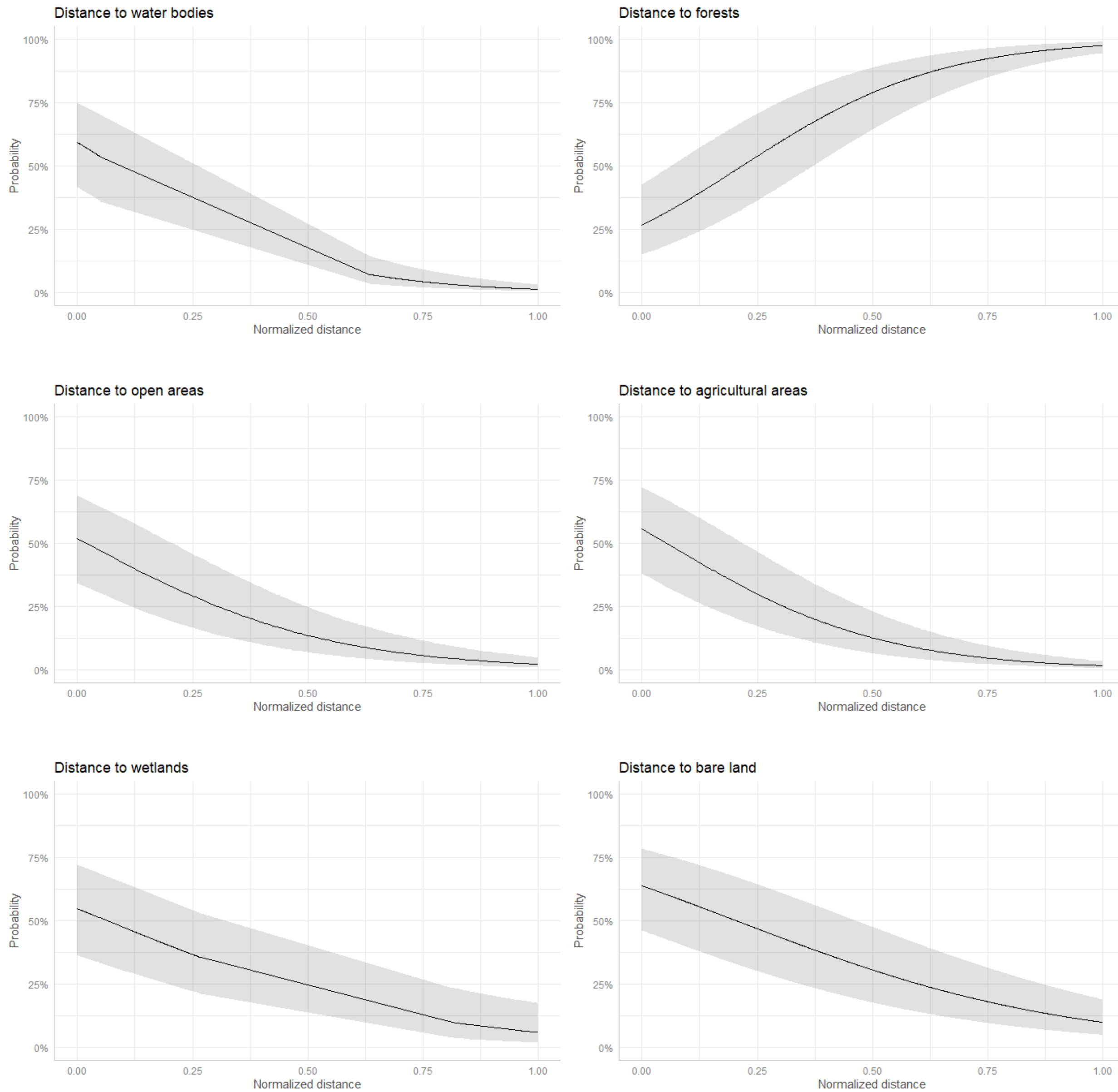

Figure 10: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories in the ospreys' wintering areas. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.4 Southward vs. northward migrations

3.4.1 Southward migrations

During their southward migrations, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests, and less in water bodies, urban areas, and bare land. Open areas and wetlands were not used significantly different than the availability (table 10). The probability of a given point being an osprey was higher than the expectation in forests, lower in water bodies, urban areas, and bare land, and it was not significantly different than the expectation in agricultural areas, open areas, and wetlands (figure 11). Meaning that during their southward migrations, the ospreys preferred being in forests, they avoided being in water bodies, urban areas, and bare land, and they used agricultural areas, open areas, and wetlands like the availability.

Table 10: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas during southward migrations (N=12954, groups: individual, 10; year, 9). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.04	0.04	0.408
Bare land	-0.59	0.06	<0.001***
Forest	0.98	0.06	<0.001***
Open	0.05	0.05	0.273
Urban	-1.04	0.25	<0.001***
Water bodies	-1.46	0.08	<0.001***
Wetland	0.63	0.35	0.069

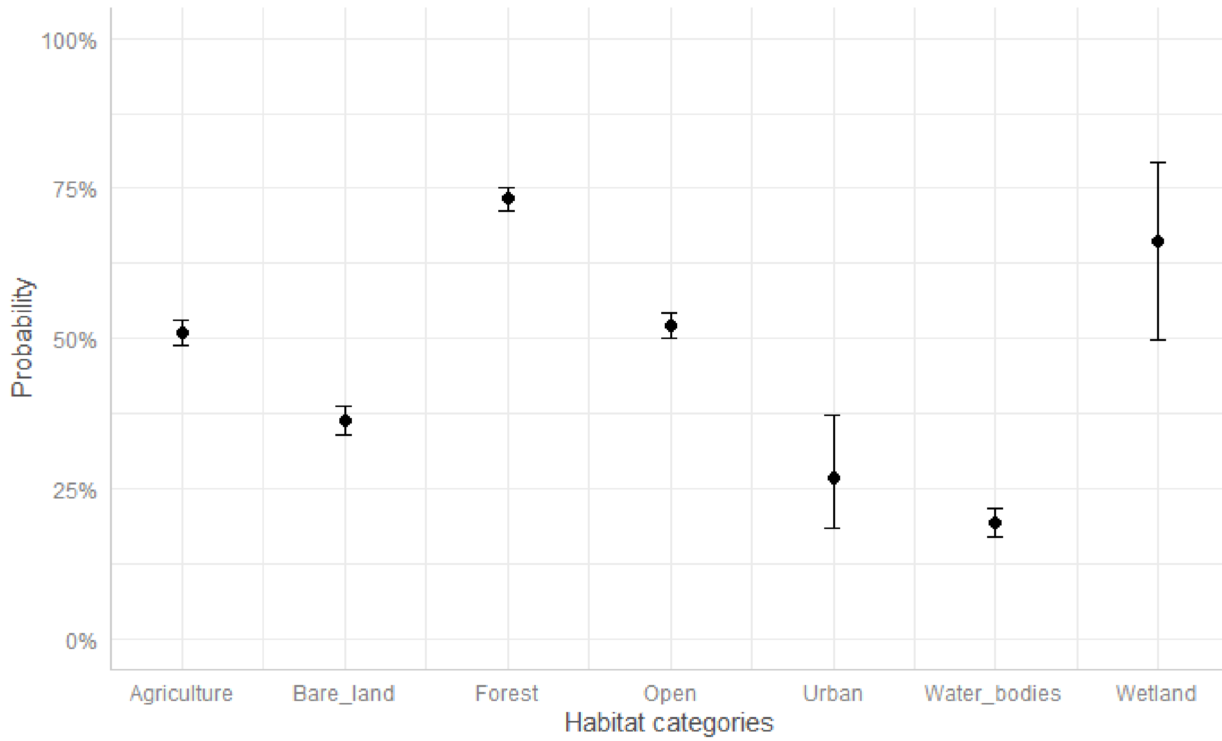

Figure 11: Predicted probabilities of a given point being an osprey in the different habitat categories during southward migration. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

During their southward migration, the ospreys were closer to open areas, urban areas, forests, agricultural areas, and water bodies, while they were further away from bare land, compared to the expectation. Distance to wetland was not significantly different than the expectation (table 11). The probability of a given point being an osprey was higher than the expectation closer to open areas, urban areas, forests, agricultural areas, and water bodies, further away from bare land, and not significantly different than the expectation further away from wetlands (figure 12). Meaning that during their southward migration, the ospreys preferred being closer to open areas, urban areas, forests, agricultural areas, and water bodies, they preferred being further away from bare land, and the distance to wetlands was like the expectation.

Table 11: Parameter estimates for distance to different habitat categories during southward migrations (N=12954, groups: individual, 10; year, 9). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.15	0.08	0.073
Distance to water bodies	-0.49	0.12	<0.001***
Distance to urban	-1.12	0.16	<0.001***
Distance to forest	-0.61	0.16	<0.001***
Distance to open	-13.50	0.90	<0.001***
Distance to agriculture	-0.53	0.20	0.009**
Distance to wetland	0.20	0.16	0.199
Distance to bare land	1.16	0.10	<0.001***

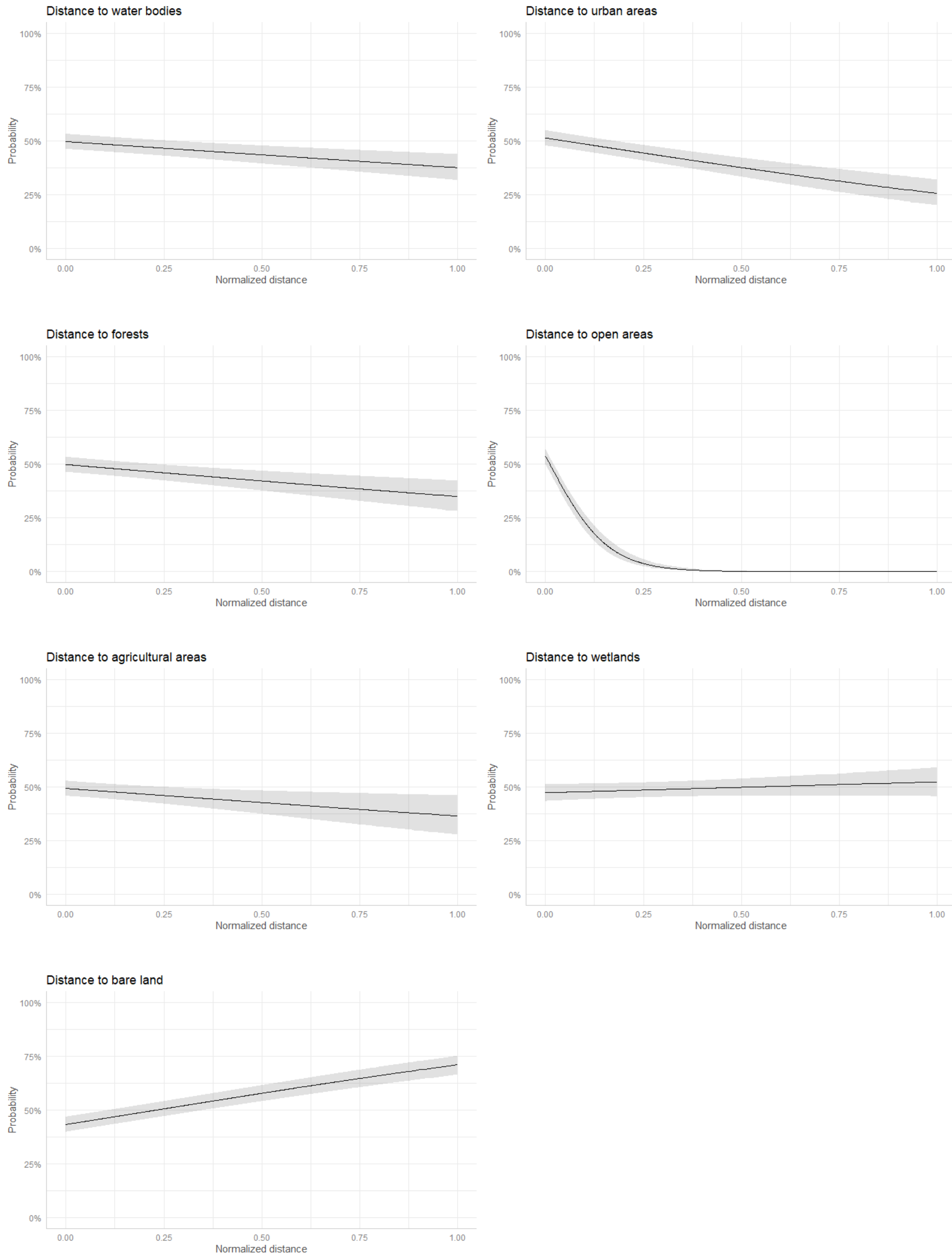

Figure 12: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories during southward migration. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.4.2 Northward migrations

During their northward migrations, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests and open areas, and less in bare land and water bodies. Urban areas and wetlands were not used significantly different than the availability (table 12). The probability of a given point being an osprey was higher than the expectation in forests and open areas, lower in bare land and water bodies, and not significantly different than the expectation in agricultural areas, urban areas, and wetlands (figure 13). Meaning that during their northward migrations, the ospreys preferred being in forests and open areas, they avoided being in bare land and water bodies, and they used agricultural areas, urban areas, and wetlands like the availability.

Table 12: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas during northward migrations (N=4254, groups: year, 6; individual, 5). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	-0.09	0.06	0.141
Bare land	-0.20	0.09	0.029*
Forest	0.55	0.10	<0.001***
Open	0.22	0.08	0.006**
Urban	0.49	0.53	0.353
Water bodies	-0.48	0.13	<0.001***
Wetland	0.22	0.52	0.672

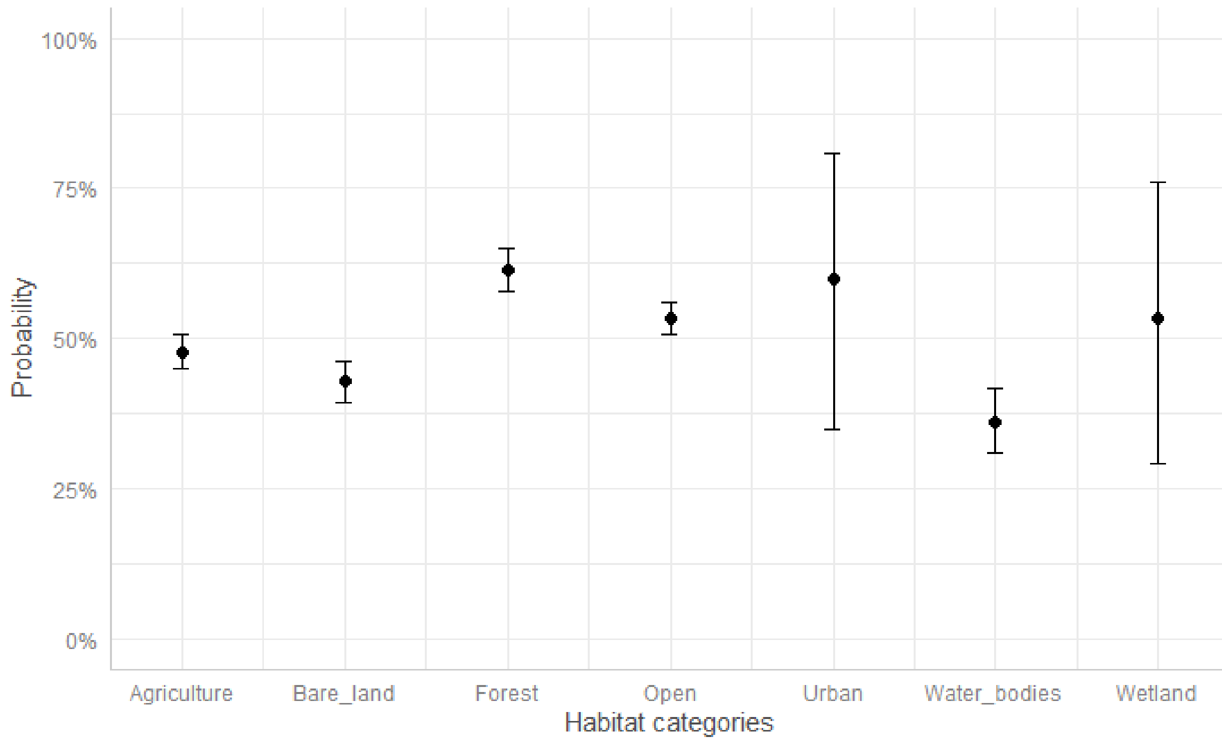

Figure 13: Predicted probabilities of a given point being an osprey in the different habitat categories during northward migration. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

During their northward migration, the ospreys were closer to open areas, urban areas, and wetlands, while they were further away from bare land, compared to the expectation. Distance to water bodies, forests, and agricultural areas was not significantly different than the expectation (table 13). The probability of a given point being an osprey was higher than the expectation closer to open areas, urban areas, and wetlands, further away from bare land, and not significantly different than the expectation at different distances to water bodies, forests, and agricultural areas (figure 14). Meaning that during their northward migrations, the ospreys preferred being closer to open areas, urban areas, and wetlands, they preferred being further away from bare land, and the distances to water bodies, forests, and agricultural areas were like the expectation.

Table 13: Parameter estimates for distance to different habitat categories during northward migrations (N=4254, groups: year, 6; individual, 5). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.27	0.08	<0.001***
Distance to water bodies	0.15	0.22	0.490
Distance to urban	-0.59	0.20	0.003**
Distance to forest	-0.42	0.24	0.073
Distance to open	-7.09	1.05	<0.001***
Distance to agriculture	0.37	0.30	0.216
Distance to wetland	-0.40	0.19	0.030*
Distance to bare land	0.34	0.15	0.022*

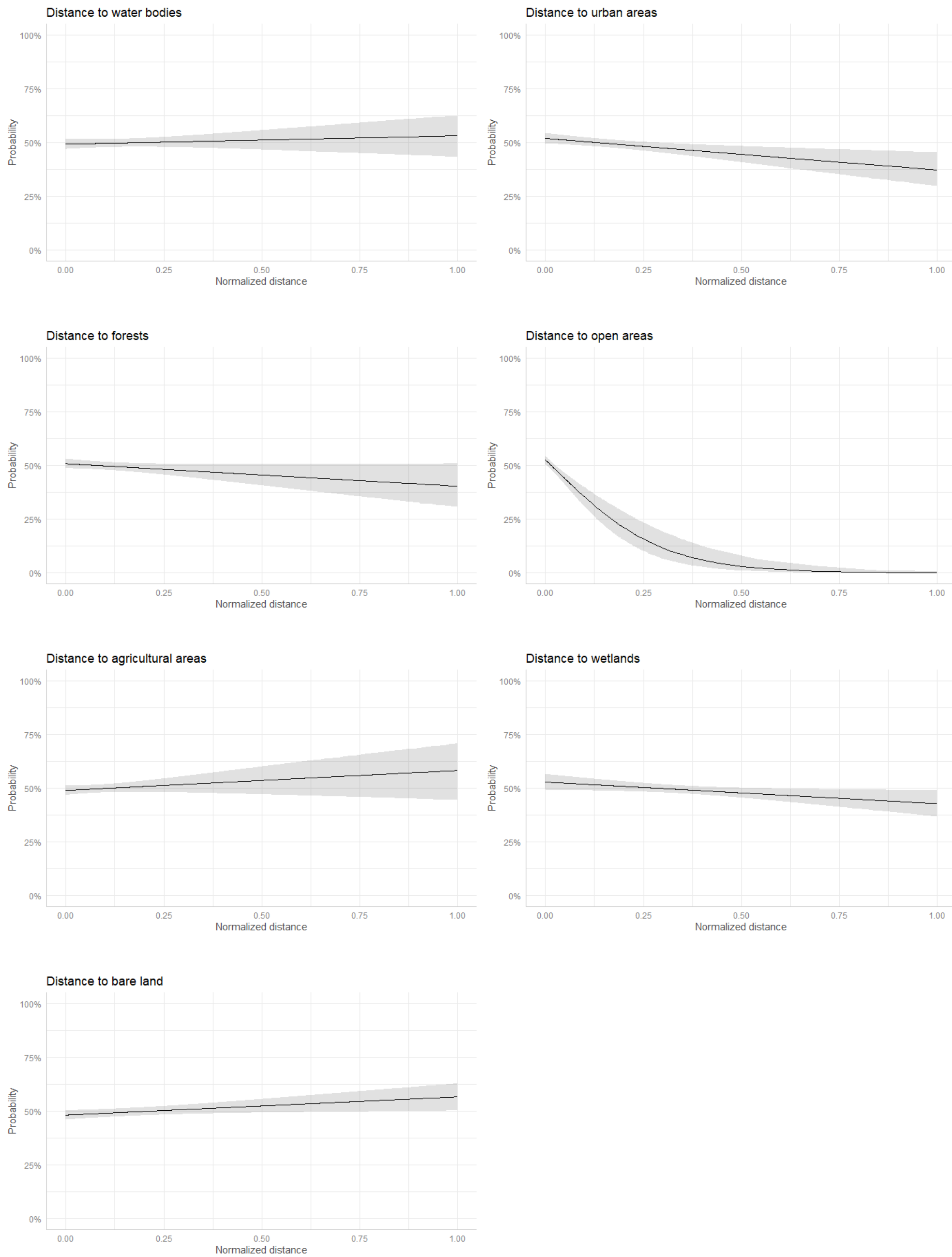

Figure 14: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories during northward migration. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.5 Adults vs. juveniles

3.5.1 Adults

Adults during southward migrations used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests, while they were less in urban areas, water bodies, and bare land. Open areas and wetlands were not used significantly different than the availability (table 14). The probability of a given point being an osprey was higher than the expectation in forests, lower in urban areas, water bodies, and bare land, and not significantly different than the expectation in agricultural areas, open areas, and wetlands (figure 15). Meaning that adults during southward migrations, preferred being in forests, they avoided being in urban areas, water bodies, and bare land, and they used agricultural areas, open areas, and wetlands like the availability.

Table 14: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas during southward migration for adults (N=11858, groups: year, 8; individual, 6). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.03	0.05	0.539
Bare land	-0.57	0.06	<0.001***
Forest	1.04	0.06	<0.001***
Open	0.06	0.05	0.230
Urban	-1.49	0.31	<0.001***
Water bodies	-1.40	0.09	<0.001***
Wetland	0.64	0.35	0.067

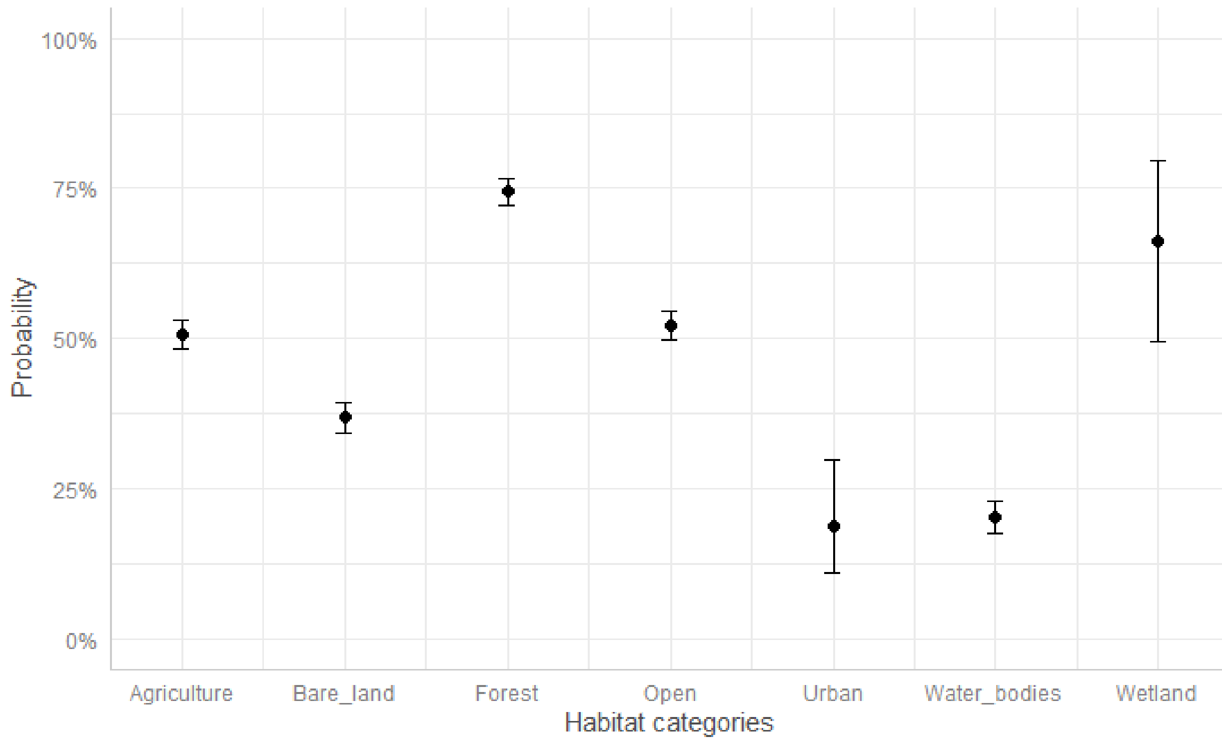

Figure 15: Predicted probabilities of a given point being an osprey in the different habitat categories for adults during southward migration. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

Adults during southward migrations were closer to open areas, urban areas, forests, water bodies, and agricultural areas, while they were further from bare land and wetlands, compared to the expectation (table 15). The probability of a given point being an osprey was higher than the expectation closer to open areas, urban areas, forests, water bodies, and agricultural areas, and further away from bare land and wetlands (figure 16). Meaning that adults during southward migrations, preferred being closer to open areas, urban areas, forests, water bodies, and agricultural areas, while they preferred being further away from bare land and wetlands.

Table 15: Parameter estimates for distance to different habitat categories during southward migration for adults (N=11585, groups: year, 8; individual, 6). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.07	0.08	0.395
Distance to water bodies	-0.63	0.13	<0.001***
Distance to urban	-1.18	0.17	<0.001***
Distance to forest	-0.69	0.16	<0.001***
Distance to open	-12.44	0.91	<0.001***
Distance to agriculture	-0.59	0.21	0.005**
Distance to wetland	0.46	0.12	<0.001***
Distance to bare land	1.24	0.10	<0.001***

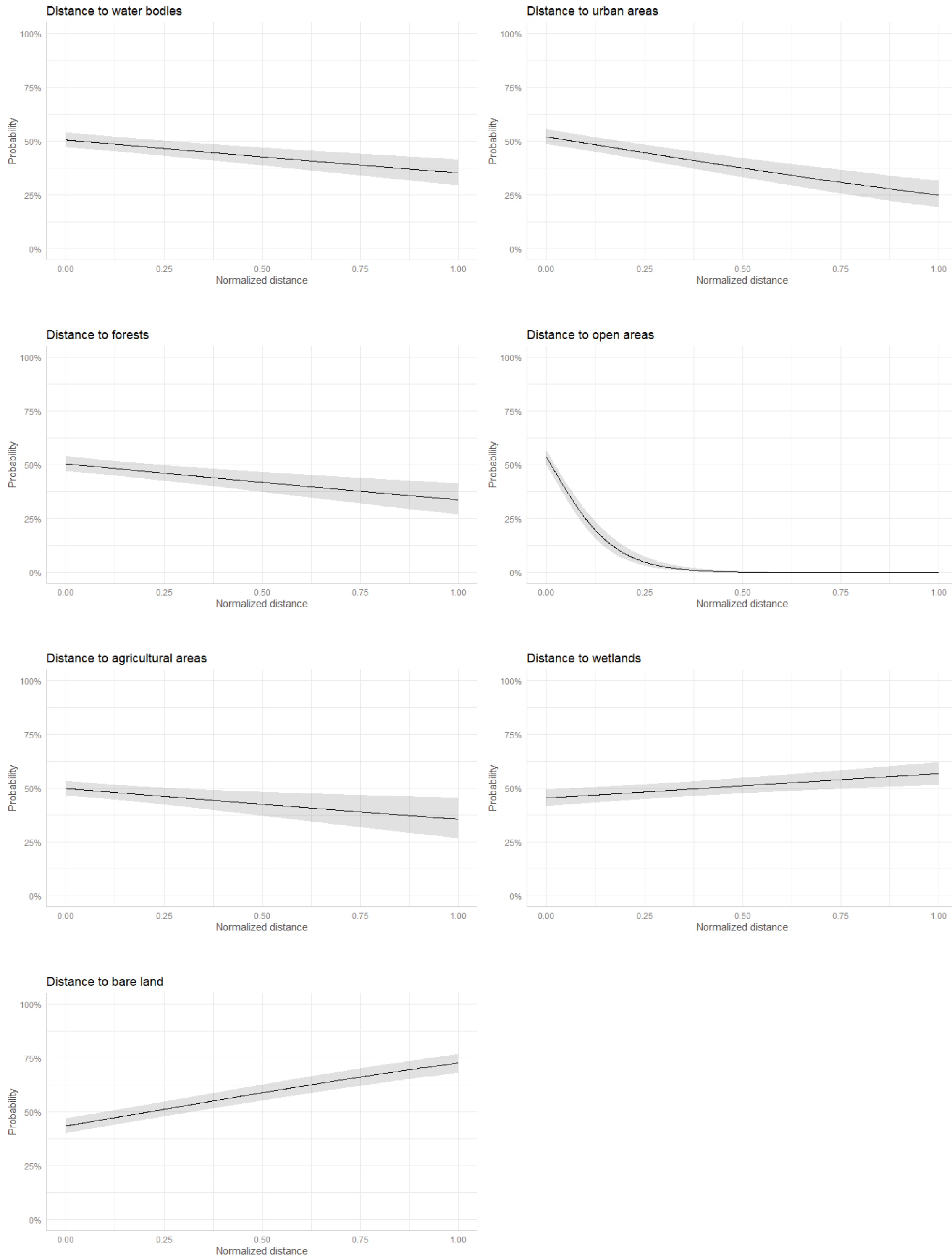

Figure 16: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories for adults during southward migration. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.5.2 Juveniles

Juveniles during their southward migrations used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the ospreys were more in forests, while they were less in water bodies and bare land. Urban areas and open areas were not used significantly different than the availability (table 16). The probability of a given point being an osprey was higher than the expectation in forests, lower in water bodies and bare land, and not significantly different than the expectation in agricultural areas, urban areas, and open areas (figure 17). Meaning that juveniles during southward migrations preferred being in forests, they avoided being in water bodies, and used agricultural areas, urban areas, and open areas like the availability.

Table 16: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas during southward migration for juveniles (N=1096, groups: individual, 4; year, 2). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.17	0.12	0.163
Bare land	-0.85	0.26	0.001**
Forest	0.54	0.17	0.001**
Open	0.07	0.22	0.760
Urban	0.34	0.53	0.523
Water bodies	-1.91	0.24	<0.001***

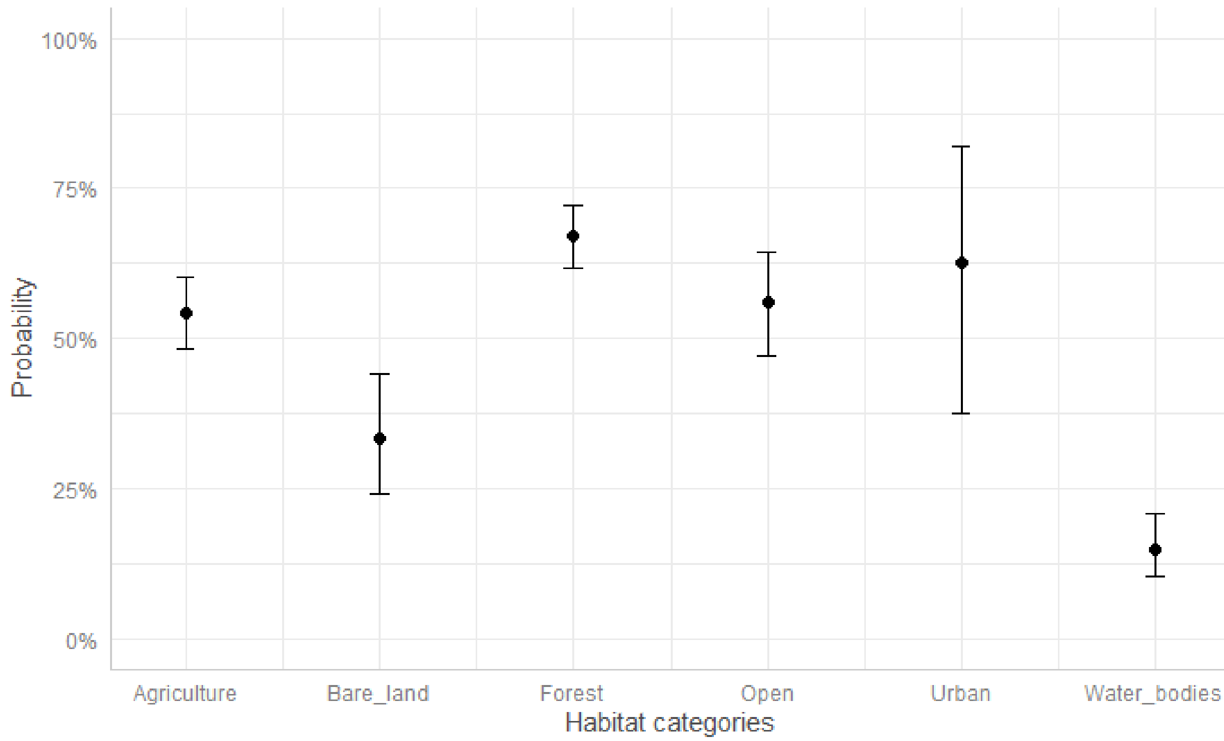

Figure 17: Predicted probabilities of a given point being an osprey in the different habitat categories for juveniles during southward migration. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

Juveniles during southward migrations were closer to open areas compared to the expectation, while distance to water bodies, urban areas, agricultural areas, bare land, and forests was not significantly different than the expectation (table 17). The probability of a given point being an osprey was higher than the expectation closer to open areas, while it was not significantly different at different distances to the rest of the habitat categories (figure 18). Meaning that juveniles during southward migration preferred being closer to open areas, while the distances to the rest of the habitat categories were like the expectation.

Table 17: Parameter estimates for distance to different habitat categories during southward migration for juveniles (N=1096, groups: individual, 4; year, 2). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.59	0.13	<0.001***
Distance to water bodies	0.37	0.39	0.332
Distance to urban	-0.40	0.43	0.352
Distance to forest	-0.64	0.46	0.163
Distance to open	-12.35	1.97	<0.001***
Distance to agriculture	-0.87	0.51	0.089
Distance to bare land	-0.66	0.34	0.052

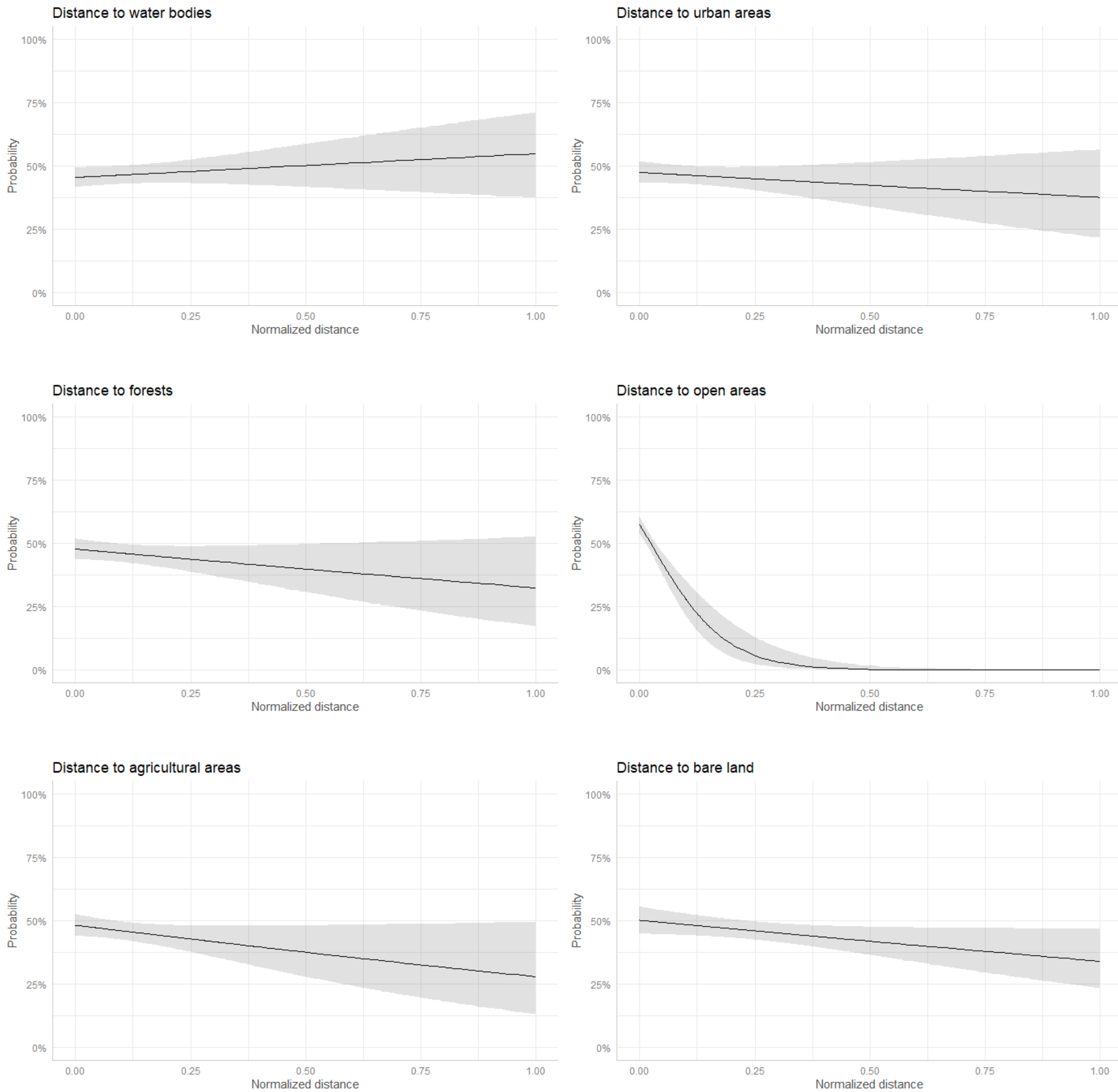

Figure 18: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories for juveniles during southward migration. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.6 Breeding years vs. non-breeding years

3.6.1 Home range

The adult ospreys used smaller areas in their home ranges in breeding years than in non-breeding years. In breeding years and non-breeding years, median MCP (95%) sizes were 83.4 km^2 and 98.8 km^2 respectively. In the same order, kernel core use areas (95%) had median sizes of 122.2 km^2 and 171.4 km^2. And kernel core use areas (50%) had median sizes of 8.1 km^2 and 12.3 km^2.

Home range in breeding years

In their home ranges in breeding years, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the use of forests, open areas, and water bodies were higher. The use of urban areas was so little that the model was not able to calculate an accurate estimate or standard error for it (table 18). Close to the nest, the probability of a given point being an osprey was higher than the expectation in forests and water bodies, it was most likely lower in urban areas, while it was not significantly different than the expectation in agricultural areas and open areas (figure 19). Meaning that in their home ranges in breeding years, the ospreys preferred being in forests and water bodies, they most likely avoided being in urban areas, while they used agricultural areas and open areas like the availability.

Table 18: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas for adults in their home ranges in breeding years (N=9220, groups: individual, 6; year, 5). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	-0.53	0.32	0.096
Forest	1.17	0.24	<0.001***
Open	0.99	0.27	<0.001***
Urban	-13.33	158.67	0.933
Water bodies	1.23	0.25	<0.001***
Distance to nest	-3.25	0.13	<0.001***

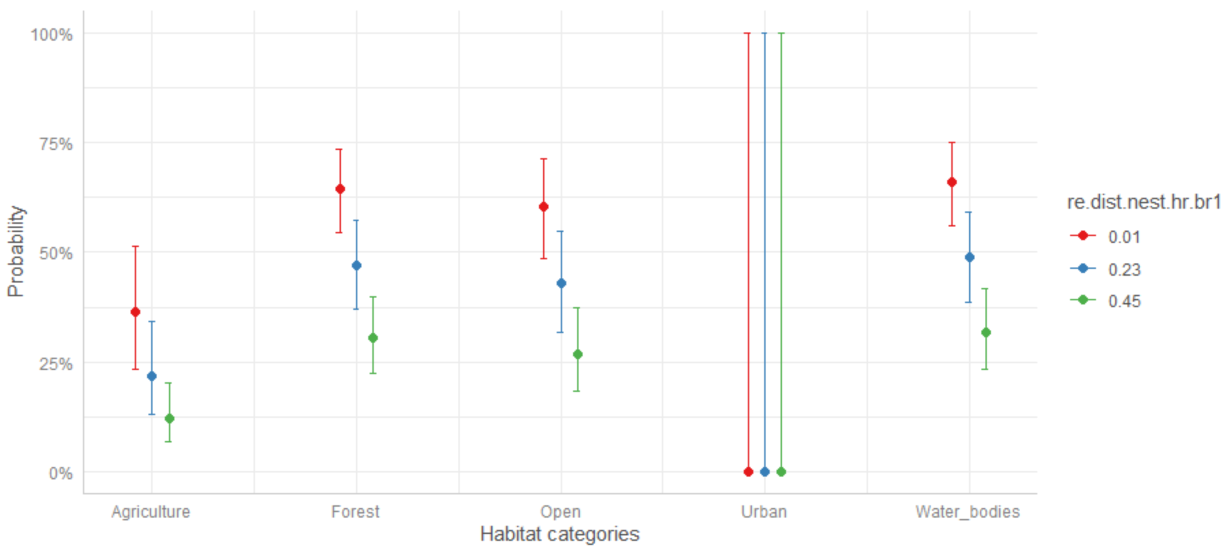

Figure 19: Predicted probabilities of a given point being an osprey in the different habitat categories in the ospreys' home ranges in breeding years, at different normalized distances to the nest (chosen automatically). Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

In their home ranges in breeding years, the ospreys were closer to forests, open areas, and water bodies, while they were further away from urban areas and agricultural areas (table 19). The probability of a given point being an osprey was higher than the expectation closer to forests, open areas, and water bodies, and further away from urban areas and agricultural areas (figure 20). Meaning that in their home ranges in breeding years, the ospreys preferred being closer to forests, open areas, and water bodies, while they preferred being further away from urban areas, and agricultural areas.

Table 19: Parameter estimates for distance to different habitat categories for adults in their home range in breeding years (N=9176, groups: individual, 6; year, 5). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	-1.89	0.75	0.012
Distance to water bodies	-0.91	0.12	<0.001***
Distance to urban	7.25	0.26	<0.001***
Distance to forest	-9.36	0.61	<0.001***
Distance to open	-4.32	0.25	<0.001***
Distance to agriculture	0.63	0.13	<0.001***
Distance to nest	-2.61	0.16	<0.001***

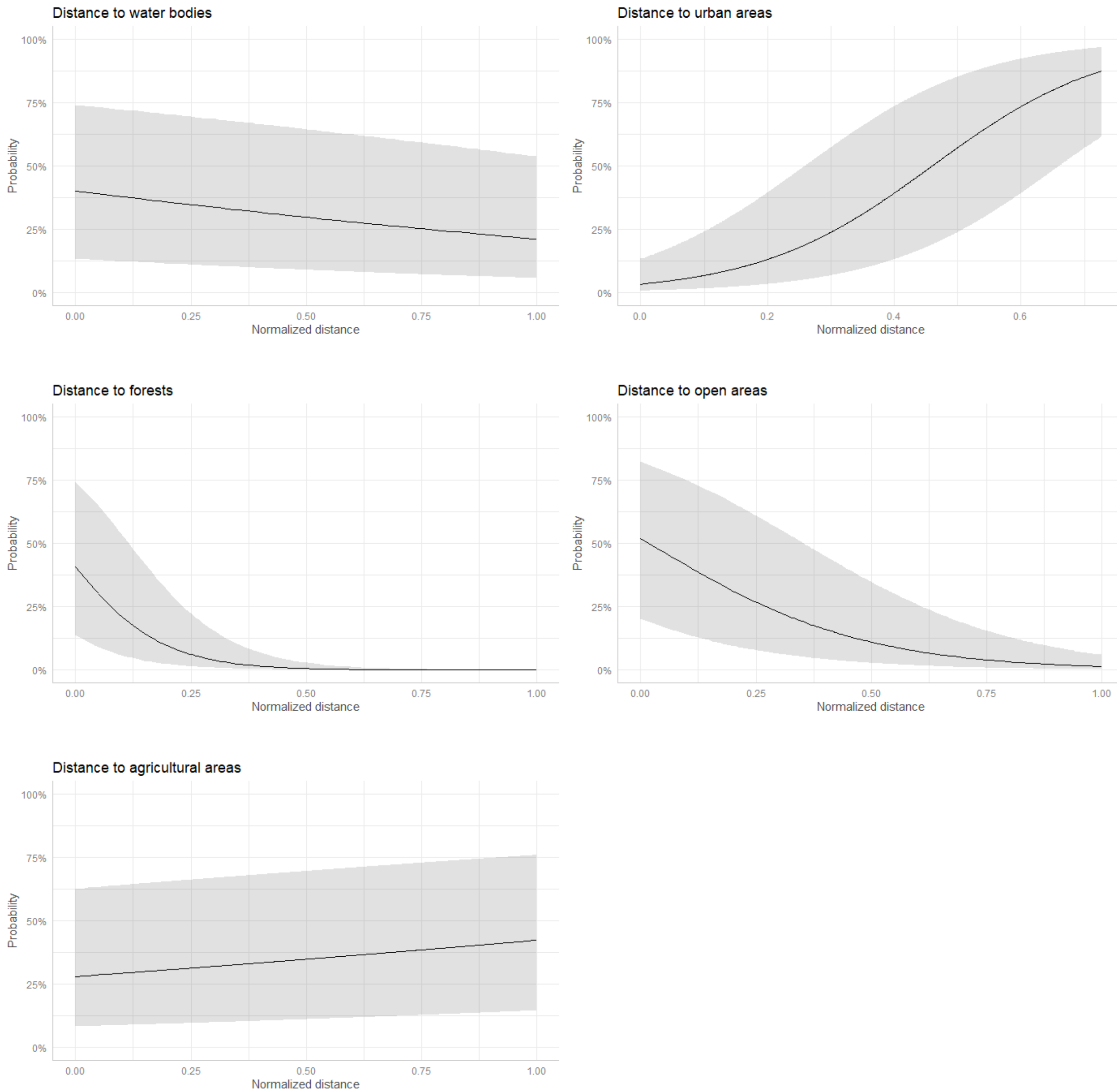

Figure 20: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories in the ospreys' home ranges in breeding years. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

Home range in non-breeding years

In their home ranges in non-breeding years, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the use of forests, open areas, and water bodies was higher, while the use of urban areas was lower (table 20). Close to the nest, the probability of a given point being an osprey was higher than the expectation in open areas and water bodies, it was lower in urban areas, while it was not significantly different in agricultural areas and forests (figure 21). Meaning that in their home ranges in non-breeding years, the ospreys preferred being in open areas and water bodies, they avoided being in urban areas, and used agricultural areas and forests like the availability.

Table 20: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas for adults in their home ranges in non-breeding years (N=11426, groups: individual, 5; year, 5). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.16	0.17	0.341
Forest	0.25	0.12	0.037*
Open	0.66	0.16	<0.001***
Urban	-4.38	1.01	<0.001***
Water bodies	0.61	0.13	<0.001***
Distance to nest	-2.00	0.13	<0.001***

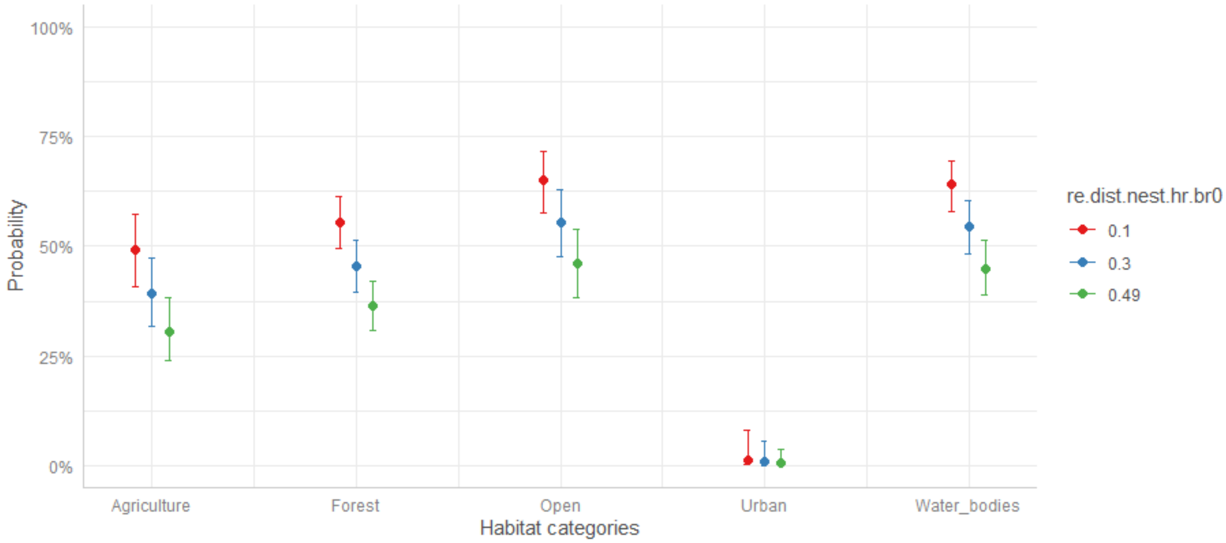

Figure 21: Predicted probabilities of a given point being an osprey in the different habitat categories in the ospreys' home ranges in non-breeding years, at different normalized distances to the nest (chosen automatically). Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

In the ospreys' home ranges in non-breeding years, they were closer to forests, open areas, water bodies, and agricultural areas, while they were further away from urban areas (table 21). The probability of a given point being an osprey was higher than the expectation closer to forests, open areas, water bodies, and agricultural areas, and further away from urban areas (figure 22). Meaning that in their home ranges in non-breeding years, the ospreys preferred being closer to forests, open areas, water bodies, and agricultural areas, and they preferred being further away from urban areas.

Table 21: Parameter estimates for distance to different habitat categories for adults in their home range in non-breeding years (N=11426, groups: individual, 5; year, 5). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	1.83	0.34	<0.001***
Distance to water bodies	-3.38	0.14	<0.001***
Distance to urban	4.18	0.22	<0.001***
Distance to forest	-9.77	0.56	<0.001***
Distance to open	-7.32	0.22	<0.001***
Distance to agriculture	-1.12	0.11	<0.001***
Distance to nest	-3.23	0.17	<0.001***

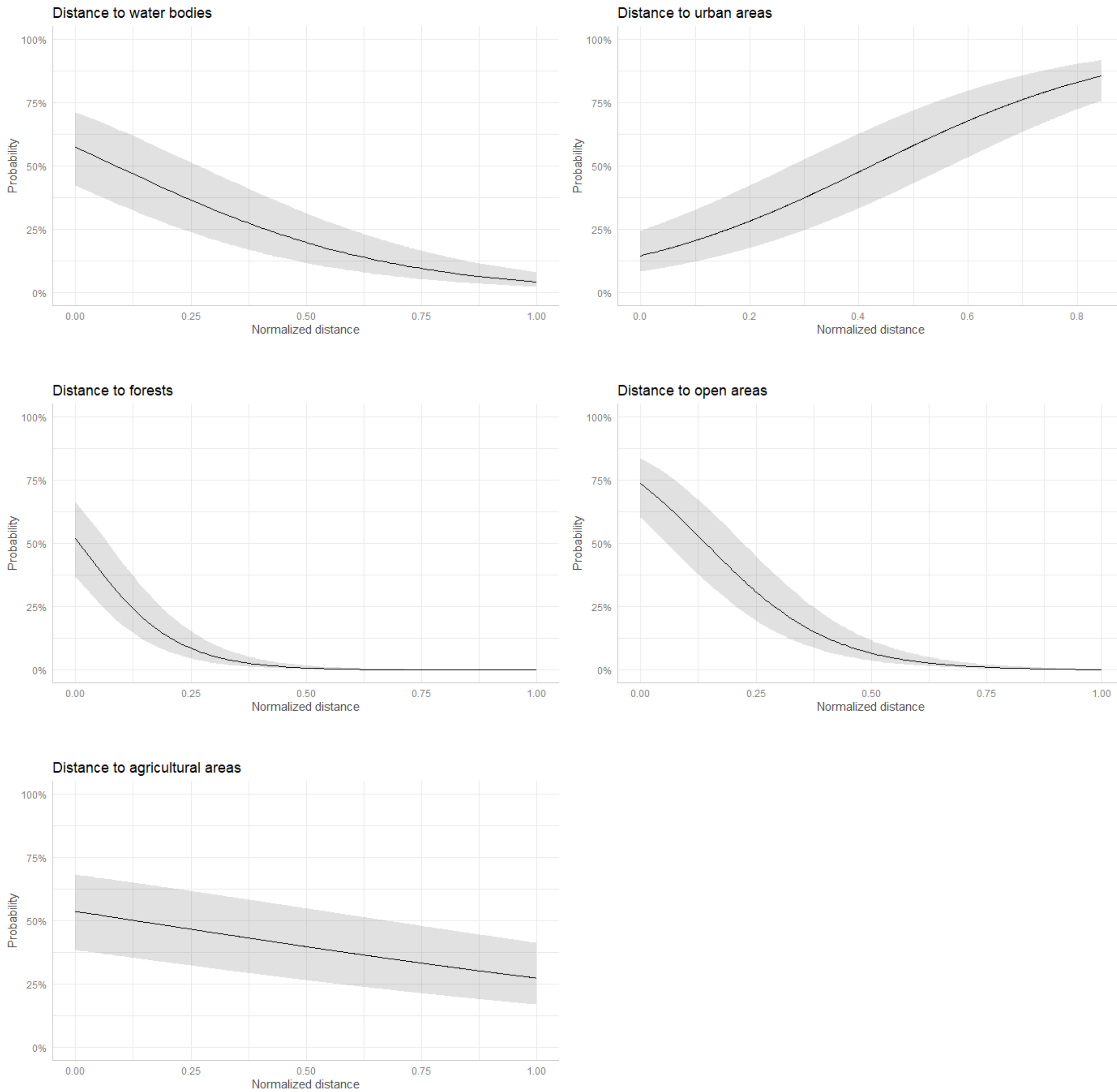

Figure 22: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories in the ospreys' home ranges in non-breeding years. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

3.6.2 Southward migration

Southward migration in breeding years

During their migration southward in breeding years, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the use of forests was higher, the use of bare land and urban areas was lower, and the use of open areas and wetlands were also like the availability (table 22). The probability of a given point being an osprey was higher than the expectation in forests, it was lower in bare land, urban areas, and water bodies, and it was not significantly different than the expectation in agricultural areas, open areas, and wetlands (figure 23). Meaning that during southward migrations in breeding years, the ospreys preferred being in forests, they avoided being in bare land, urban areas, and water bodies, while they used agricultural areas, open areas, and wetlands like the availability.

Table 22: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas for adults during southward migration in breeding years (N=6090, groups: individual, 6; year, 5). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	0.05	0.06	0.374
Bare land	-0.55	0.09	<0.001***
Forest	0.92	0.09	<0.001***
Open	-0.02	0.07	0.736
Urban	-1.20	0.44	0.006**
Water bodies	-1.27	0.11	<0.001***
Wetland	0.57	0.37	0.116

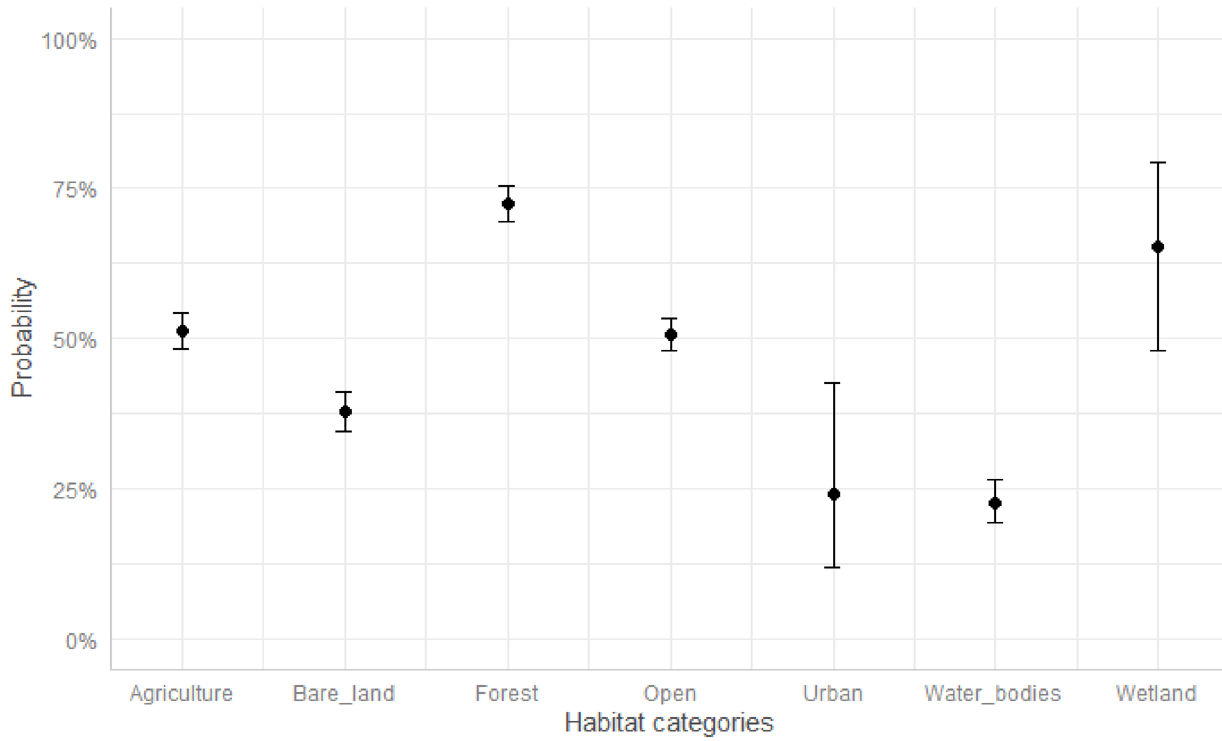

Figure 23: Predicted probabilities of a given point being an osprey in the different habitat categories during southward migration in breeding years. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

During their migrations southward in breeding years, the ospreys were closer to water bodies, forests, and open areas, while they were further away from bare land. Distances to urban areas, agricultural areas and wetlands were not significantly different than the expectation (table 23). The probability of a given point being an osprey was higher than the expectation closer to water bodies, forests, and open areas, further away from bare land, and not significantly different at different distances to urban areas, agricultural areas, and wetlands (figure 24). Meaning that during southward migrations in breeding years, the ospreys preferred being closer to water bodies, forests, and open areas, they preferred being further away from bare land, while distances to urban areas, agricultural areas, and wetlands were like the expectation.

Table 23: Parameter estimates for distance to different habitat categories for adults during southward migration in breeding years (N=6090, groups: individual, 6; year, 5). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	0.12	0.08	0.139
Distance to water bodies	-0.58	0.18	0.001**
Distance to urban	-0.23	0.24	0.340
Distance to forest	-1.12	0.28	<0.001***
Distance to open	-8.85	0.84	<0.001***
Distance to agriculture	-0.06	0.34	0.853
Distance to wetland	0.10	0.17	0.555
Distance to bare land	1.09	0.15	<0.001***

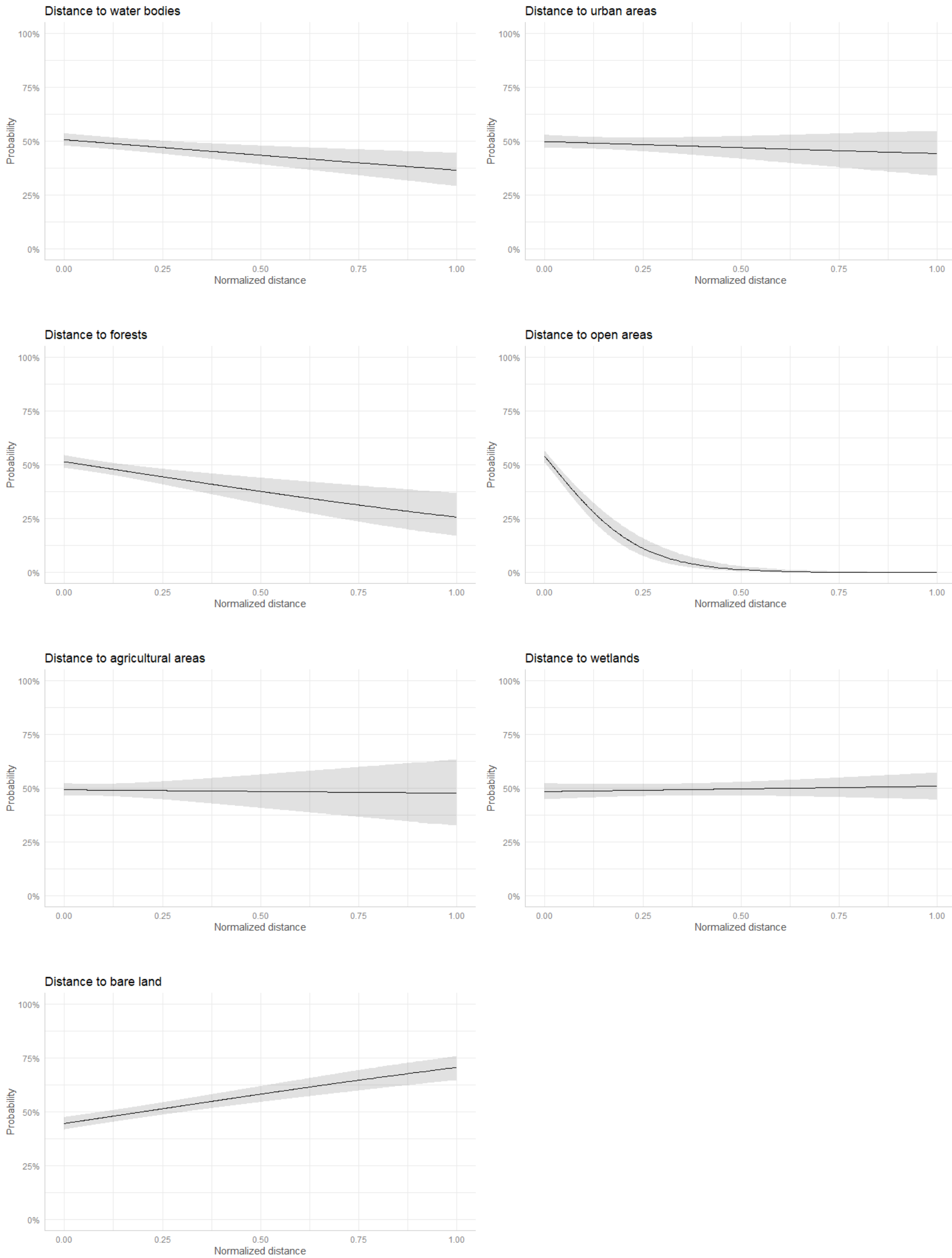

Figure 24: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories during southward migration in breeding years. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

Southward migration in non-breeding years

During their migrations southward in non-breeding years, the ospreys used agricultural areas like the availability. Compared to the use vs. availability of agricultural areas, the use of forests was higher, it was lower in bare land, urban areas, and water bodies, while wetlands and open areas were also used like the availability (table 24). The probability of a given point being an osprey was higher than the expectation in forests, it was lower in bare land, urban areas, and water bodies, while it was not significantly different than the expectation in agricultural areas, open areas, and wetlands (figure 25). Meaning that during southward migrations in non-breeding years, the ospreys preferred being in forests, they avoided being in bare land, urban areas, and water bodies, while they used agricultural areas, open areas, and wetlands like the availability.

Table 24: Parameter estimates for the use vs. availability of different habitat categories compared to agricultural areas for adults during migration in non-breeding years (N=5768, groups: individual, 5; year, 5). A positive or negative estimate of the intercept means that the ospreys used agricultural areas more or less than the availability, and a positive estimate of the other habitat categories means they used the habitat more compared to the availability compared to agricultural areas. Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Agriculture (intercept)	-0.05	0.09	0.587
Bare land	-0.58	0.09	<0.001***
Forest	1.18	0.09	<0.001***
Open	0.14	0.07	0.067
Urban	-1.74	0.45	<0.001***
Water bodies	-1.57	0.14	<0.001***
Wetland	0.78	1.20	0.517

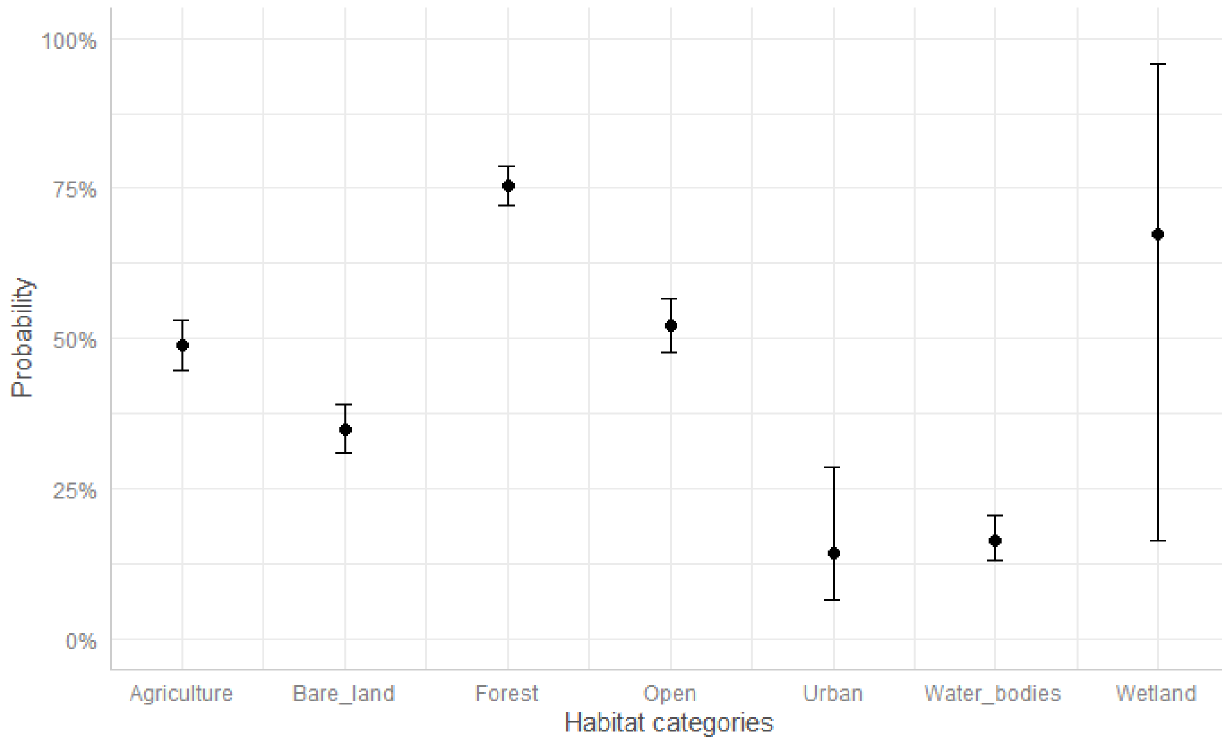

Figure 25: Predicted probabilities of a given point being an osprey in the different habitat categories during southward migrations in non-breeding years. Brackets show the 95% confidence interval. A preference or avoidance is seen if the entire confidence interval is over or under the expectation (50%). The expectation is that the ospreys use the habitat category like the availability.

During their southward migrations in non-breeding years, the ospreys were closer to water bodies, urban areas, forests, open areas, and agricultural areas, while they were further away from wetlands and bare land, compared to the expectation (table 25). The probability of a given point being an osprey was higher than the expectation closer to open areas, urban areas, agricultural areas, water bodies, and forests, and it was higher further away from bare land and wetlands (figure 26). Meaning that during southward migrations in non-breeding years, the ospreys preferred being closer to open areas, urban areas, agricultural areas, water bodies, and forests, while they preferred being further away from bare land and wetlands.

Table 25: Parameter estimates for distance to different habitat categories for adults during southward migration in non-breeding years (N=5768, groups: individual, 5; year, 5). A negative estimate means that the ospreys were closer to the habitat category than the expectation (random points). Significance codes: <0.001***, <0.01**, <0.05*.

Fixed effects	**Estimate**	**Std. error**	**P**
Intercept	-0.04	0.11	0.736
Distance to water bodies	-0.62	0.18	<0.001***
Distance to urban	-2.11	0.24	<0.001***
Distance to forest	-0.51	0.20	0.012*
Distance to open	-10.15	1.15	<0.001***
Distance to agriculture	-0.85	0.26	0.001**
Distance to wetland	0.91	0.19	<0.001***
Distance to bare land	1.27	0.13	<0.001***

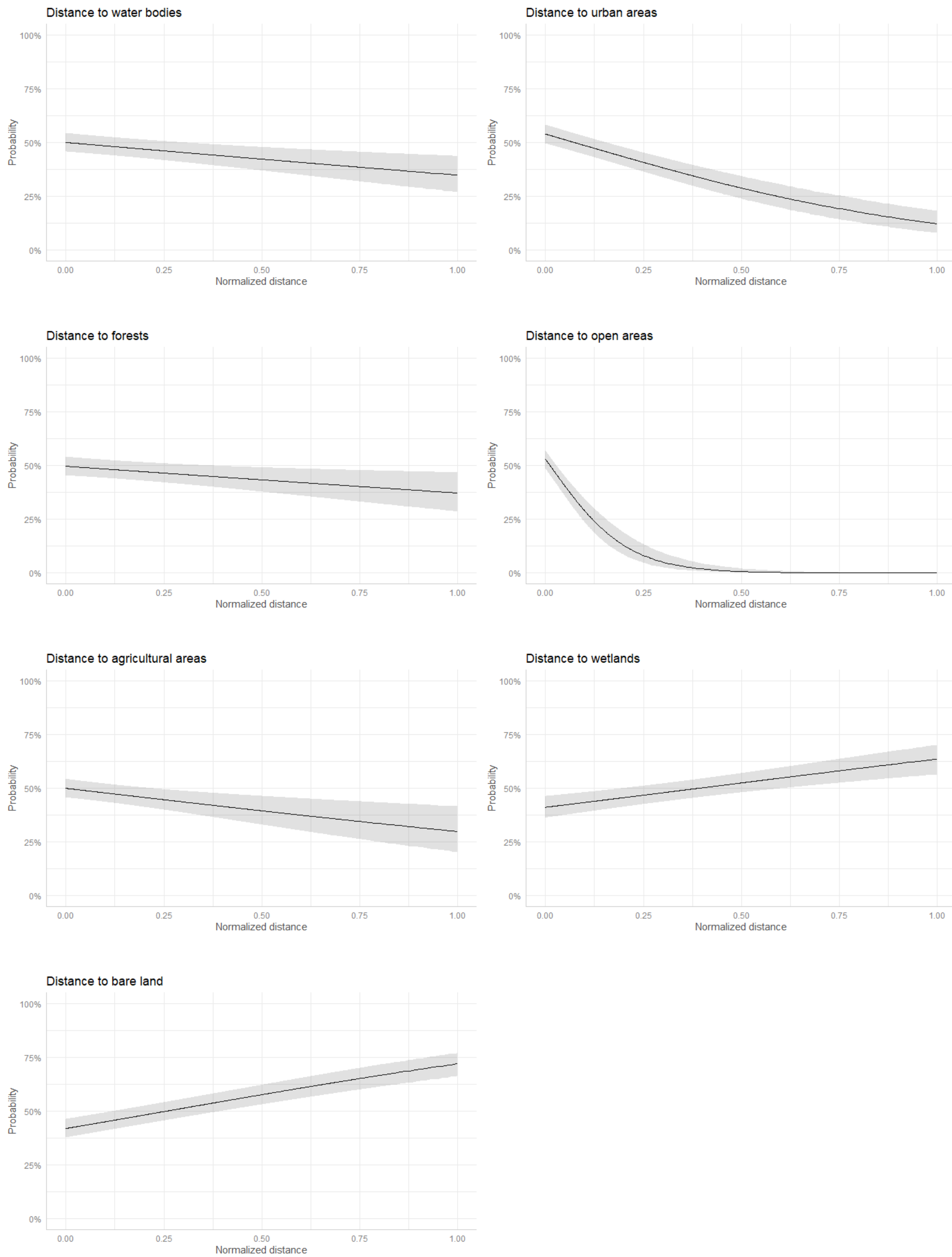

Figure 26: Predicted probabilities of a given point being an osprey at different normalized distances to the different habitat categories during southward migration in non-breeding years. The buffer shows the 95% confidence interval. The expectation is that the probability is the same at any distance to the habitat category (50%), and a preference is seen if the probability changes significantly at different distances.

4. Discussion

4.1 Habitat preferences in the different seasons

4.1.1 Home range

When analyzing the ospreys' home ranges using the detailed map, some differences were seen from the analysis with the world map. However, the analysis on the more detailed map could only include ospreys that had home ranges exclusively in Norway, meaning that only two adults and three juveniles were included. The three juveniles were mostly in the nest or very close to it and a preliminary analysis of all juveniles' habitat preferences in their home ranges showed that they had no significant preferences. One of the two adults had a special behavior, where it would fly great distances over open sea regularly, to forage on the opposite side of the fjord (maps 9-10 in Appendix 1). This individual's habitat preferences alone, would show an avoidance of water bodies, due to the large amount of open sea in the available area. This had a large effect and led to the analysis of all the ospreys' habitat preferences in their home ranges with the detailed map, showing an avoidance of water bodies, and no preference for being closer to water bodies, due to the analysis not including enough individuals. Highlighting the common problem of having few individuals in satellite telemetry studies (Hebblewhite & Haydon, 2010). Therefore, the analyses of different habitat preferences between breeding years and non-breeding years for adults in their home ranges was done using the world map, and only the results from the analysis of all ospreys' habitat preferences in their home ranges with the world map will be discussed hereafter.

In their home ranges, the ospreys preferred being in forests, open areas, and water bodies, they avoided being in urban areas, and they used agricultural areas like the availability. They also preferred being closer to forests, open areas, water bodies, and agricultural areas, and they preferred being further away from urban areas. Bai et al. (2009) found that ospreys preferred landscapes with more water bodies and forest for their nest locations, and that pairs with nests surrounded by more agricultural land and less forest had higher breeding success. The ospreys' preferences to be in forests and water bodies, and their preference to be closer to agricultural areas, confirmed what Bai et al. (2009) found in their study. Toschik et al. (2006) found that ospreys preferred to nest over water, coastal marshes, or shrubs, and avoided agricultural and urban areas. The preferred habitats found for nesting ospreys by Toschik et al. (2006) were all the same or very similar to land cover classes that were aggregated into habitat categories in this study: coastal marshes would go under wetlands in this study and shrubs was a land cover class that went under the habitat category open areas in this study. Meaning that the habitat preferences of ospreys in their home ranges found in this study were in agreement with what earlier studies have found. The ospreys' preferences for forests could be explained by nests primarily being built in forests (Saurola, 1997), forests providing shelter, allowing the ospreys to rest (Galarza & Dennis, 2009), and forests being used while perch hunting (Clancy, 2005). The ospreys' preferences for open areas, could be explained by the use of thermal updrafts for soaring, while foraging "on the wing" (Clancy, 2005). The ospreys' preferences for water bodies were unsurprising given their biology. The ospreys' preference to be closer to agricultural areas, could be explained by more efficient foraging in eutrophic lakes (Bai et al., 2009). And the ospreys' avoidance of urban areas was of course to avoid human disturbance.

4.1.2 Migration

During their migrations, the ospreys preferred being in forests and open areas, they avoided being in bare land, urban areas, and water bodies, and used agricultural areas and wetlands like the availability. They also preferred being closer to open areas, urban areas, forests, and water bodies, they preferred being further away from bare land, and their distances to agricultural areas and wetlands were like the expectations. Crawford and Long (2017) found that juvenile ospreys during migration generally preferred being close to rivers and lakes and avoided urban areas, while some of the individuals preferred forests and others avoided them, some individuals preferred being in water bodies at stopover sites, and open areas were avoided by some individuals and used like the availability by others. However, open areas in their study included land cover classes which would go under agricultural areas, wetlands, and bare land in this study. Since Crawford and Long (2017) studied only juvenile ospreys, and analyzed individual habitat preferences, their study is not optimal to compare with the results of all ospreys' habitat preferences during migrations. However, the results were generally in agreement, other than the differences in preferences for open areas, which was due to different classification of the habitat category, and the differences in preferences for water bodies, which was due to only stopovers being analyzed in their study. A study on a single osprey's stopover during spring migration (Galarza & Dennis, 2009), showed that the osprey was primarily in wooded areas and had quick daily foraging trips to feeding areas in marshland and the sea, and stayed more than 200 m from roads and buildings. These results were in agreement with the results found in this study, that during migration the ospreys preferred forests, avoided being in urban areas, used wetlands like the availability, and preferred being closer to water bodies.

What was different from in their home ranges, was that during the ospreys' migrations, they avoided being in water bodies but still preferred being closer to them, they preferred being closer to urban areas but still avoided being in them, and they did not prefer being closer to agricultural areas. Additionally, bare land and wetlands were in the available area, bare land was avoided, and wetlands were used like the availability. Large water bodies represent a difficult barrier during migration for most migratory birds, even though ospreys are a bit of an exception in this regard (Duriez et al., 2018). Oceans were crossed as quickly as possible, leaving few observed points and many random points in water bodies, leading to the avoidance of being in water bodies during the ospreys' migrations. The ospreys still preferred being closer to water bodies, due to stopovers being close to water bodies and foraging in water bodies during migration. That the ospreys preferred being closer to urban areas during migration could be because most stopover sites were made in Europe, like Hake et al. (2001) and Kjellen et al. (2001) also found, while fewer observed points were from crossing the Mediterranean and the Sahara Desert, as examples where distances to urban areas were great. The largest area of bare land in the study area was the Sahara Desert, which is hazardous for migratory birds (Strandberg et al., 2010), making the avoidance of bare land unsurprising. The ospreys preferences for forests, being closer to water bodies, and their non-significant use of wetlands, could all be explained by ospreys using forests close to foraging areas, to have a safe place to rest while making quick feeding trips, improving refueling rates and survival during migration (Galarza & Dennis, 2009). The ospreys preferences for open areas during migration, could again be explained by the use of thermal updraft for soaring flight (Kjellen et al., 2001).

4.1.3 Wintering areas

In their wintering areas, the ospreys preferred being in forests and wetlands, they avoided being in bare land and water bodies, and they used agricultural areas and open areas like the availability. They also preferred being closer to water bodies, agricultural areas, open areas, wetlands, and bare land, while they preferred being further away from forests. Washburn et al. (2014) found that wintering North American ospreys stayed in forest dominated areas (50.6%), agricultural areas (25.3%), wetlands (13.9%), grasslands (6.3%), and residential areas (3.8%). Which was very similar to what this study has found, except for agricultural areas seeming to be used more and wetlands seeming to be used less by the North American ospreys. However, their study did not take the availability of the different habitat categories into account, meaning that the uses could be similar, since agricultural areas are a more dominant land cover in most of the world (Ritchie & Roser, 2013), and wetlands are known to be important foraging habitats for ospreys (BirdLife, 2019).

Ospreys are known to be more stationary during their wintering period, staying close to foraging areas, and resting most of the day (Alerstam et al., 2006; Hake et al., 2001; Monti et al., 2018b; Washburn et al., 2014). Therefore, the ospreys' preferences for forests and wetlands in their wintering areas was due to the ospreys resting in forests close the foraging areas and as shown in Zwarts et al. (2009): resting and foraging in wetlands. That the ospreys also preferred being further away from forests, could be because the same forest patches were used most of the time, while many other unused forests were in the available areas. That the ospreys avoided being in water bodies during their wintering period, was because ospreys spend more time perched next to water bodies than actually being in them (Zwarts et al., 2009, p. 295). This effect was seen in the ospreys' wintering areas, but not in their home ranges, possibly due to the different movement patterns that led to smaller areas used in their wintering areas, which were close to their foraging grounds. Meaning that their wintering areas contained larger proportions of water bodies, and therefore more random points being in water bodies (see maps of home ranges: 1-22 vs. wintering areas: 30-44). That the ospreys used agricultural areas and open areas like the availability, and preferred being closer to both habitat categories, could be explained by some use of "foraging on the wing" during their wintering period, which the "larger than usual" wintering areas found in this study also suggest (further discussed in sub-chapter 4.5). That the ospreys preferred being closer to bare land is hard to explain but could be due to more wintering areas being closer to the Sahara Desert, two wintering area were surrounded by bare land (figure 27).

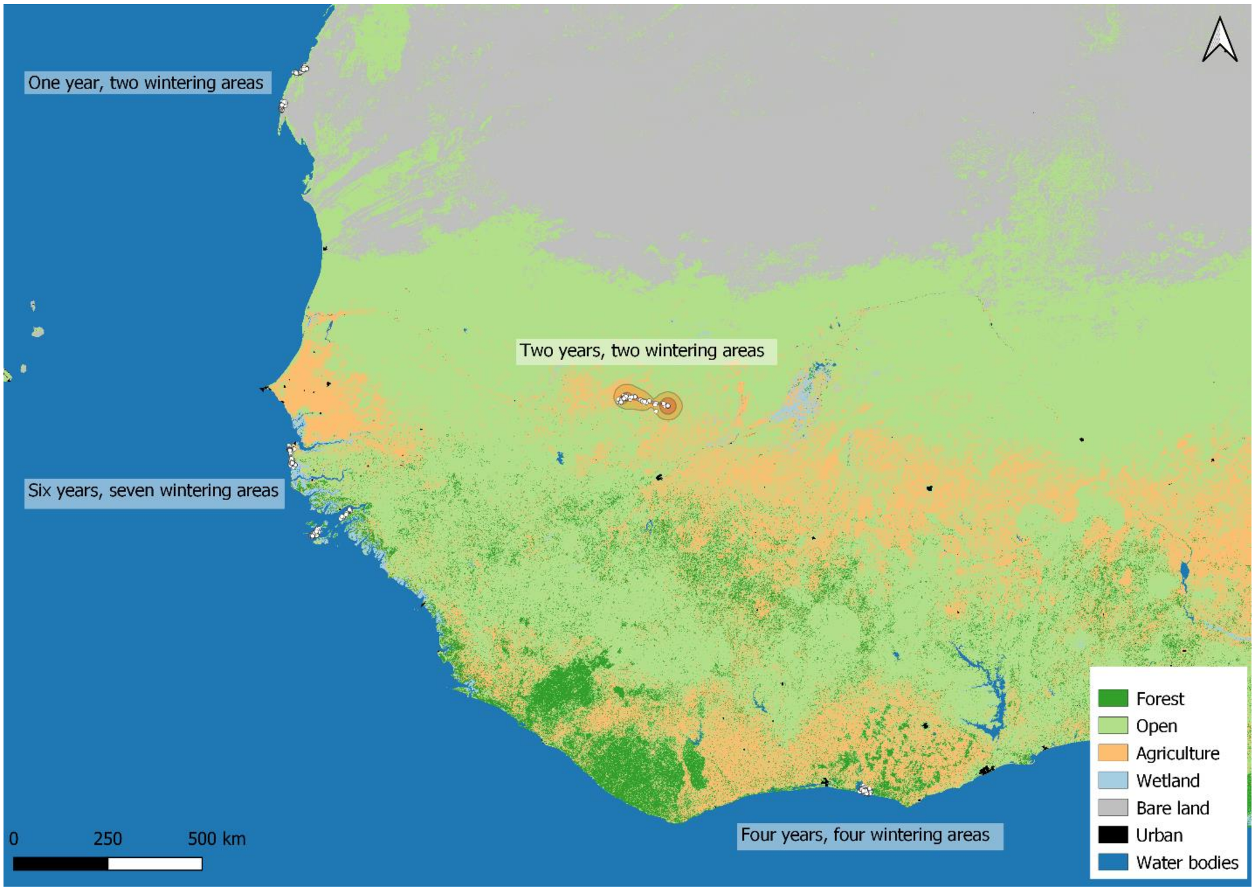

Figure 27: Wintering areas of all individuals in all years. Several individuals used the same wintering areas in several years.

4.2 Southward migrations vs. northward migrations

Differences in habitat preferences were found between southward migrations and northward migrations. These differences could be explained by the fact that ospreys typically have longer duration migrations, with longer stopovers on their way south, compared to their northward migrations (Alerstam et al., 2006; Monti et al., 2018a; Strandberg & Alerstam, 2007).

Open areas were preferred during northward migrations, while they were used like the availability during southward migrations. This difference could be explained by a higher proportion of use of open areas for thermal updrafts during northward migrations, due to soaring while covering migration distance and soaring while “foraging on the wing” (Clancy, 2005; Strandberg & Alerstam, 2007). While more time spent at stopovers on the southward migration led to a higher proportion of use of other habitat categories. Alerstam et al. (2006) showed that the differences in total duration between migrations were mainly due to more stopover days being spent during southward migrations, while no or only minor differences in flight behavior/performance were seen. Meaning that the days spent at stopover sites during southward migrations were the reason open areas were only used like the availability.

The ospreys avoided water bodies during both migrations but preferred being closer to them only during southward migrations, while the distance was like the expectation during northward migrations. This could also be explained by more time spent at stopovers during southward migrations, close to water bodies, cancelling out the effect of the avoidance of large water bodies. While the quicker northward migrations did not contain enough points close to water bodies to cancel out the effect. Hake et al. (2001) showed that even though ospreys are especially well adapted to flight over open sea (Duriez et al., 2018), they still avoid the risks associated with it to some degree. Meaning that during the northward migration, containing less observed points close to water bodies than during stopovers on southward migrations, the ospreys’ habitat preferences showed they avoided large water bodies completely.

The ospreys used wetlands like the availability during both migrations, while the ospreys only preferred being closer to them during northward migrations. This could be due to some wetlands being used and others being skipped during southward migrations, because the energy accumulated at stopovers allowed the ospreys to continue flying over other wetlands close to and after stopovers. While during northward migration, the ospreys probably used more different wetlands for quick foraging stops. Strandberg and Alerstam (2007) showed that more ospreys deviated from their flight paths during spring migration than during autumn migration, to forage in a lake. Supporting my suggestion that when ospreys have recently made a stopover, they will not deviate from their flight path to visit other foraging areas.

During southward migrations, the ospreys avoided being in urban areas, while during northward migrations the ospreys used them like the availability. Which could be explained by ospreys sometimes flying over urban areas during both migrations, but only southward migrations including enough use of other habitat categories during stopovers to show an avoidance of urban areas. And perhaps ospreys use deflection updrafts over urban areas during migration (Fenner et al., 2014).

Agricultural areas were used like the availability during both migrations, while the distances to agricultural areas were significantly lower than the expectation only during southward migration. This could also be due to more time spent at stopovers during southward migrations, which were closer to agricultural areas than for example the middle of Sahara or the Mediterranean, leading to the distances to agricultural areas during northward migrations being like the expectation. As Hake et al. (2001) and Kjellen et al. (2001) also showed, most stopovers were made in Europe, where agricultural areas are prominent.

4.3 Adults vs. juveniles

Differences in habitat preferences were found between adults and juveniles during southward migration, which could be explained by juveniles lacking experience. The juveniles did not use wetlands at all and did not prefer being closer to water bodies or forests as the adults did, possibly a result of the juveniles not being able to find good resting and foraging areas. Previous studies have shown that juvenile ospreys have less straight migration paths toward wintering areas compared to adults (Hake et al., 2001), and that juveniles are less capable of compensating for wind drift during migration (Thorup et al., 2003). Mackrill (2017) also showed that juvenile ospreys had more variable flight paths, they spent more energy during migration, they were less hesitant of crossing oceans, and they were heavily affected by crosswinds. Additionally, adult ospreys' migrations are based on past experiences and they navigate with familiar landmarks (Alerstam et al., 2006). Crawford and Long (2017) found that juvenile ospreys showed individual habitat preferences during migration, some juveniles preferred forests and avoided open areas, while others preferred open areas and avoided forests. The opposite preferences of some of the juveniles found in their study, showed that the habitat preferences of juveniles were probably more dependent on other factors than the preferences of adults. I found that the juveniles did have one habitat category they preferred being closer to, open areas. Which suggests that juveniles were using soaring flight like the adults during migration, but since they did not already know good resting and foraging areas during their first migration, they ended up in different areas and therefore had different habitat preferences than adults.

4.4 Breeding vs. non-breeding years

Home range

Differences in area uses and habitat preferences were found between breeding years and non-breeding years for adults in their home ranges, which could be explained by the need to be closer to the nest in breeding years. This was shown by both the larger home ranges in non-breeding years and the stronger preference of being closer to the nest in breeding years. Additionally, the preferences for different habitats were more similar at different distances to the nest in non-breeding years. During breeding years in their home ranges, the ospreys preferred forests and water bodies, while during non-breeding years they preferred open areas instead of forests. During breeding years, the ospreys preferred being further away from agricultural areas, and during non-breeding years the ospreys preferred being closer to them, while during both years they used agricultural areas like the availability. These differences could all be explained by more use of thermal updrafts for exploring and foraging "on the wing" during non-breeding years.

To my knowledge, no previous study has researched differences in behavior between breeding years and non-breeding years. Many studies have researched site occupancy and distribution patterns based on the ideal free distribution theory, which simply put explains how a species distribution will prioritize sites of high quality, and therefore the presence in a site compared to the distribution reflects its quality (e.g. Bai et al., 2009; Bretagnolle et al., 2008; Lohmus, 2001). And others have studied breeding success in an osprey population (e.g. Clancy, 2006; Eriksson & Wallin, 1994; Poole, 1985). Researching ospreys' behavior in years where breeding fails, would be a step further in understanding their ecology.

Southward migration

Some small differences were seen in habitat preferences during southward migration between breeding and non-breeding years. However, the preferences or avoidances of being in different habitat categories were the same between years, while distances to different habitat categories showed some differences. During southward migration in non-breeding years, the ospreys preferred being closer to agricultural areas and urban areas, and further away from wetlands, which were all like the expectation in breeding years. However, the preferences during non-breeding years were most likely due to one individual making many stopovers close to agricultural areas and urban areas during several non-breeding years (see maps 50 and 52 in Appendix 1). That the ospreys preferred being further away from wetlands only during non-breeding years, could then be explained by the same effect as suggested for southward migrations for all individuals, since one individual, who had many non-breeding years, made many stopovers during these years. Having individual and year as random effects in the GLMM, did account for the pseudo replication of data from the one individual and in the different years. However, the estimates for the fixed effects provided by the model were averages between the different individuals and the different years, and the analysis only included five individuals and five years, where one of those years only included one individual with many stopovers (while other years included several individuals). Meaning that the estimate was affected by one individual, again highlighting the problem of having few individuals in satellite telemetry studies. Since the differences in preferences were small between years, and they seemed to be more affected by different individuals breeding or not breeding, the conclusion was that no differences were seen in adults' habitat preferences during southward migration between breeding years and non-breeding years.

The only mention I have found of differences in southward migration between breeding years and non-breeding years was that male ospreys who had failed to breed, departed significantly earlier in autumn than successful breeders (Kjellen et al., 2001). However, no further differences were analyzed in their study. Candler and Kennedy (1995) suggested that under certain conditions, a nonstop migration may be energetically possible for North American ospreys, assuming a large deposition of energy prior to migration. More research on differences in energy deposition prior to migration, and temporal and spatial aspects during southward migration between breeding years and non-breeding years could improve our understanding of ospreys' behavior. And a larger sample size is necessary to study differences in habitat preferences during southward migration between breeding and non-breeding years.

4.5 Range sizes

The median sizes of the ospreys' home ranges were 87.20 km^2 (95% MCP), 110.23 km^2 (95% kernel), 8.90 km^2 (50% kernel). Even though northern latitude osprey populations are widely studied in their breeding grounds (Saurola, 1997), I did not find any study which has calculated and provided home range sizes on these populations. I found one study that calculated home range sizes of translocated juvenile ospreys in central Italy, which showed they had median home range sizes of 5.0 km^2 (95% kernel) and 0.9 km^2 (50% kernel) in one year, and 0.58 km^2 (95% kernel) and 0.09 km^2 (50% kernel) from other individuals the year after (Monti et al., 2012). These home range sizes were similar to the median home range sizes found for juveniles in this study: 4.4 km^2 (95% kernel) and 0.26 km^2 (50% kernel). Bedrosian et al. (2015) found that adult North American ospreys in Lake Yellowstone, Wyoming had home ranges with mean sizes (95% MCP) of 1.76 km^2 (SD=3.01 km^2). The sizes of the ospreys' home ranges found in this study were much larger than what Bedrosian et al. (2015) had found, perhaps due to differences in behavior between sub-species, and/or differences in food availability and competition with other nesting pairs. Swenson (1978) showed in their study that ospreys, also from Lake Yellowstone, had high food abundance and needed little time for foraging for each fish caught. Lohmus (2001) showed in their study that ospreys in Estonia foraged primarily in smaller eutrophic lakes, despite having large lakes and coastal seas available. Some of the ospreys in this study foraged in both lakes and in the sea, with one individual crossing the outer

Oslo-fjord (>20 km) regularly to forage on the coast on the other side (maps 9-10 in Appendix 1). While some of the ospreys foraged in several large lakes during the breeding season (see maps 1-22 in Appendix 1). This suggests that differences in behavior between populations and/or subspecies, and differences in food availability, are the reason for the much larger home range sizes found in this study. Perhaps this is the first study to have calculated and provided home range sizes in northern latitude ospreys breeding grounds and can be used to compare sizes found in later studies, home range sizes should be included when researching ospreys in their breeding grounds in the future.

The median sizes of the ospreys' stopover sites found in this study were: 2.50 km^2 (95% MCP), 12.21 km^2 (95% kernel), 2.21 km^2 (50% kernel). Crawford and Long (2017) found that juvenile ospreys had stopover sites that ranged from 43.4 km^2 to 208 km^2 (70% kernel). The largest stopover site found in this study was that of a juvenile, which was 31.22 km^2 (95% kernel). However, looking at the maps of the juveniles' stopover sites in Crawford and Long (2017)'s study, the stopovers looked very similar to the stopovers seen in this study. The reason for the differences in sizes was that stopovers were classified differently. Crawford and Long (2017) used a classification of stopover sites as movement <100 km during 24 hours and included all points that were within that margin. Meaning that points during migration before and after the stopover site was included, leading to very large kernel core use areas, with such large distances between the points. While I included only points that were at the stopover site and excluded points that were during migration before or after the stopover area. Therefore, I assume that the stopover sizes would have been similar if we had used the same method of classifying a stopover. I argue that only points from the actual stopover site should be included in calculating the sizes and when analyzing stopover sites, as the points during migration before or after stopovers are from an entirely different movement pattern. The reason stopovers were much smaller than home ranges, was that ospreys roost close to foraging areas during stopovers, as explained earlier.

The median sizes of the ospreys wintering areas found in this study were: 57.43 km^2 (95% MCP), 90.05 km^2 (95% kernel), 10.10 km^2 (50% kernel). Some earlier studies have separated smaller locations that the ospreys use during their wintering period and calculated the sizes of these (e.g. Kjellen et al., 1997; Washburn et al., 2014). For example, Washburn et al. (2014) found that female ospreys had wintering areas that ranged from 18.3 to 26.0 km^2 (95% kernel) and 1.9 to 2.5 km^2 (50% kernel), and males' wintering areas ranged from 2.2 to 14.5 km^2 (95% kernel) and 0.7 to 0.9 km^2 (50% kernel). While the ospreys in this study had wintering areas that ranged from 0.01 to 9576.86 km^2 (95% kernel) and 0.02 to 1911.00 km^2 (50% kernel). In this study I have separated only those areas that were used exclusively in their own time periods (e.g. maps 30, 31, 34, 35 in Appendix 1), while areas that were used interchangeably throughout the wintering period were treated as one whole wintering area. I argue that several locations used interchangeably throughout the wintering period are similar to how ospreys use several locations interchangeably in their home ranges, and wintering areas should therefore be calculated as a whole area like home ranges are.

In this study, a few very small home ranges were found for adults, and one very large and one very small wintering area were found. The first small home range of an adult was that of Mrs. Søndre in 2015 where something went wrong with the transmitter and only points between July 12^{th}-30^{th} were included, meaning that she was mostly in the nest or very close to it (see map 3 in Appendix 1). The second and third small home ranges were those of Lotta in 2011 and 2012, where in both years she spent the first half of the breeding season at the nest brooding, and the other half in a completely different area (see maps 17-20 in Appendix 1). Which meant that the small home ranges were again only from points at or around the nest. The one very large wintering area was that of Mrs. Søndre in 2019, where she interchanged between two locations that were quite far apart, throughout the wintering period (see map 37 in Appendix 1). This could be because of competition from other ospreys, disturbances, or poor food availability. The one very small wintering area was that of Mr. Søndre in 2015, which is a perfect example of how stationary an osprey can be in its wintering area (see map 39 in Appendix 1). He stayed at one roost the entire wintering period, only making short trips to the water close by, making both the 95% and 50% kernel very small, while the 95% MCP was a bit larger.

4.6 Weaknesses of this study

The analysis of the whole migration led to a very large available area and included many points that were during flight. With the large and general habitat categories the analysis showed the differences in larger areas that the ospreys preferred or avoided, but with more detailed habitat data the available area would most likely contain many other habitats than the ones used. One could argue that all points during flight are not in preferred habitats, and that an analysis of the whole migration would include too many of these. I argue that these points during flight are the same as points during flight in the ospreys' home ranges, where including points from the entire period is common practice. The only reason that the points during flight would be different during migration is that these are in a much larger available area and would include too many observations from not used habitats. However, since the migrations are much shorter in time than the home range season, I argue that the effect evens out. Additionally, including all points from the migration included points from short foraging and overnight stops which would not be included in an analysis of only stopover sites. I assumed that habitat used in daily stops and stopovers during the entire migration would show the same preferences as only within the stopover sites. A previous study has shown that habitat preferences are linked between smaller scales and larger scales (Hutto, 1985).

The available area during migration was not the same size throughout the migration. The fact that the analyses were done in such a large area, meant that a world-wide coordinate system had to be used to locate points. Therefore, values of coordinates did not correspond to real world distances throughout the study area, making the buffer smaller in northern latitudes than by the equator. One could argue that since the ospreys do have a fixed point in their home ranges to leave from and return to, the ospreys would likely have a more direct path with less deviation, the closer they are to the nest. This was seen in one osprey returning to the breeding area in spring (Alerstam, 2006), and Alerstam et al. (2006) found that the ospreys had wider migration corridors further south. However, some of the juveniles in this study dispersed in other directions before migrating south, and the available area should be uniform for all individuals and the same size throughout the study area (Beyer et al., 2010). A possible solution would be to separate the buffer by latitude, project a local map and generate a corresponding buffer in each part.

4.7 Conclusion

The ospreys had preferences for habitat on land, and these preferences were different between seasons. Forests were preferred by the ospreys in all seasons. Open areas were preferred by the ospreys in their home ranges and during migrations, and they were used like the availability and the ospreys preferred being closer to them in their wintering areas. Wetlands were preferred by the ospreys in their wintering areas, and they were used like the availability during migrations. Agricultural areas were used like the availability in all seasons, and the ospreys preferred being closer to them in their home ranges and wintering areas. Bare land and urban areas were generally avoided in all seasons, but the ospreys showed a weak preference to be closer to urban areas during migration, and to bare land in their wintering areas. Water bodies were avoided during migrations and in their wintering areas, while the ospreys preferred being closer to them in all seasons.

The ospreys had different habitat preferences between southward and northward migrations, due to differences in temporal and spatial aspects between the migrations. Adult and juvenile ospreys had different habitat preferences during southward migrations, due to juveniles lacking experience. Adult ospreys had different area uses and habitat preferences in their home ranges between breeding years and non-breeding years, while they had no differences in habitat preferences during southward migrations between breeding years and non-breeding years.

The large and general habitat categories used in these analyses are of limited practicality for conservation work for ospreys but serve as a baseline in the knowledge of the area and habitat needs of ospreys throughout the year. More research is needed on differences in ospreys' behavior between breeding years and non-breeding years, as these differences could further improve our understanding of the species. The methodology used in this study is a promising way of conducting research on a migrating species, allowing us to gather information and improve our understanding of a species, using much less resources.

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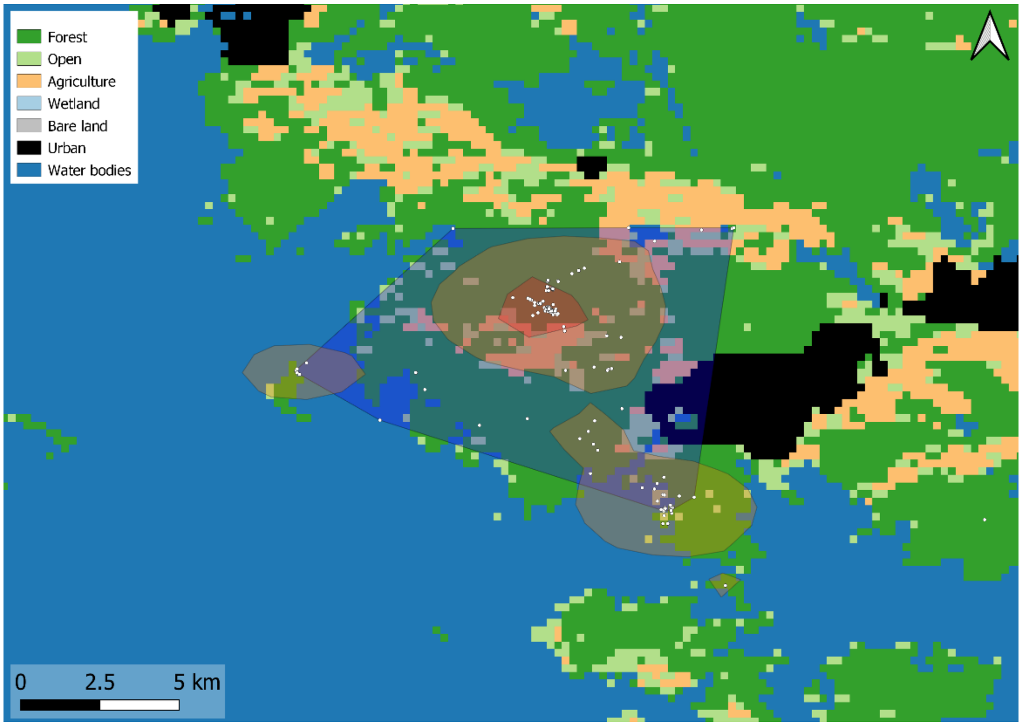
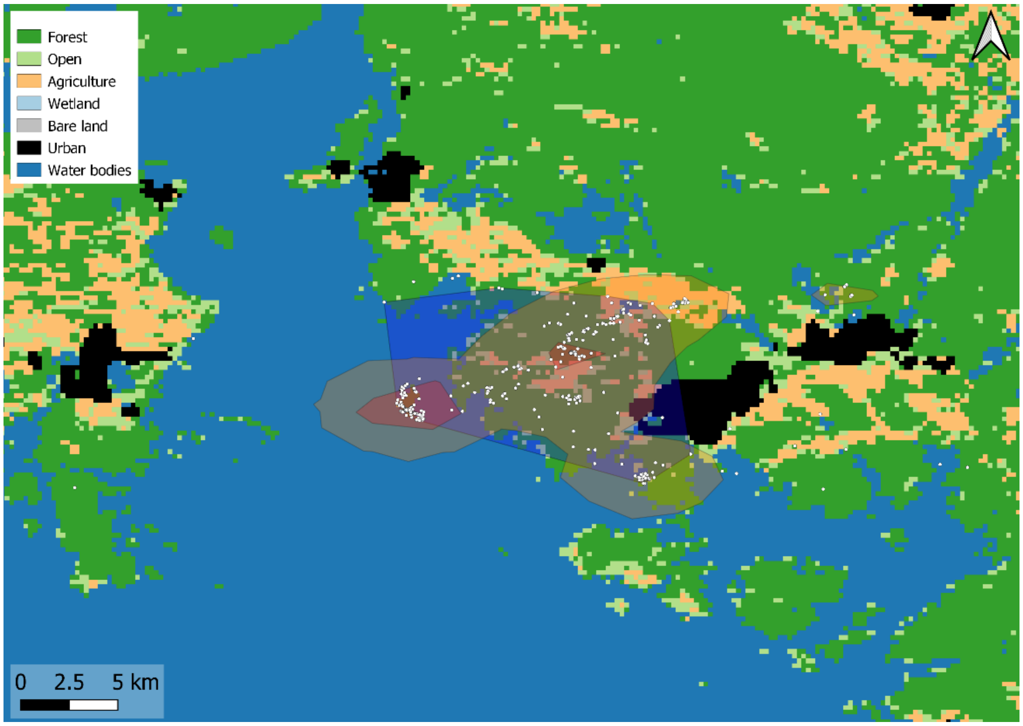
Appendix 1

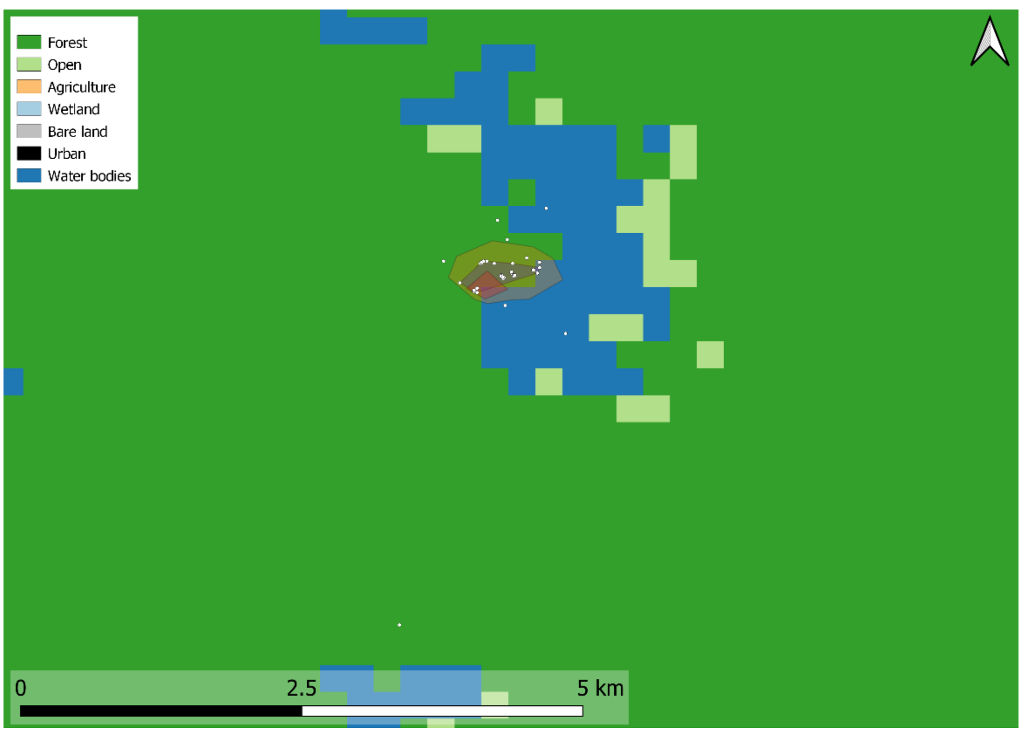
Maps of all individuals' home ranges, migrations, and wintering areas, in all years.



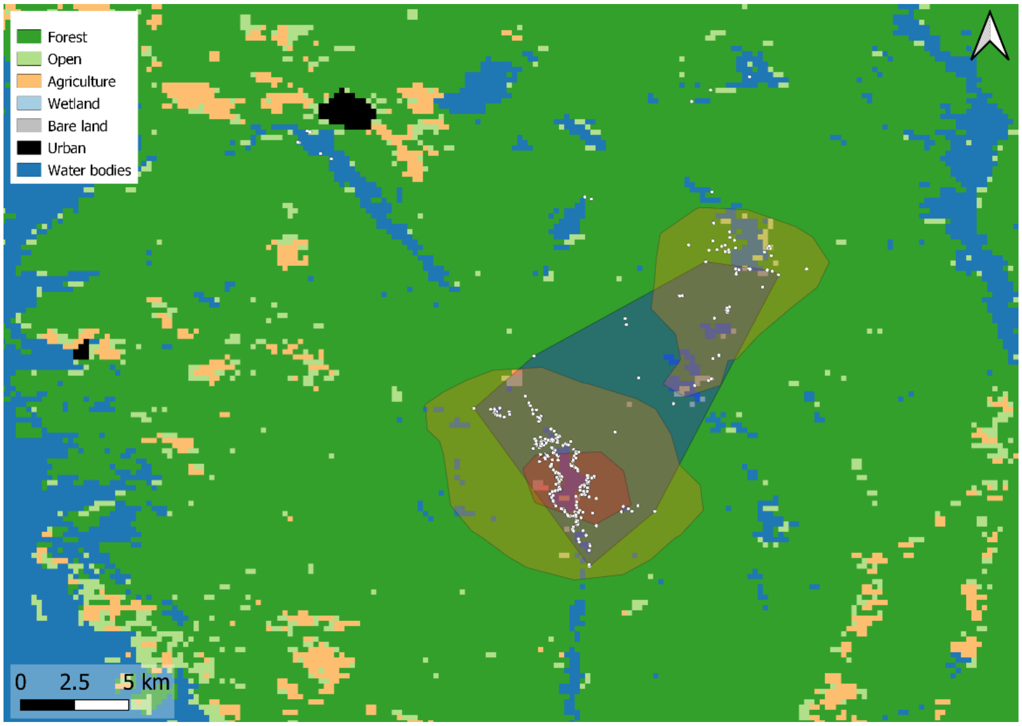
Map 1: Home range of Mrs. Huseby in 2019 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



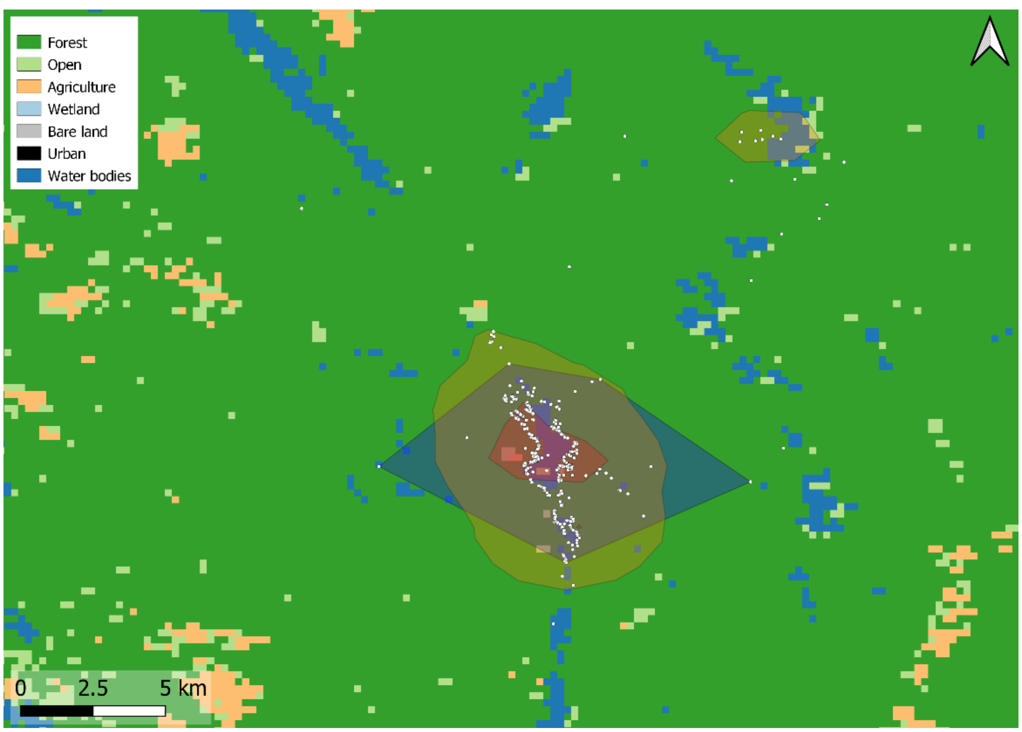
Map 2: Home range of Mrs. Huseby in 2020 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



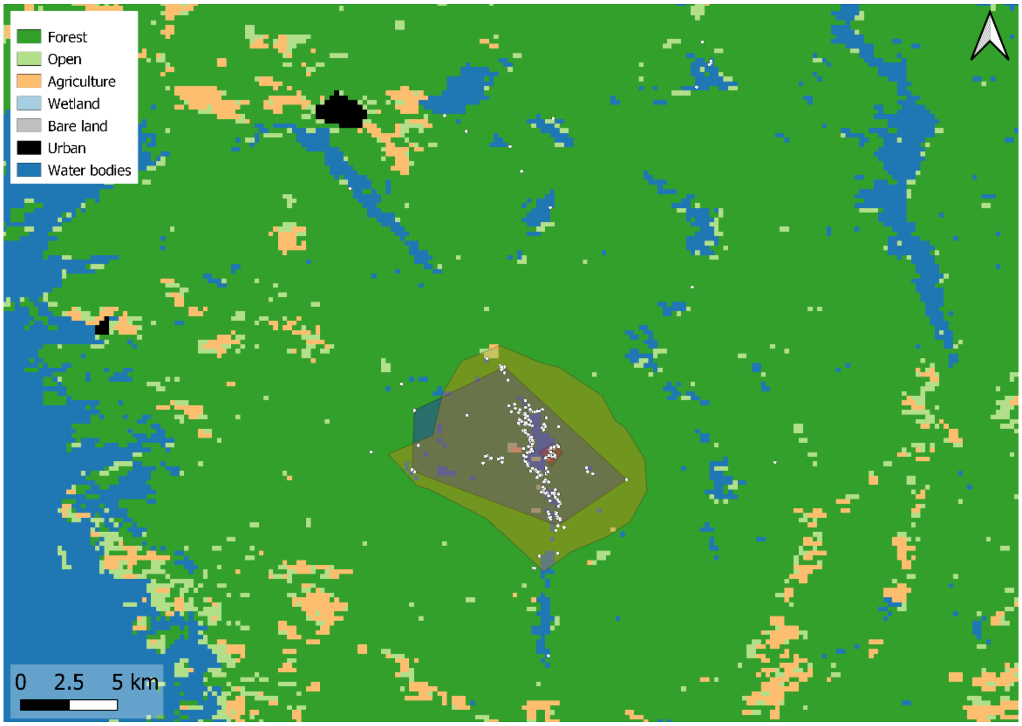
Map 3: Home range of Mrs. Søndre in 2015 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



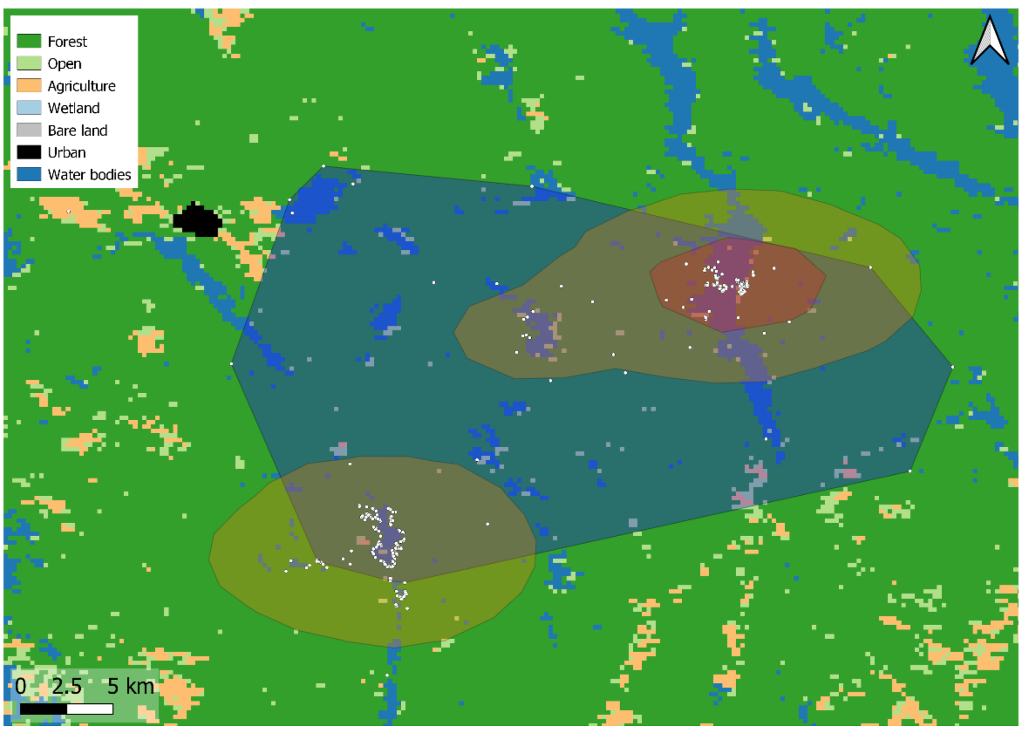
Map 4: Home range of Mrs. Søndre in 2016 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



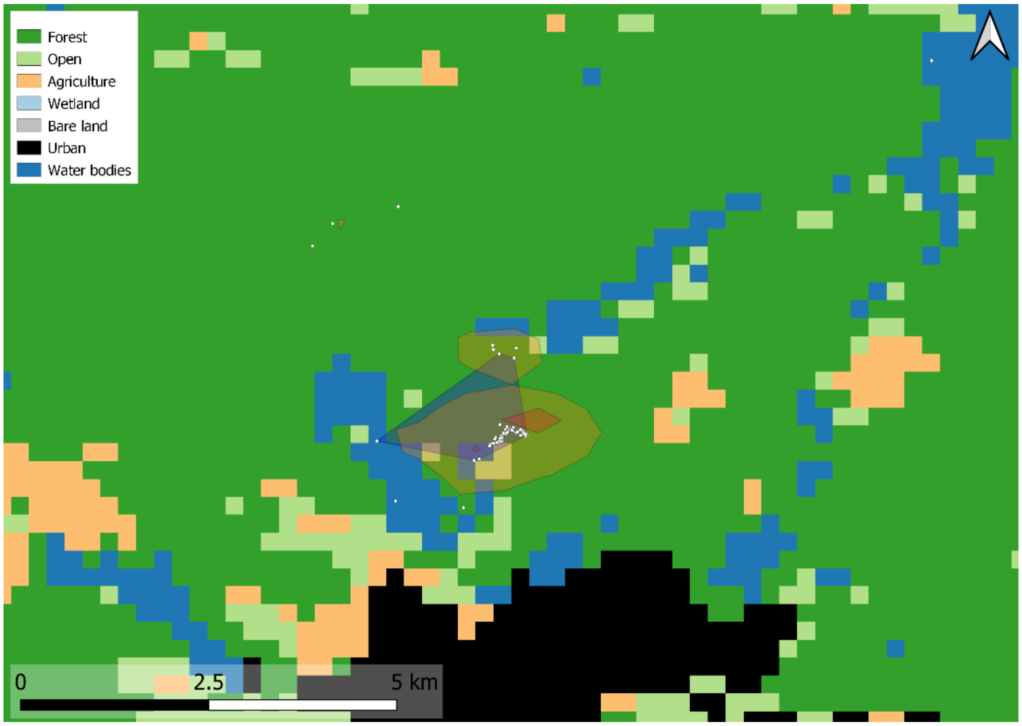
Map 5: Home range of Mrs. Søndre in 2017 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



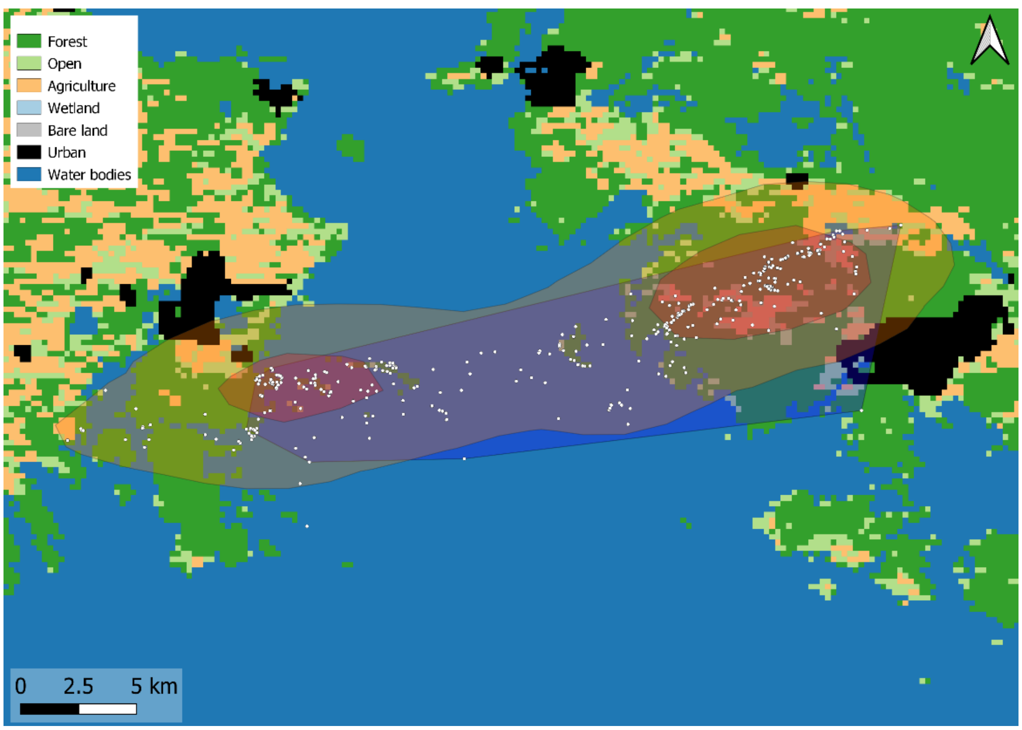
Map 6: Home range of Mrs. Søndre in 2018 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



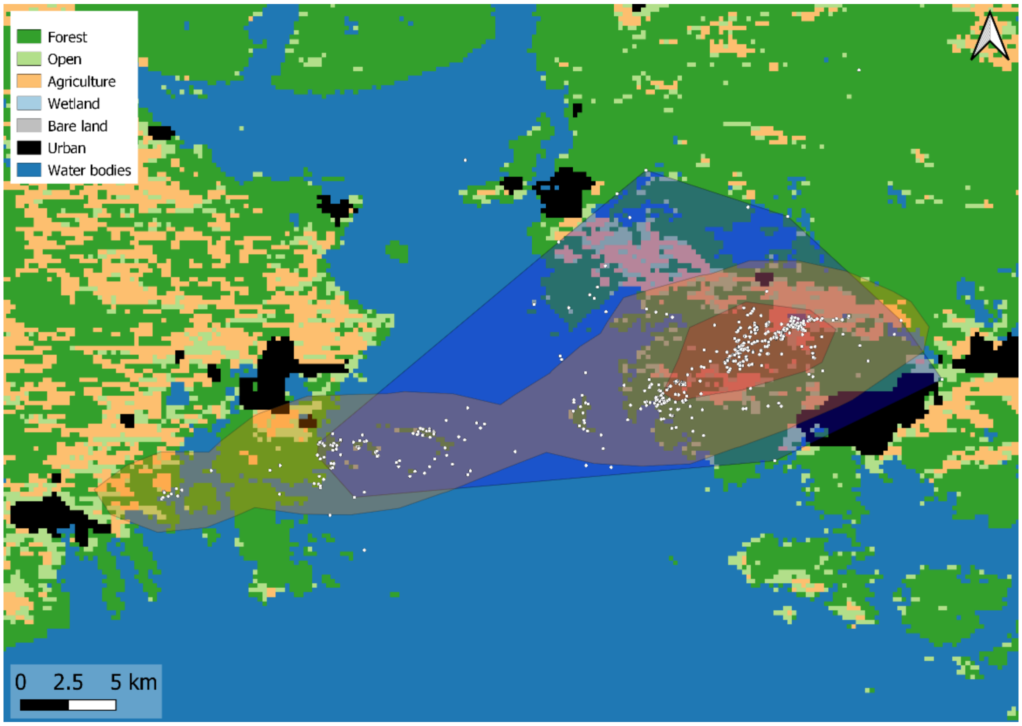
Map 7: Home range of Mrs. Søndre in 2019 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



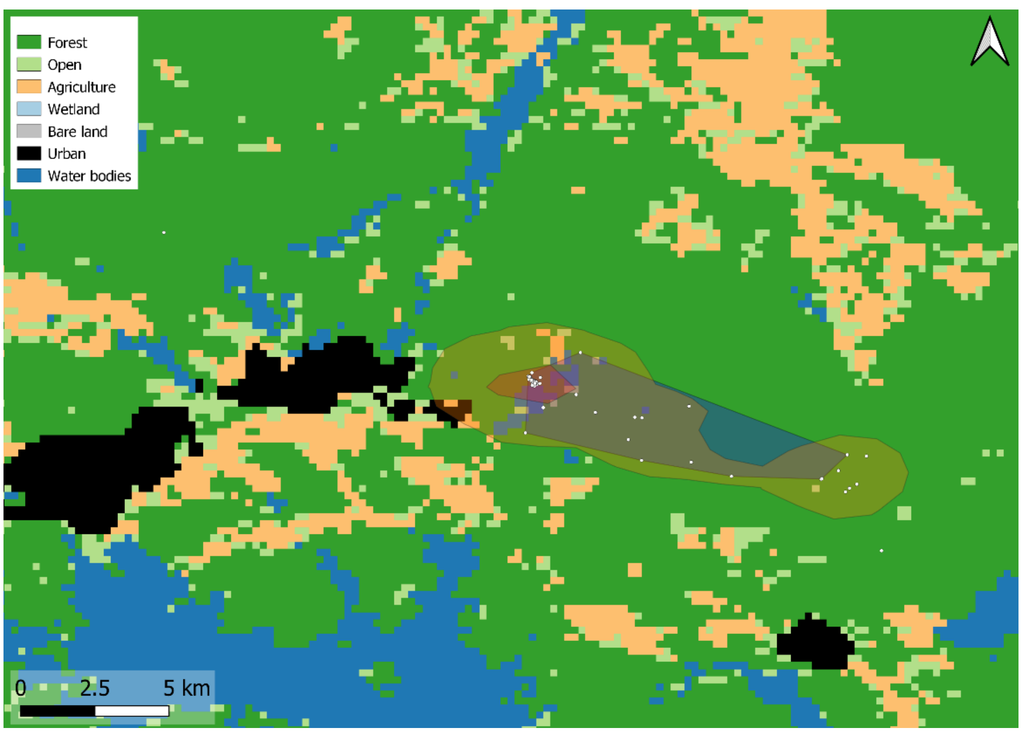
Map 8: Home range of Mr. Bjørnlandsevja (juvenile) in 2013. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



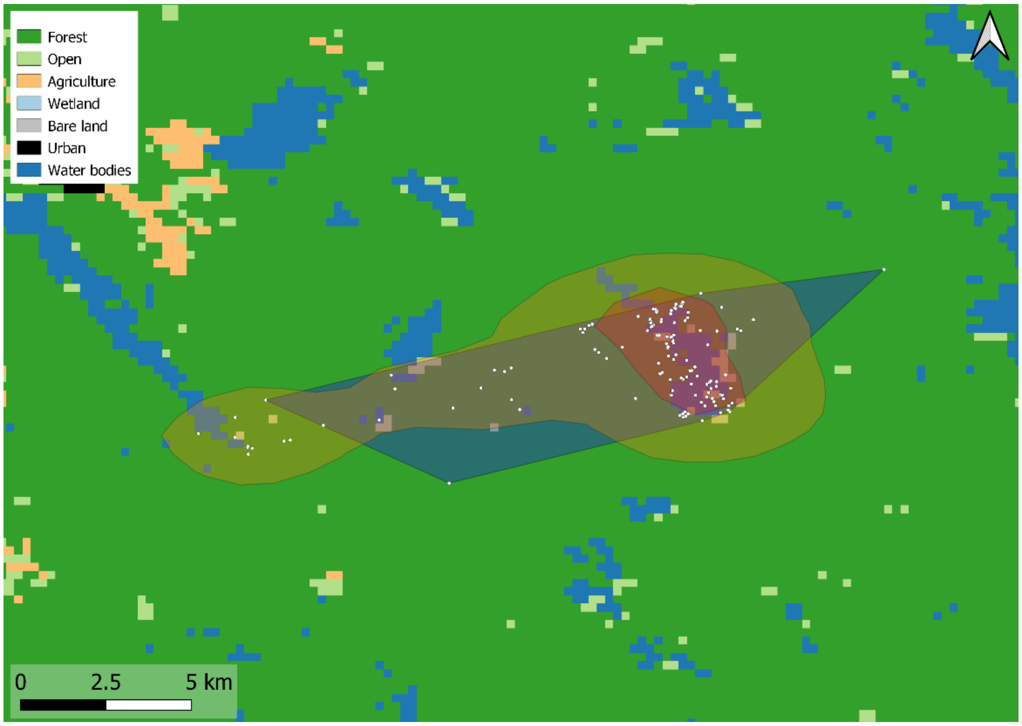
Map 9: Home range of Mr. Huseby in 2019 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



Map 10: Home range of Mr. Huseby in 2020 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

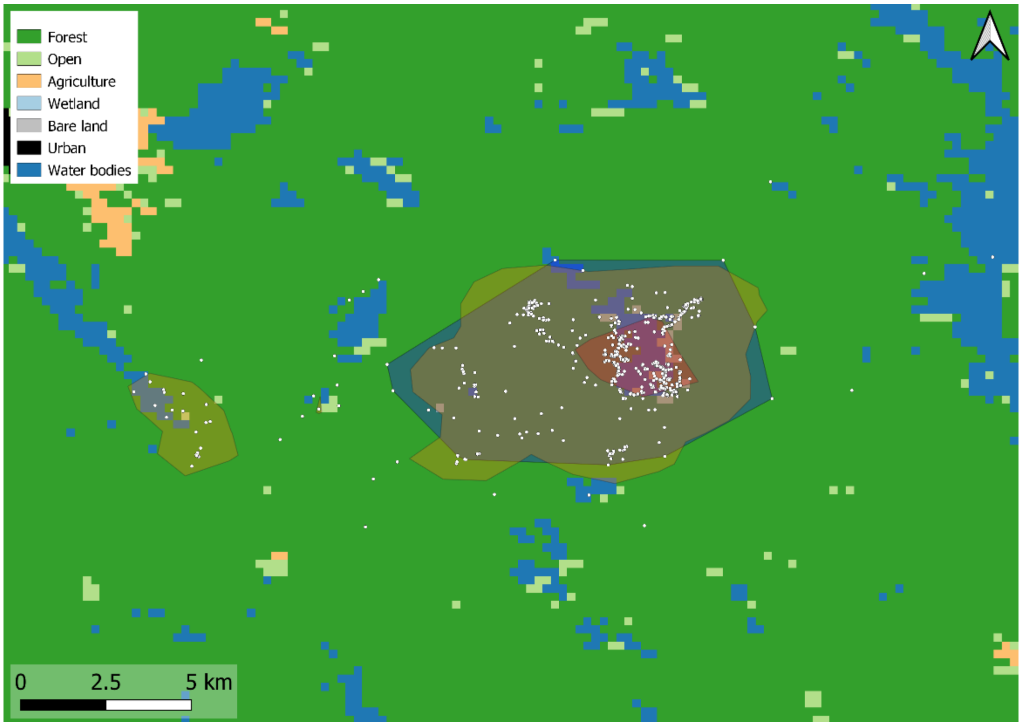


Map 11: Home range of Mr. Ise (juvenile) in 2013. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

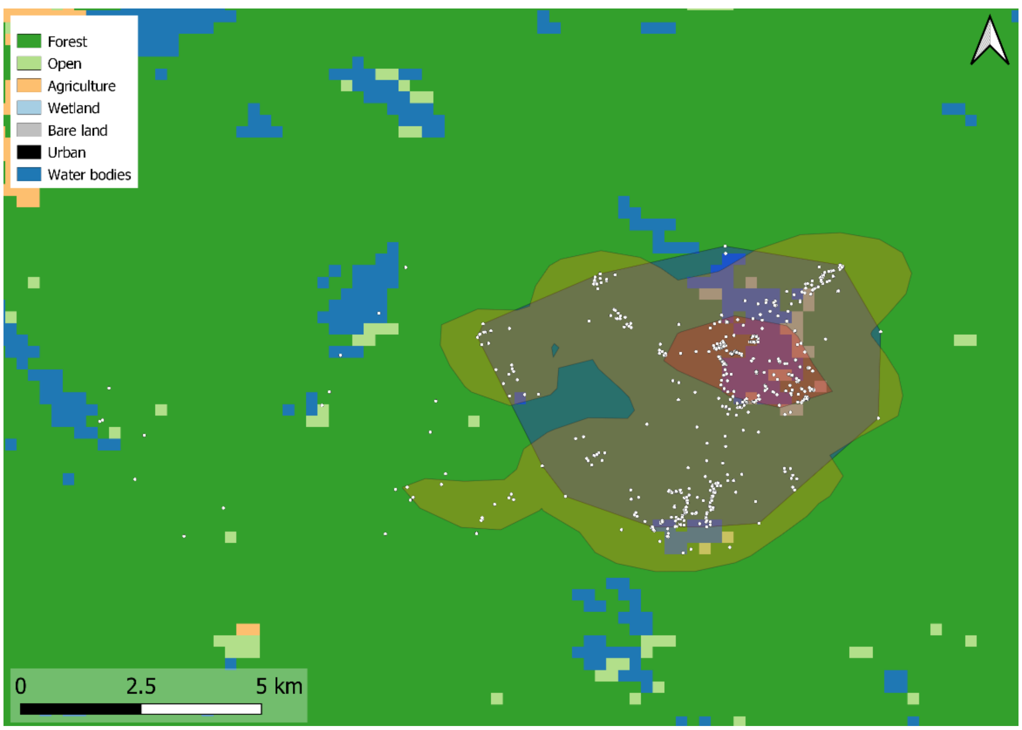


Map 12: Home range of Mr. Søndre in 2015 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

Map 13: Home range of Mr. Søndre in 2016 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



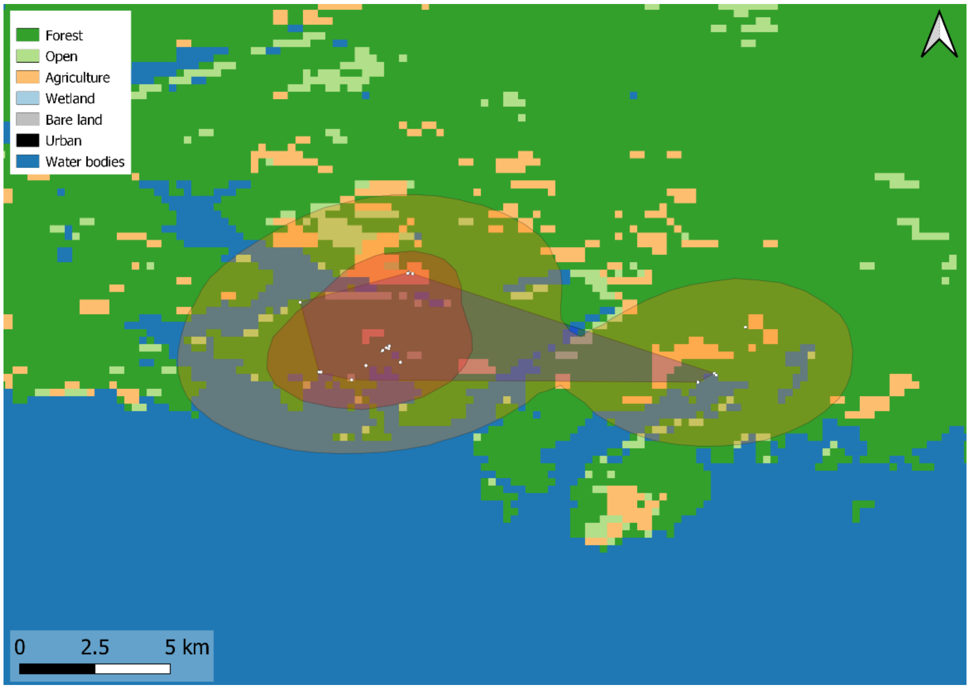
Map 14: Home range of Mr. Søndre in 2017 (non-breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



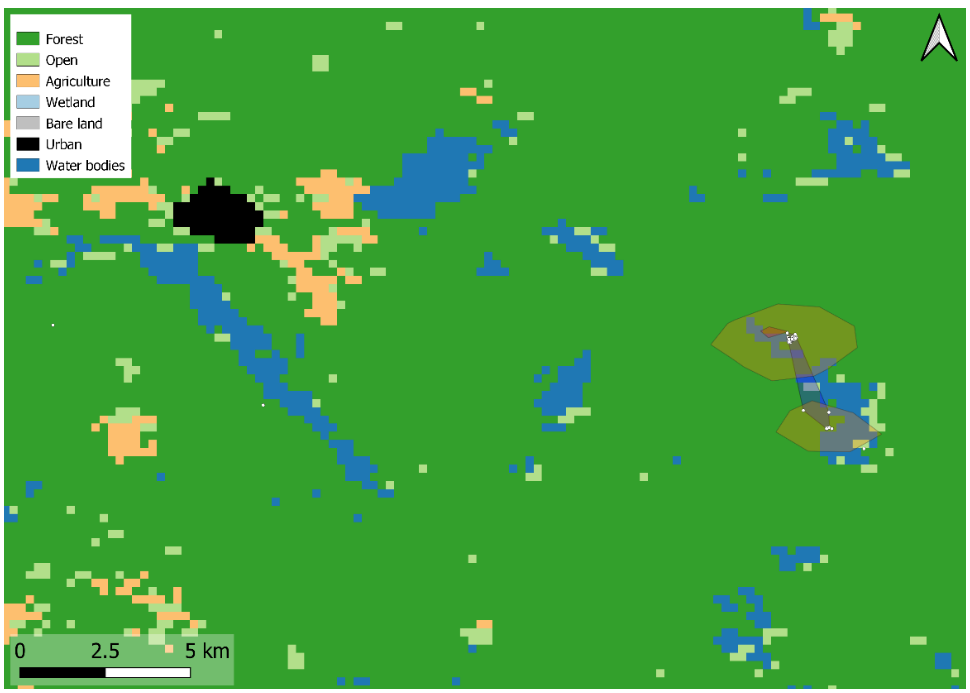
Map 15: Home range of Mr. Søndre in 2018 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

Map 16: Home range of Huse (juvenile) in 2013. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

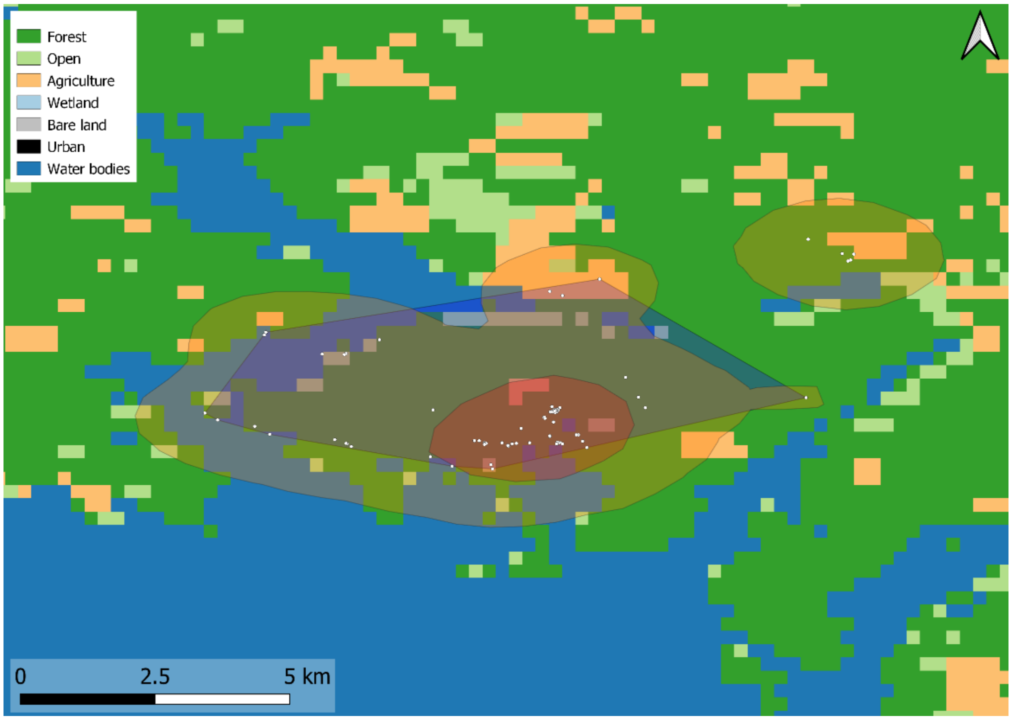
Map 17: Home range of Lotta in 2011 (breeding year). First half of the breeding season, while she was brooding. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



Map 18: Home range of Lotta in 2011 (breeding year). Second half of the breeding season, in a different area than the nest. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

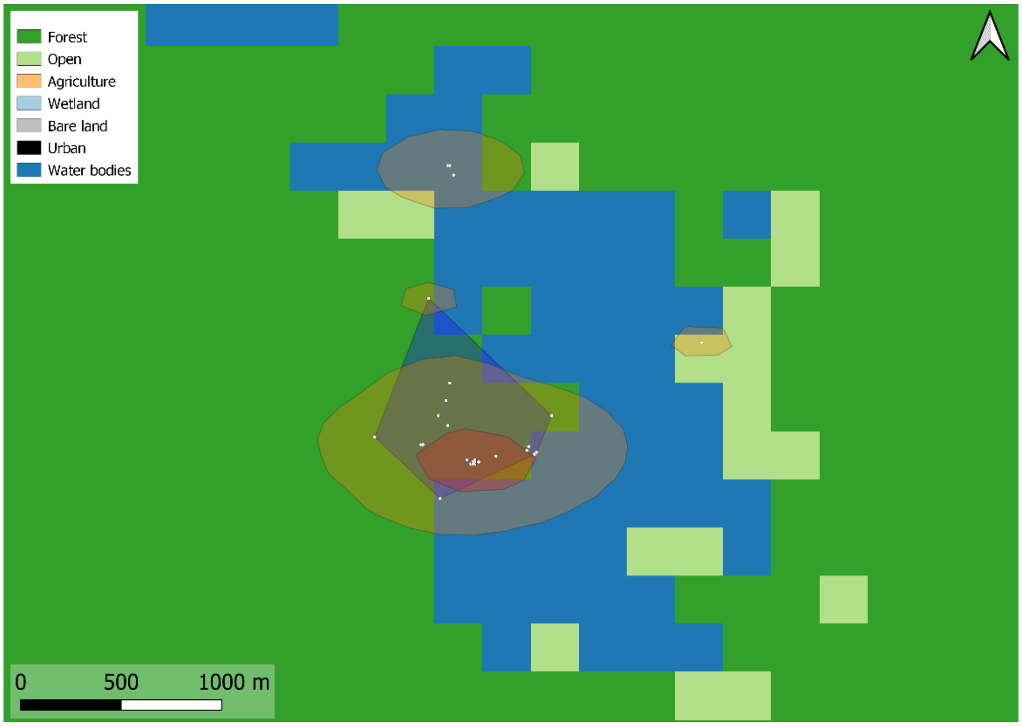


Map 19: Home range of Lotta in 2012 (non-breeding year). First half of the breeding season, while she was brooding. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

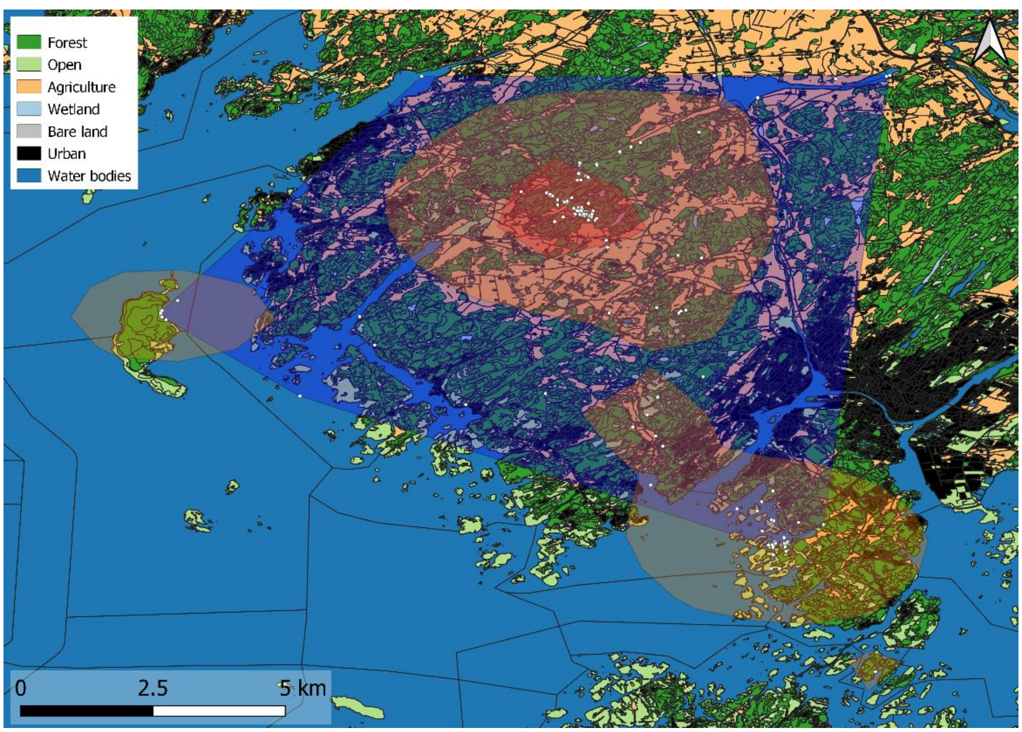


Map 20: Home range of Lotta in 2012 (non-breeding year). Second half of the breeding season, in a different area than the nest. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

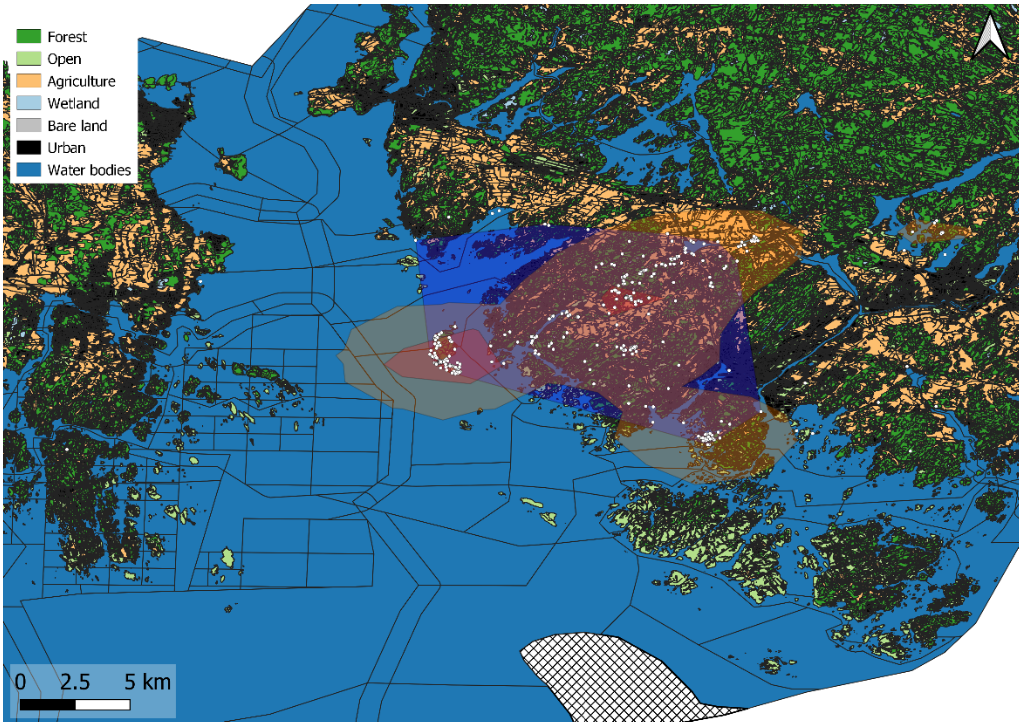
Map 21: Home range of Mikael in 2011 (breeding year). With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



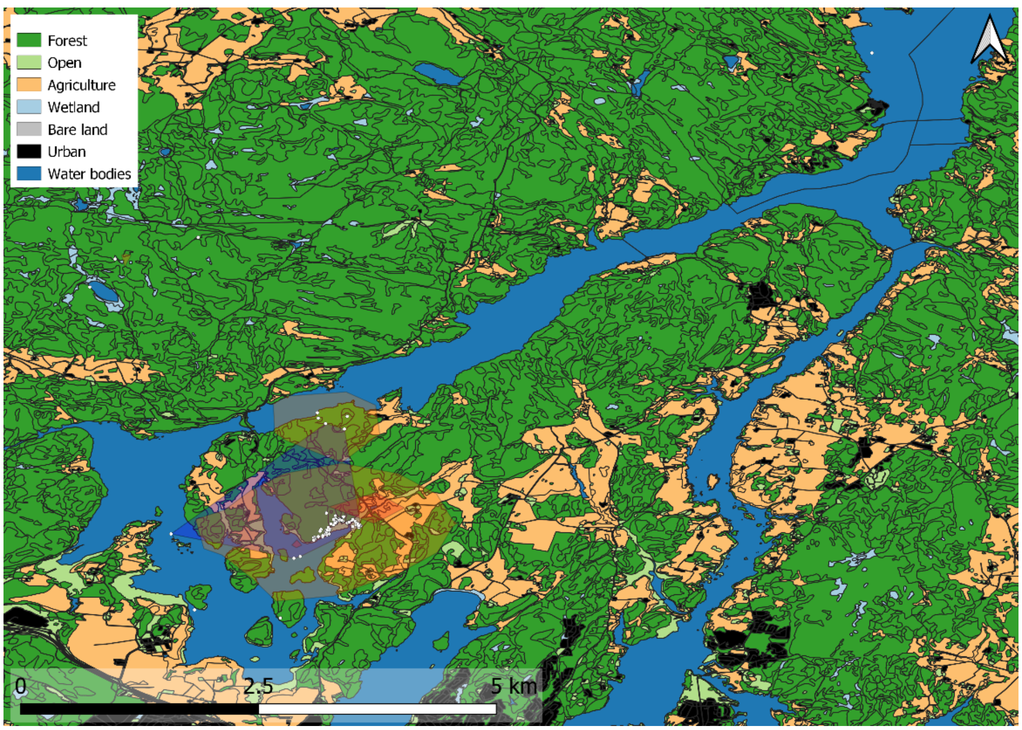
Map 22: Home range of Signe (juvenile) in 2011. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



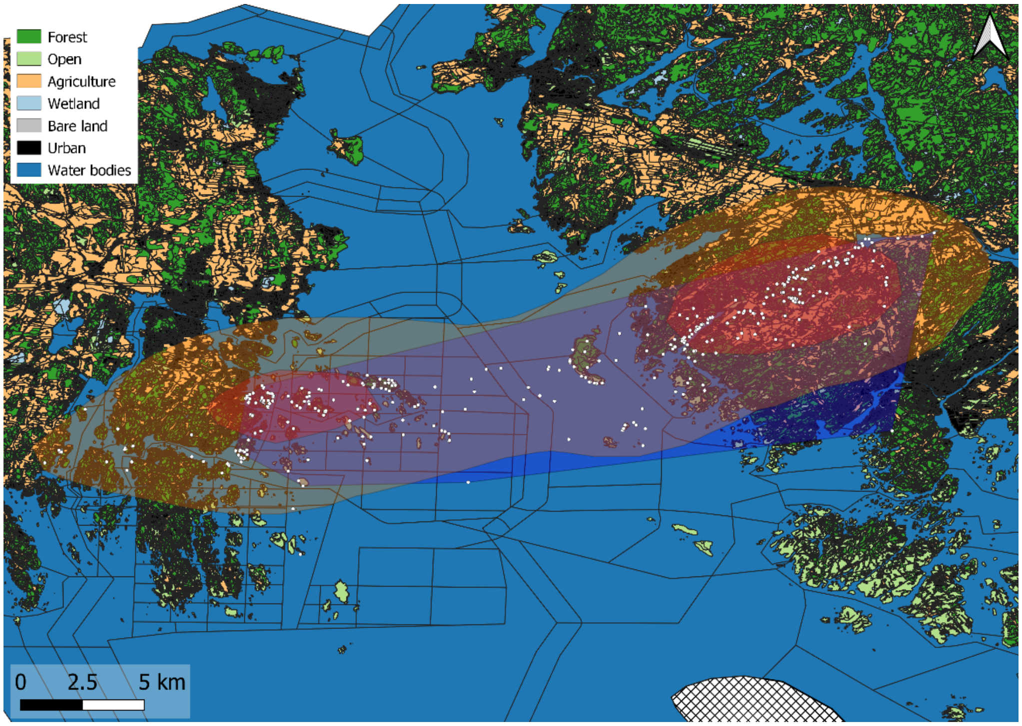
Map 23: Home range of Mrs. Huseby in 2019 (breeding year) on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



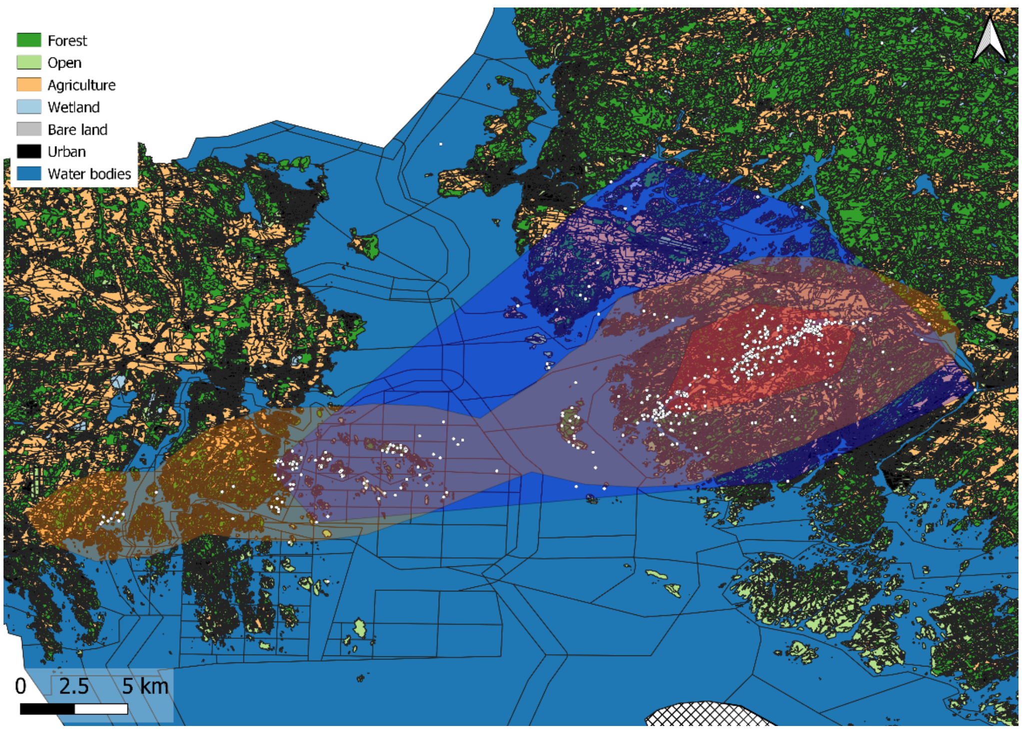
Map 24: Home range of Mrs. Huseby in 2020 (non-breeding year) on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



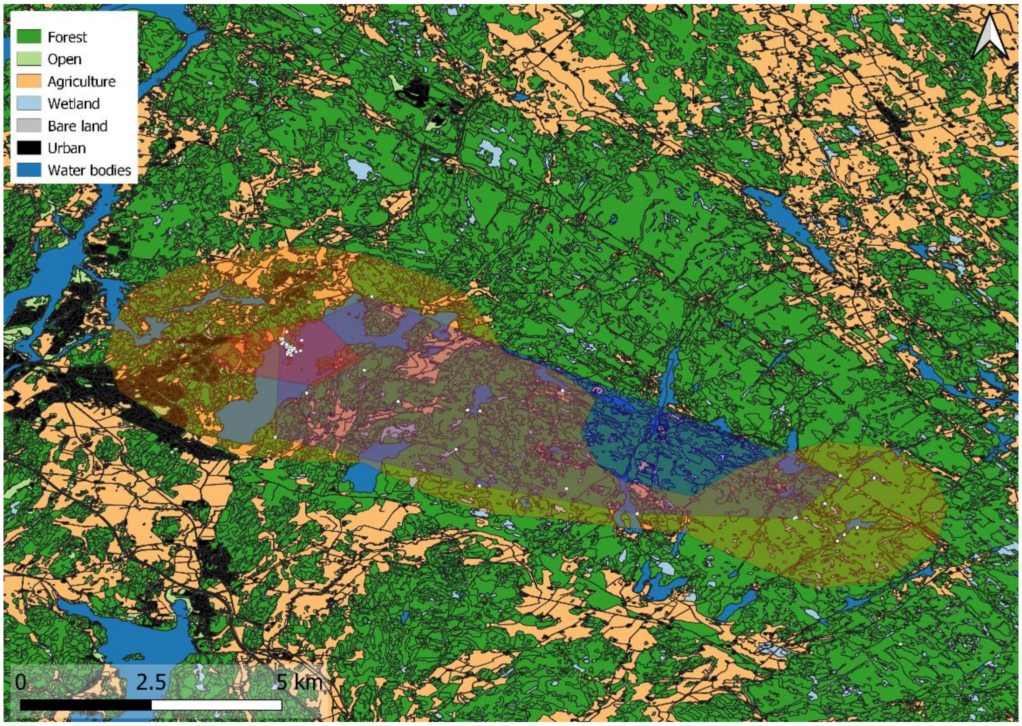
Map 25: Home range of Mr. Bjørnlandsevja (juvenile) in 2013 on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



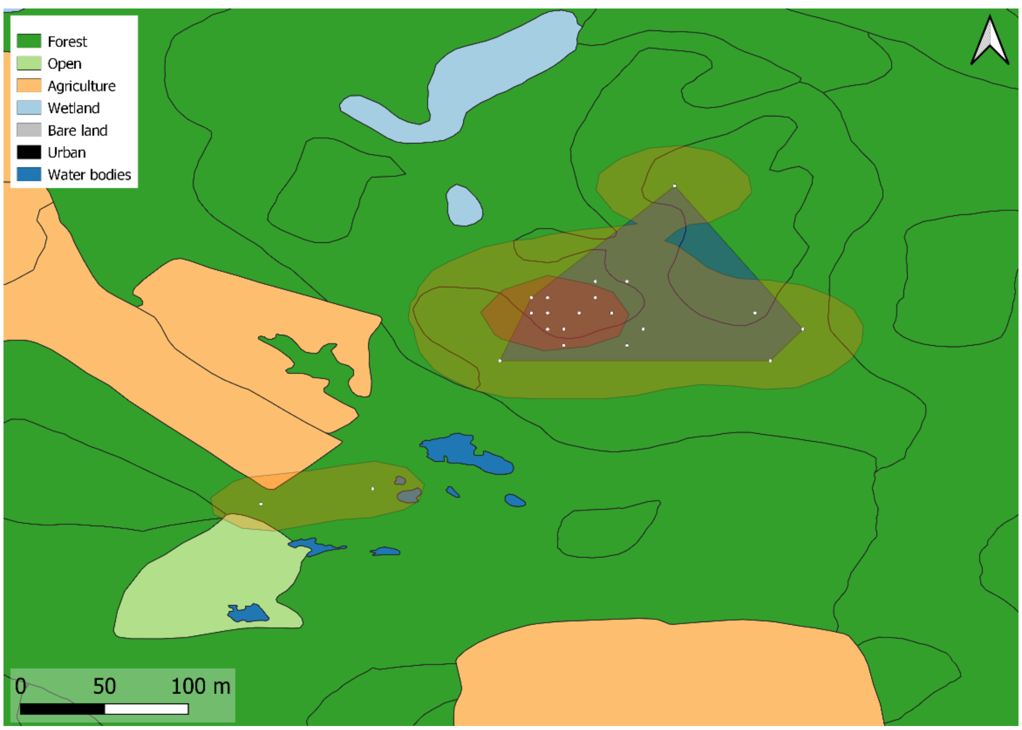
Map 26: Home range of Mr. Huseby in 2019 (breeding year) on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



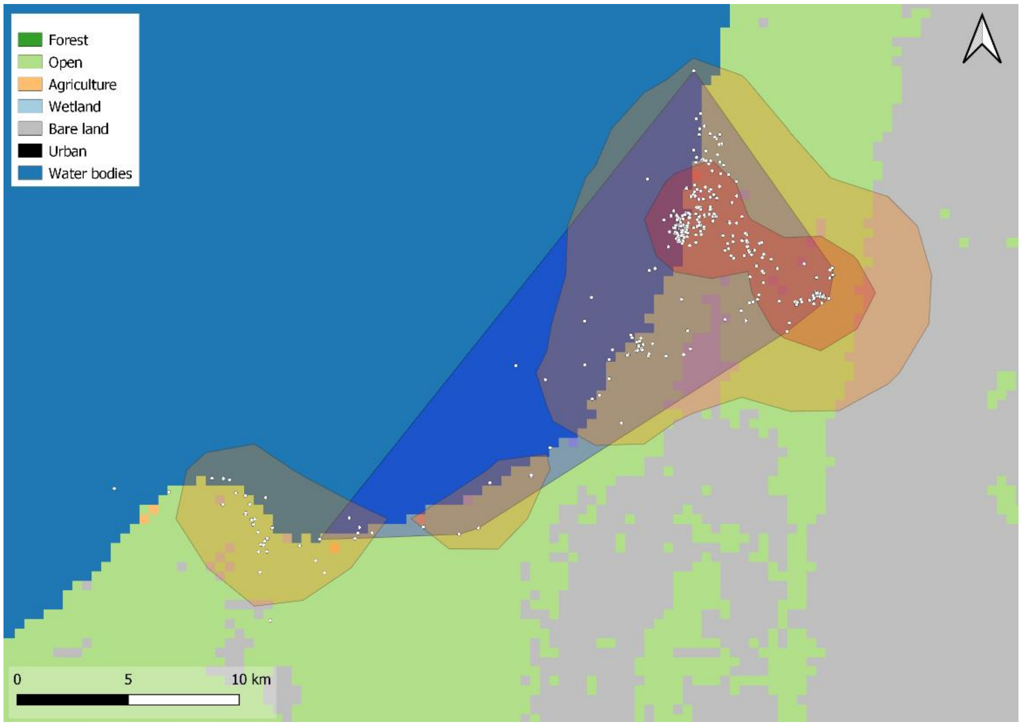
Map 27: Home range of Mr. Huseby in 2020 (non-breeding year) on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



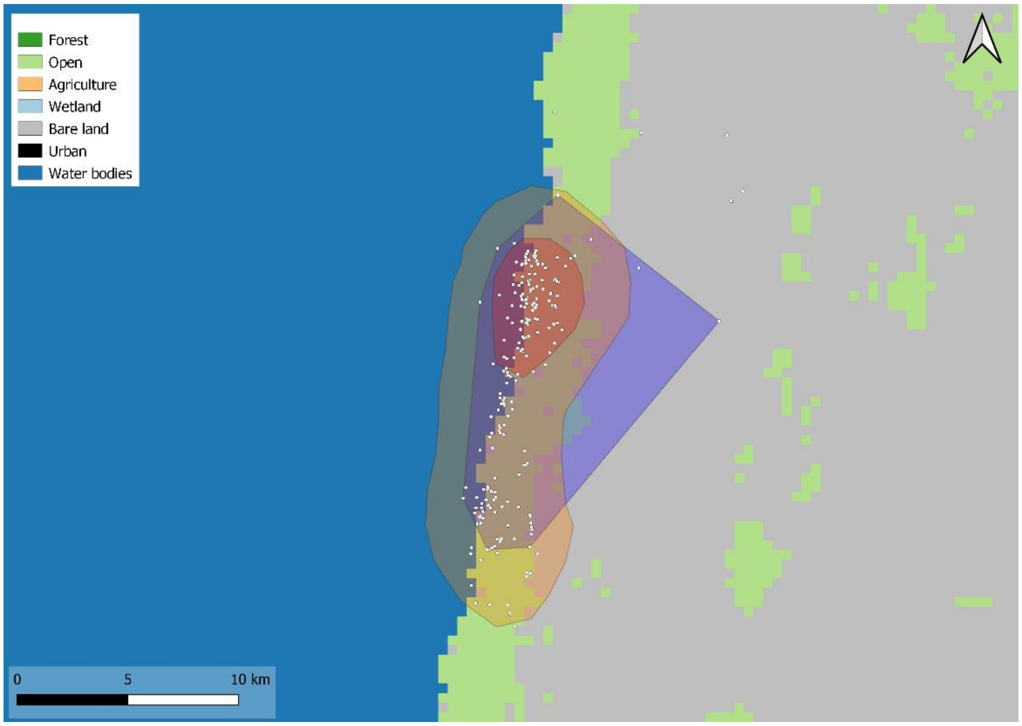
Map 28: Home range of Mr. Ise (juvenile) in 2013 on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



Map 29: Home range of Huse (juvenile) in 2013 on the detailed map. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

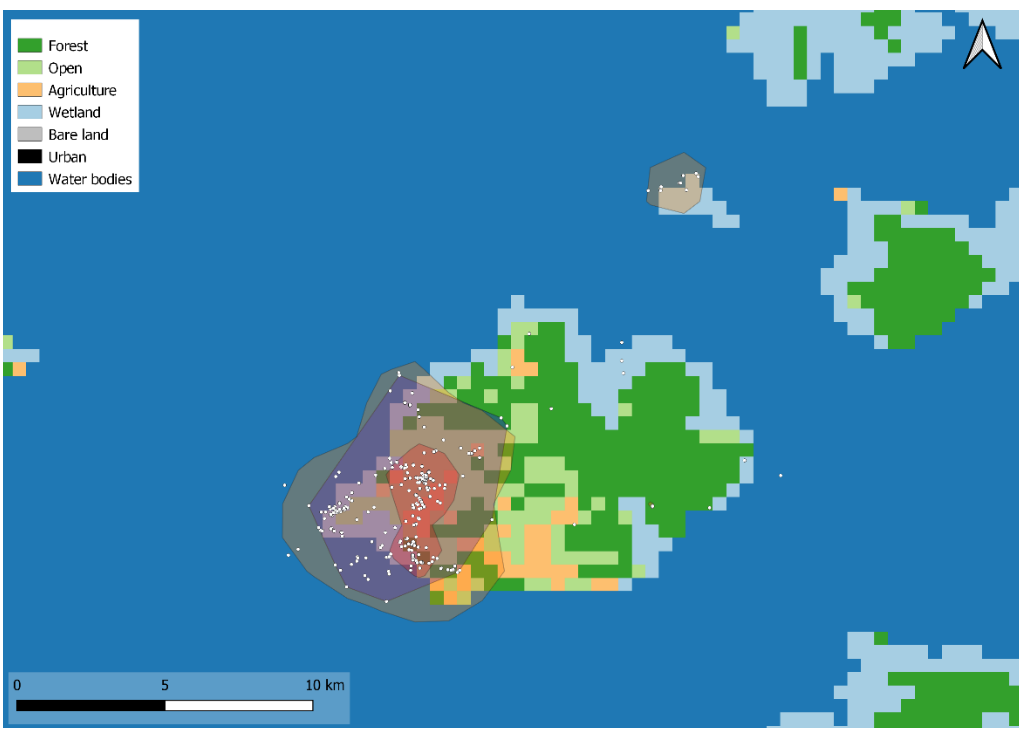


Map 30: Wintering area of Mrs. Huseby in 2019, first half of the wintering season. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

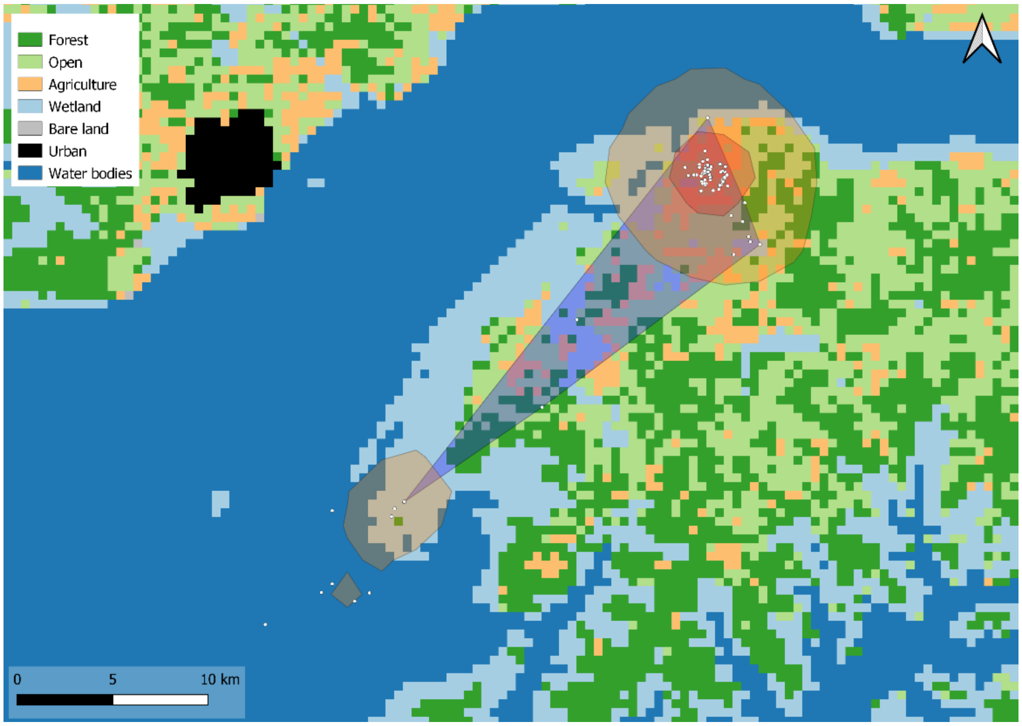


Map 31: Wintering area of Mrs. Huseby in 2019, second half of the wintering season. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

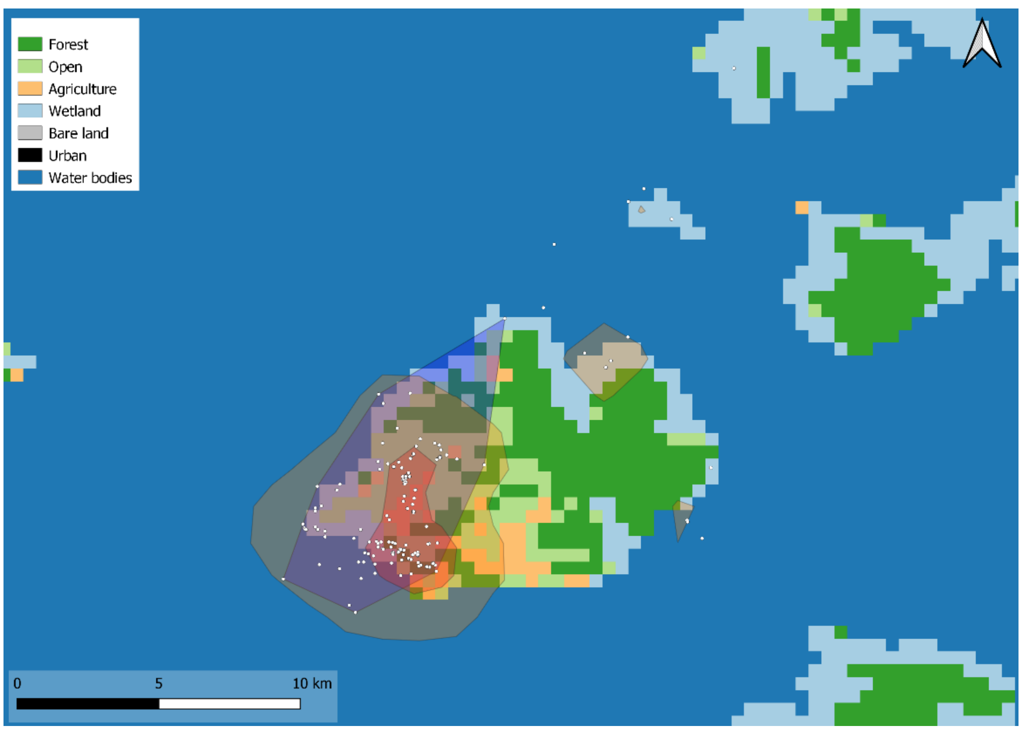
Map 32: Wintering area of Mrs. Søndre in 2015. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



Map 33: Wintering area of Mrs. Søndre in 2016. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

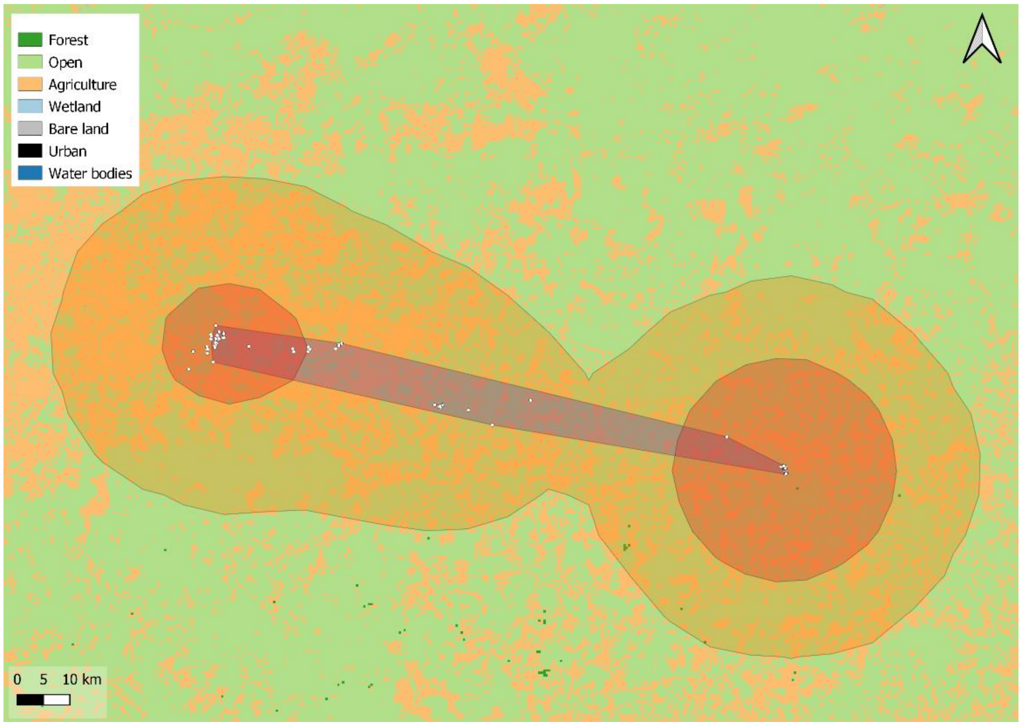


Map 34: Wintering area of Mrs. Søndre in 2017, first half of the wintering season. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

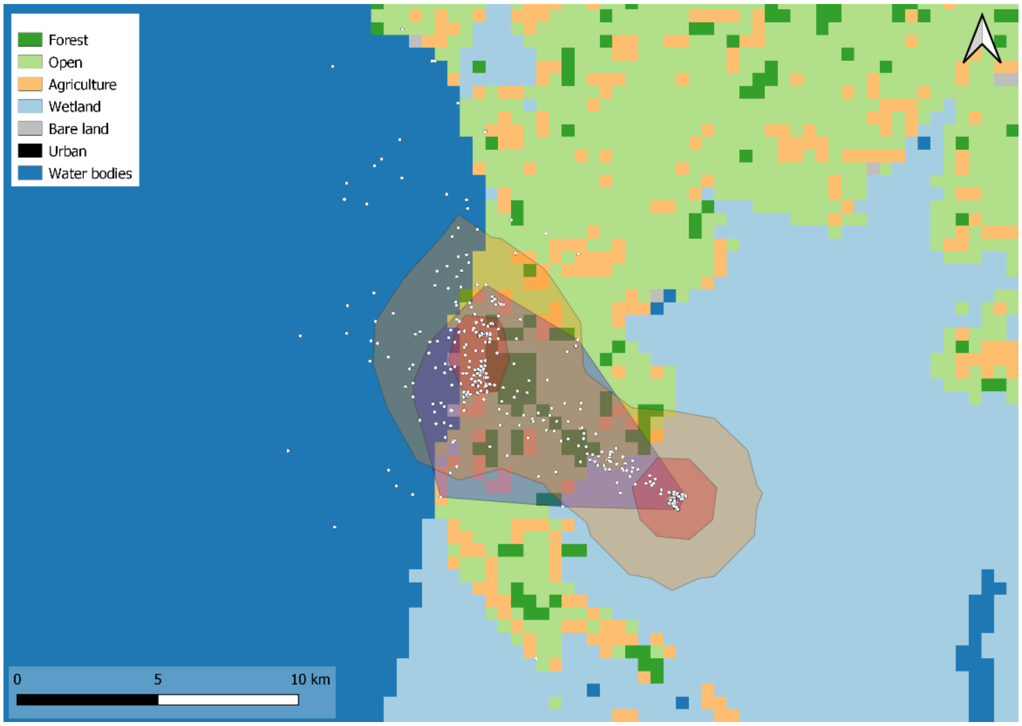


Map 35: Wintering area of Mrs. Søndre in 2017, second half of the wintering season. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

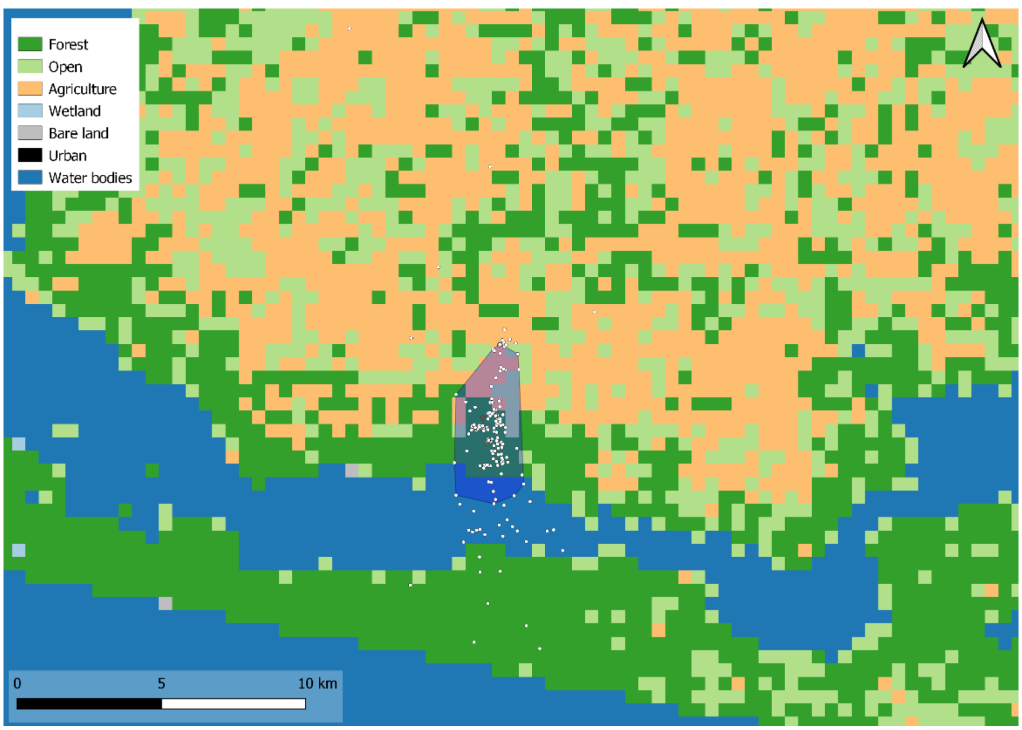
Map 36: Wintering area of Mrs. Søndre in 2018. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



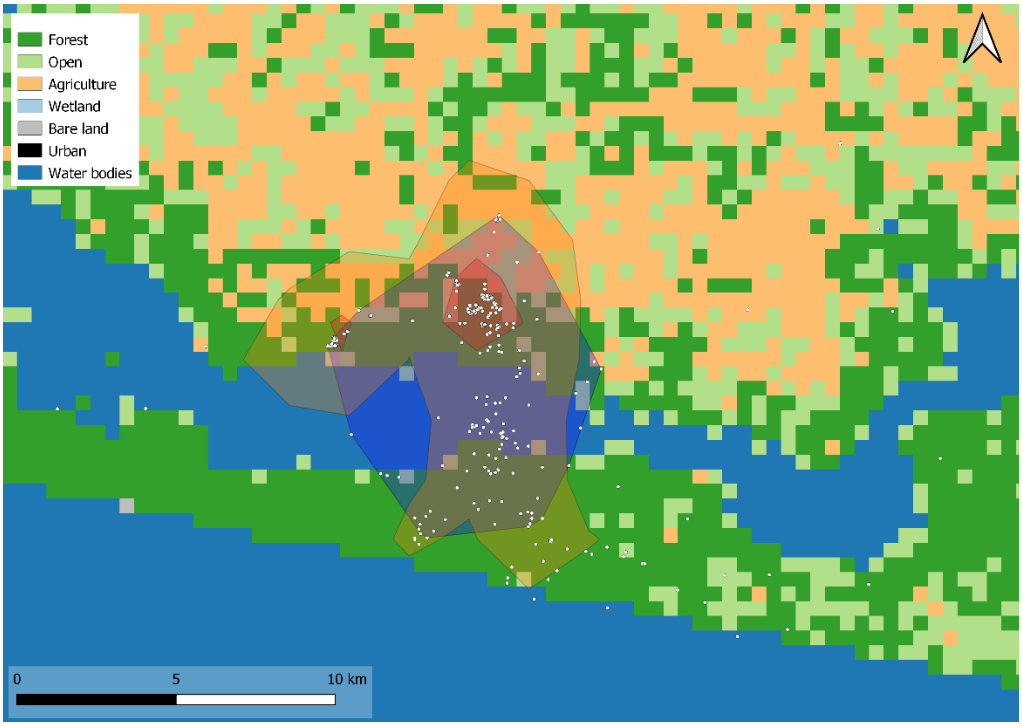
Map 37: Wintering area of Mrs. Søndre in 2019. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



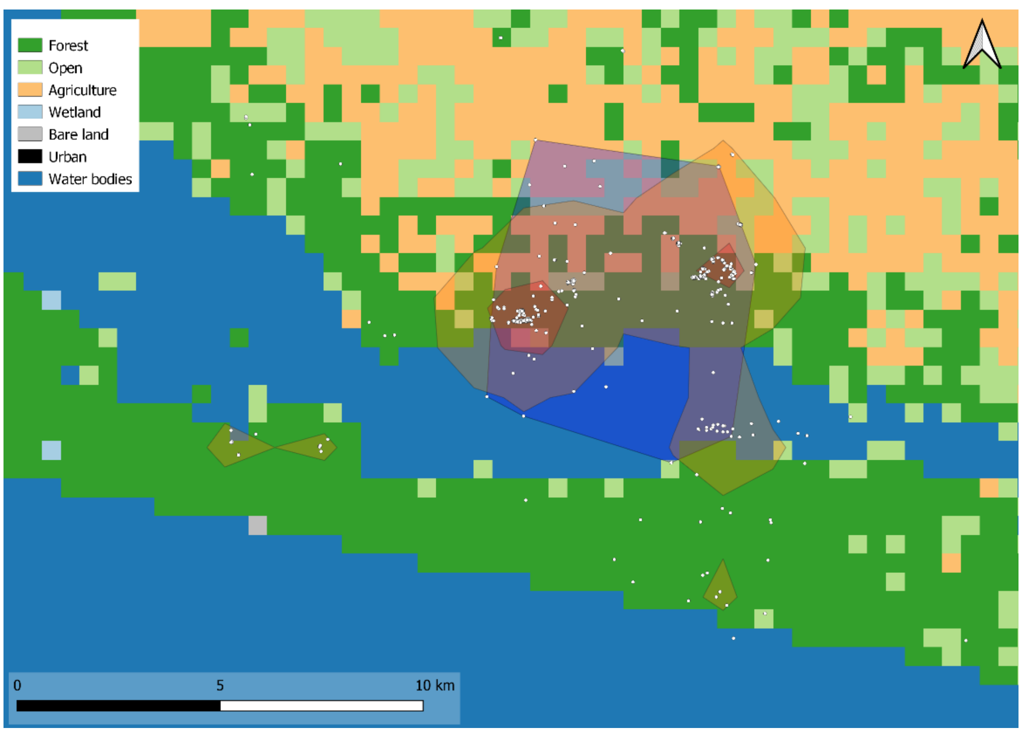
Map 38: Wintering area of Mr. Huseby in 2019. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



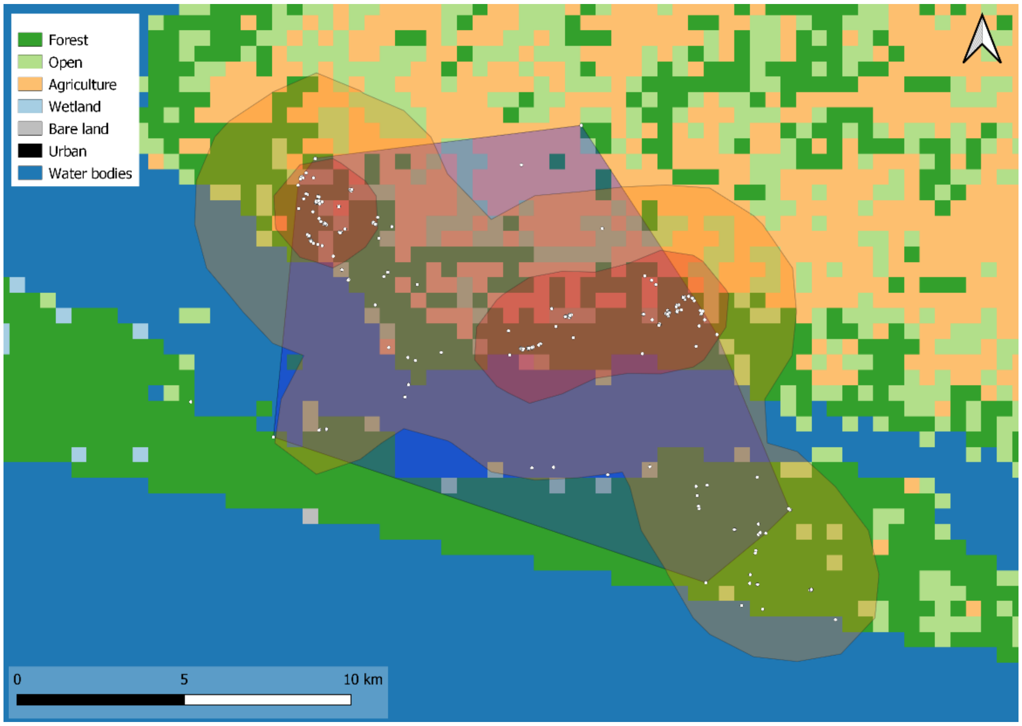
Map 39: Wintering area of Mr. Søndre in 2015. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



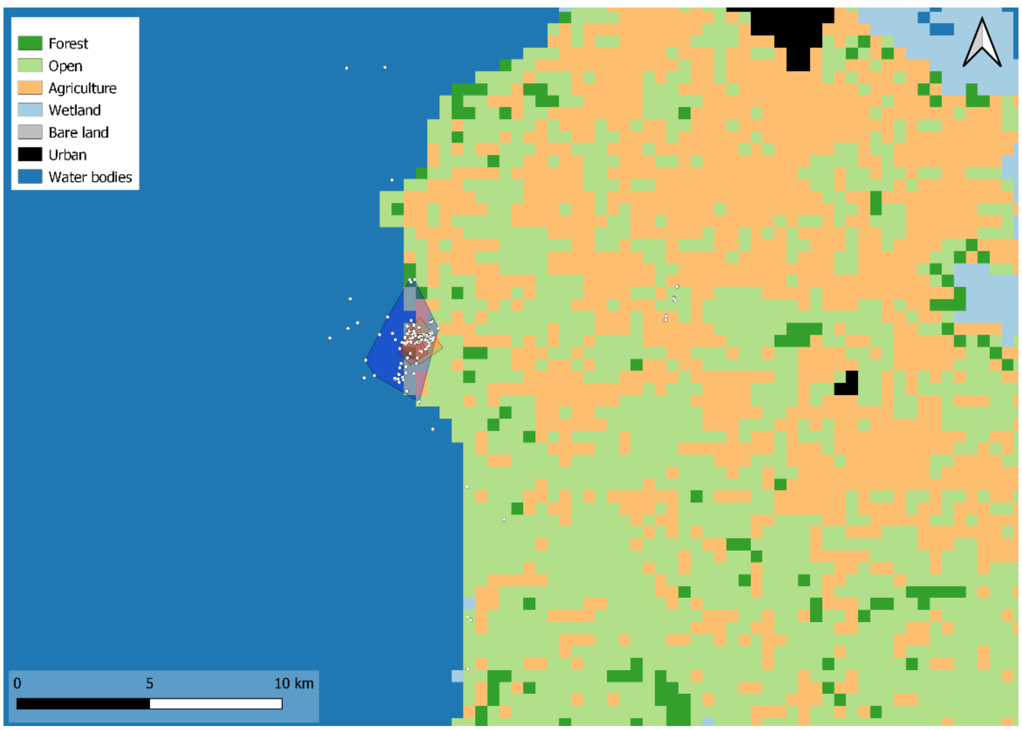
Map 40: Wintering area of Mr. Søndre in 2016. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



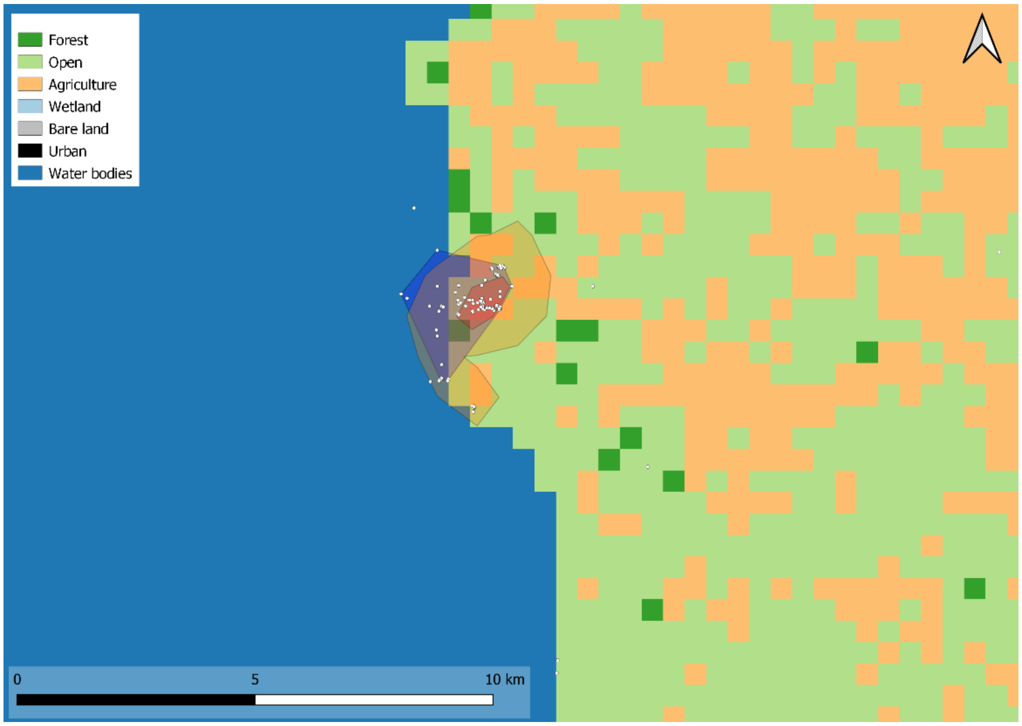
Map 41: Wintering area of Mr. Søndre in 2017. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



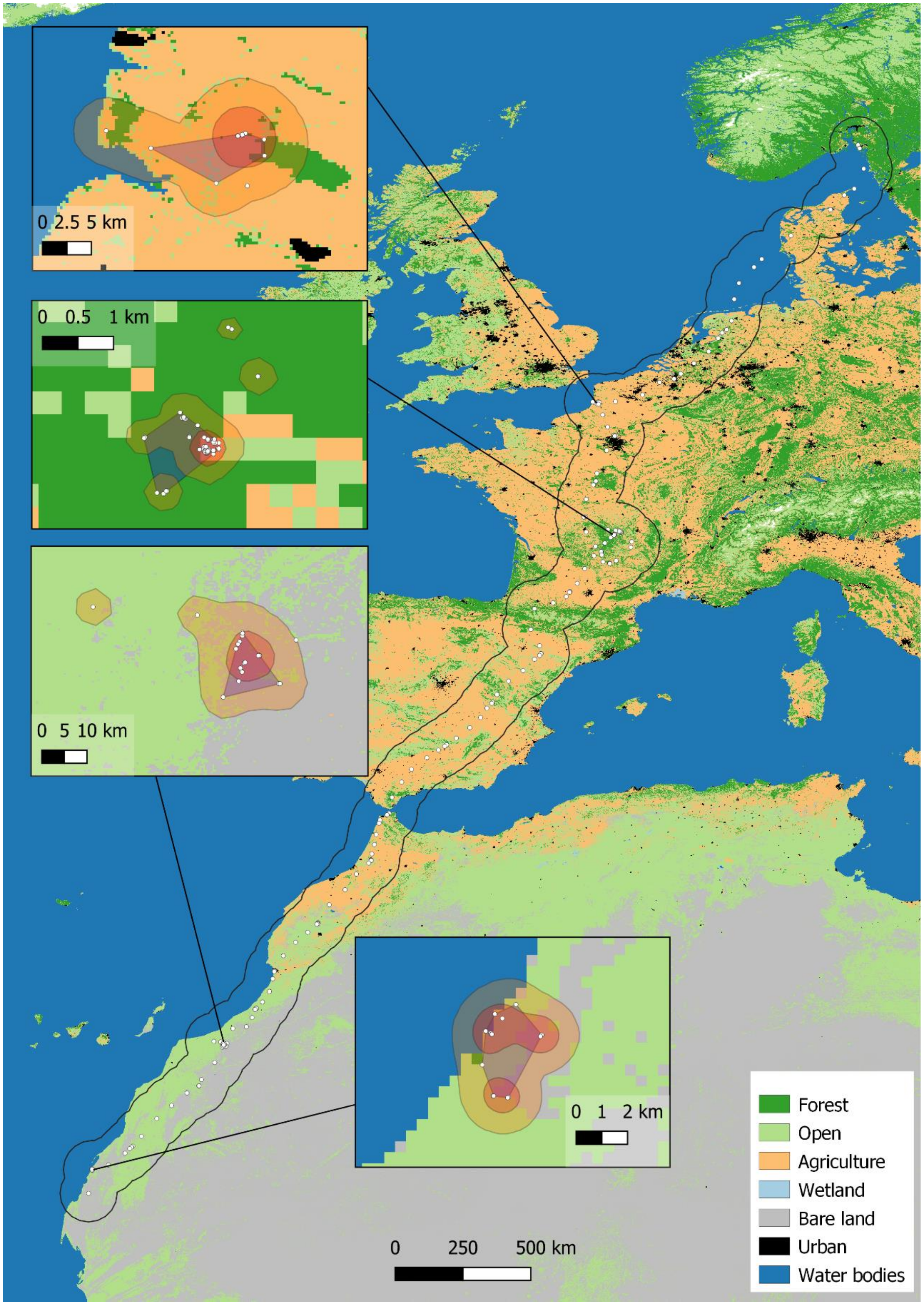
Map 42: Wintering area of Mr. Søndre in 2018. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



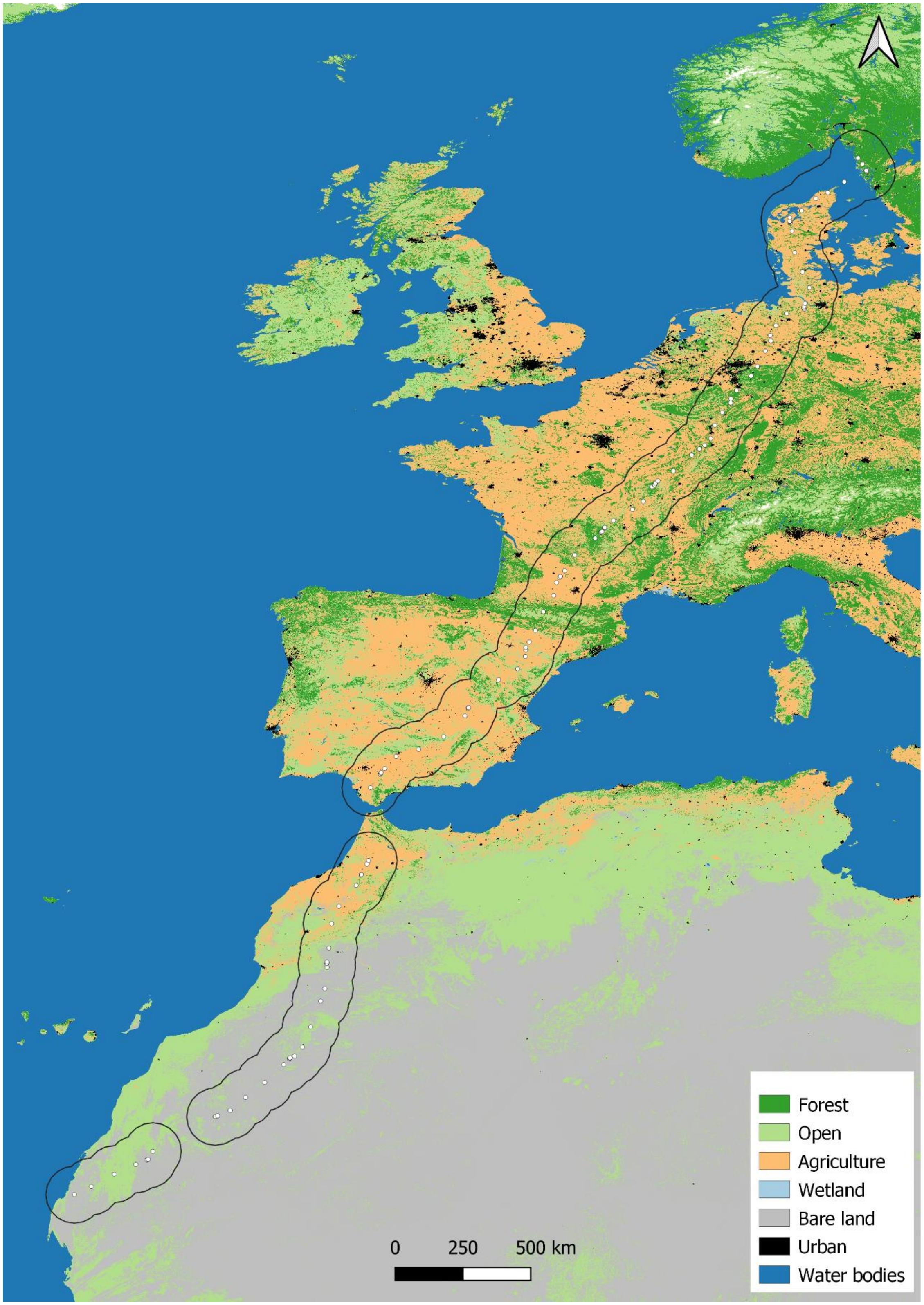
Map 43: Wintering area of Lotta in 2011. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



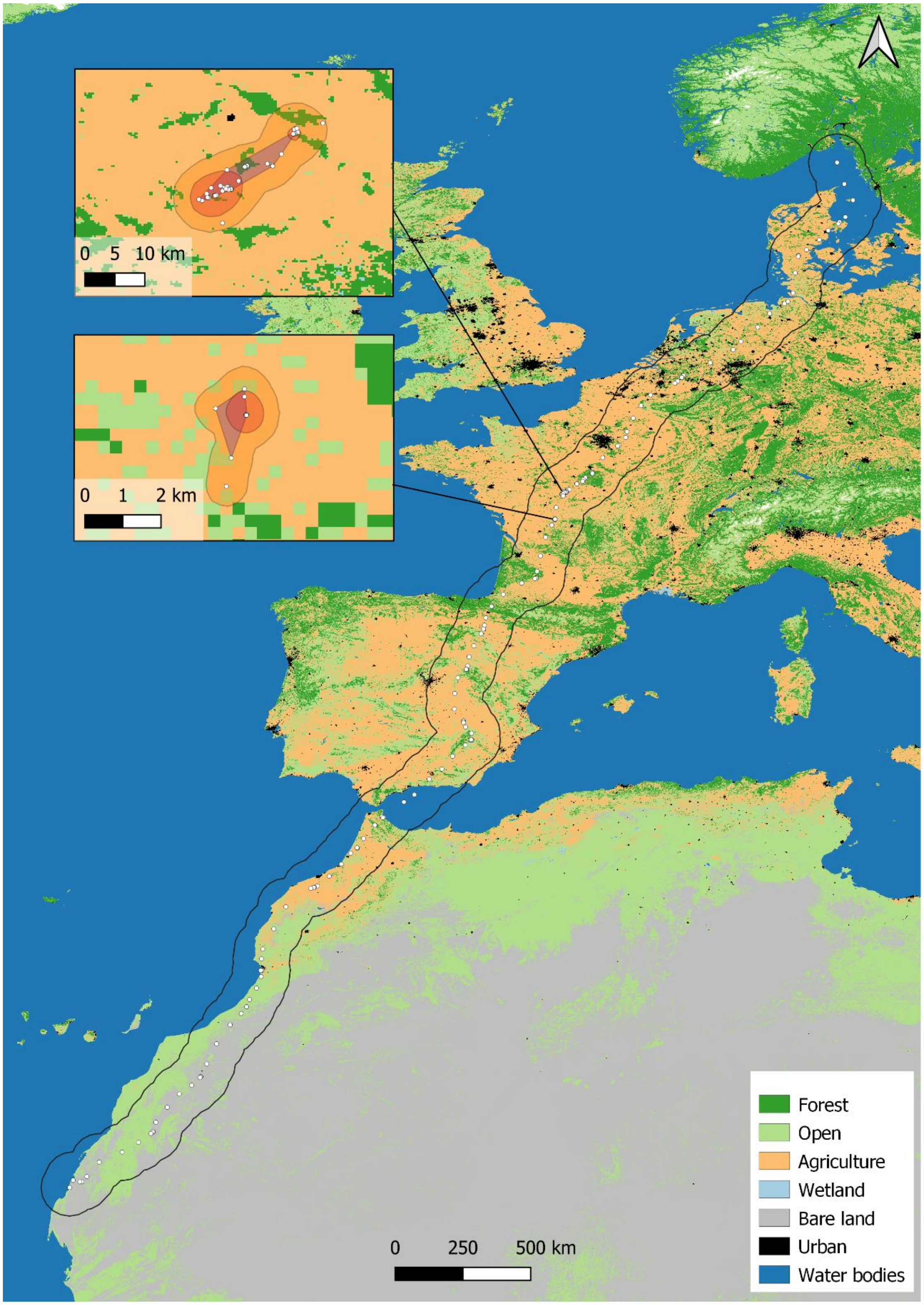
Map 44: Wintering area of Lotta in 2012. With observed points in white, MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



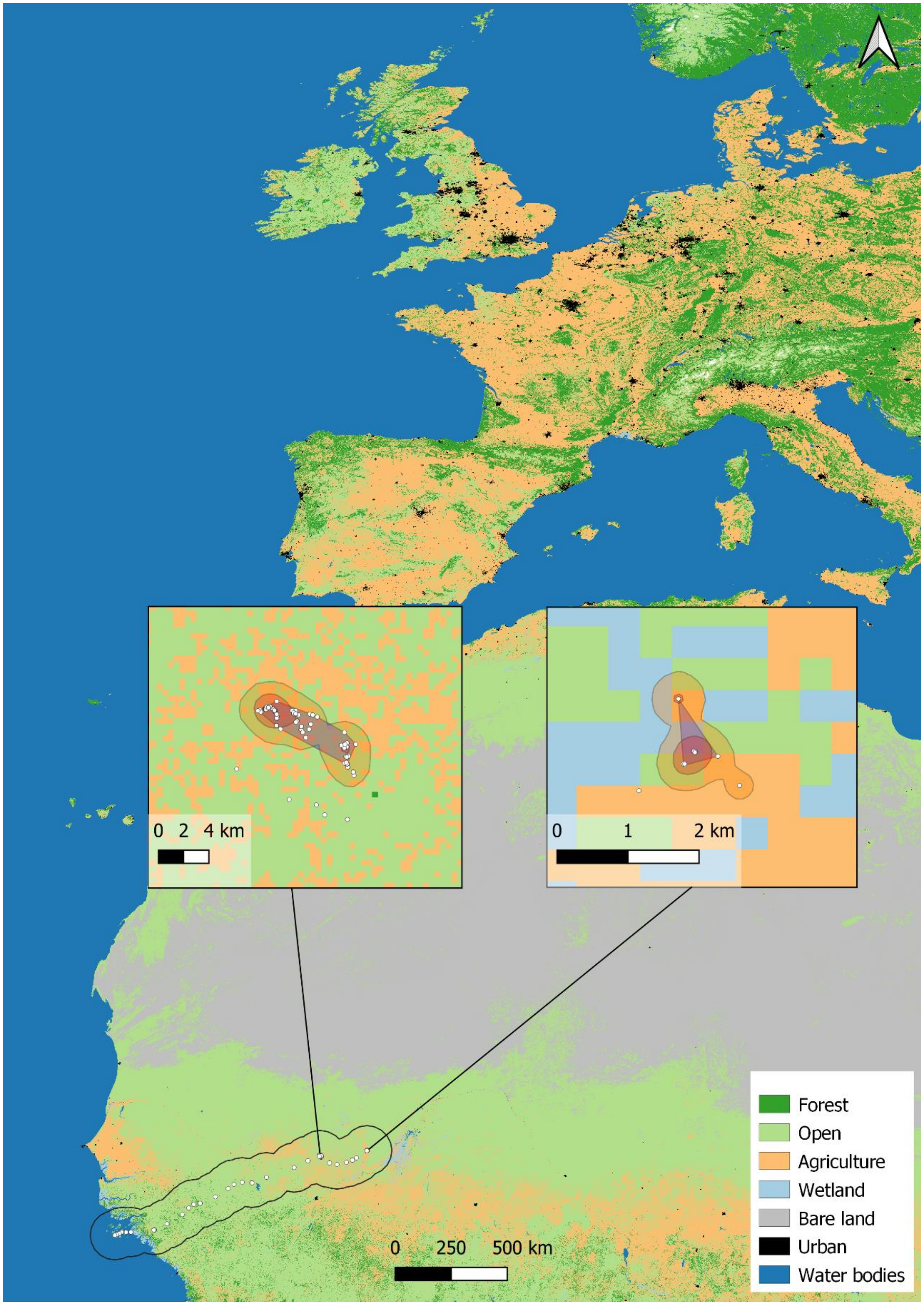
Map 45: Southward migration of Mrs. Huseby in 2019 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



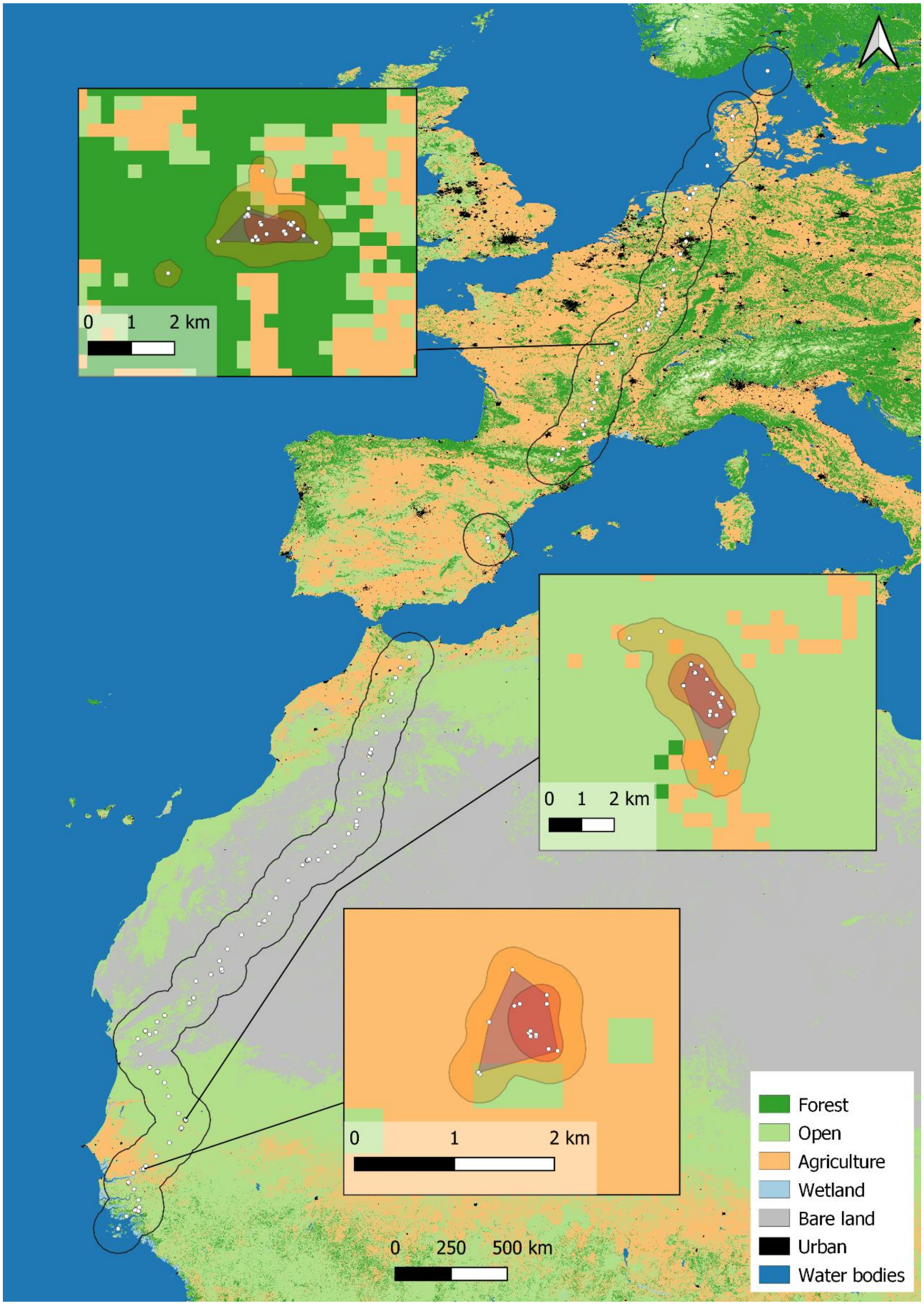
Map 46: Northward migration of Mrs. Huseby in 2020, with observed points in white and the buffer. No stopovers were made during this migration.



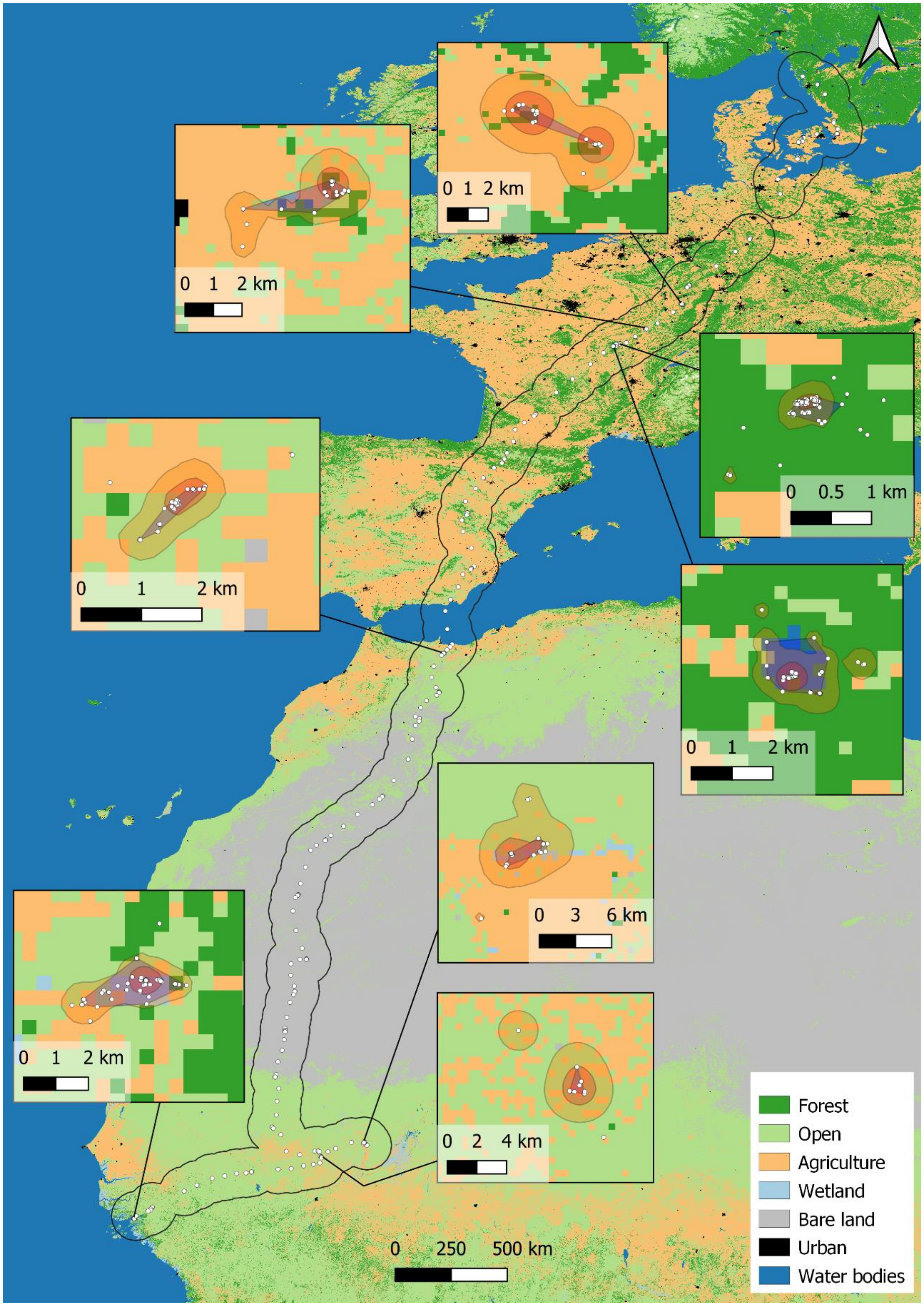
Map 47: Southward migration of Mrs. Huseby in 2020 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



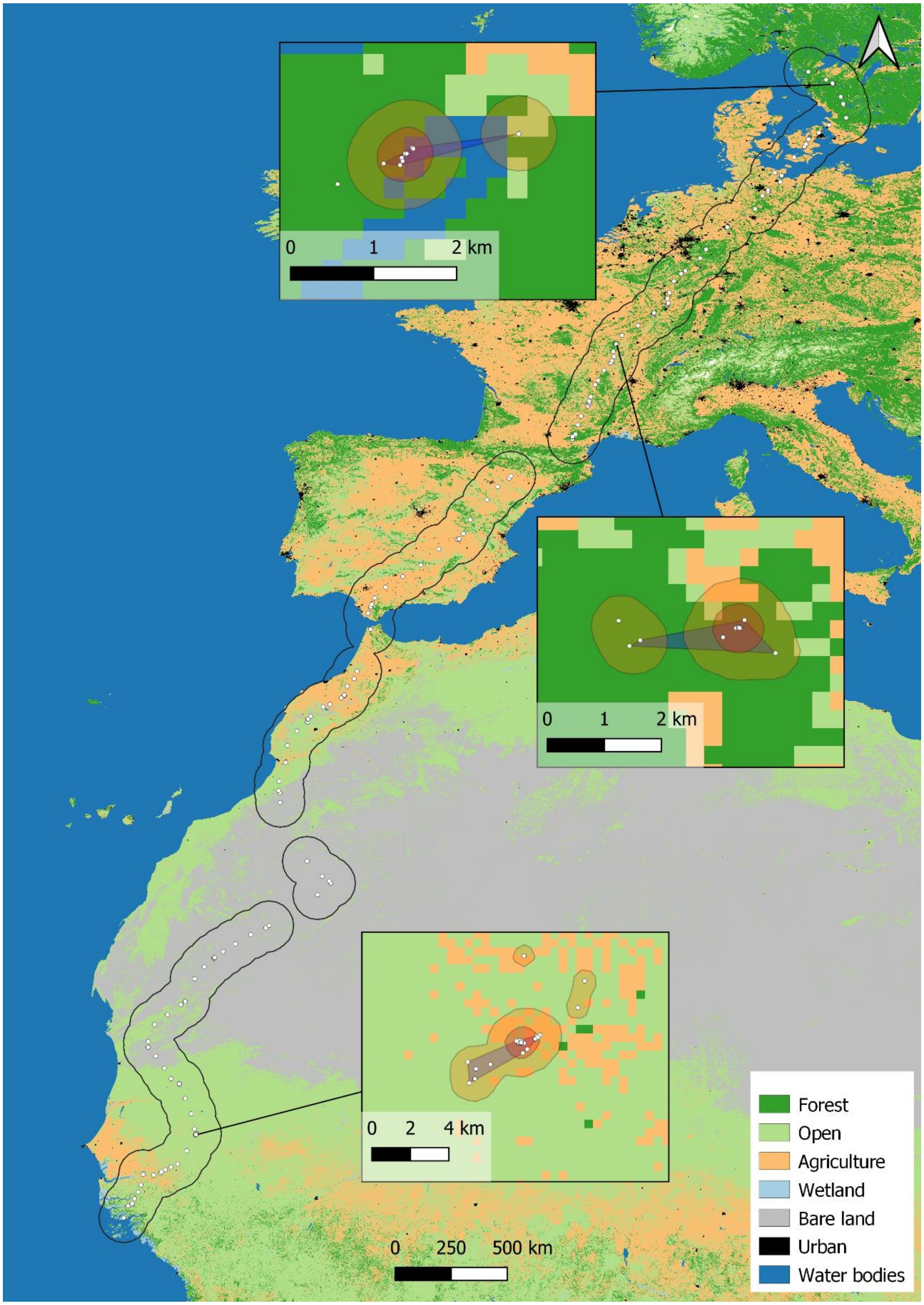
Map 48: Southward migration of Mrs. Søndre in 2015 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



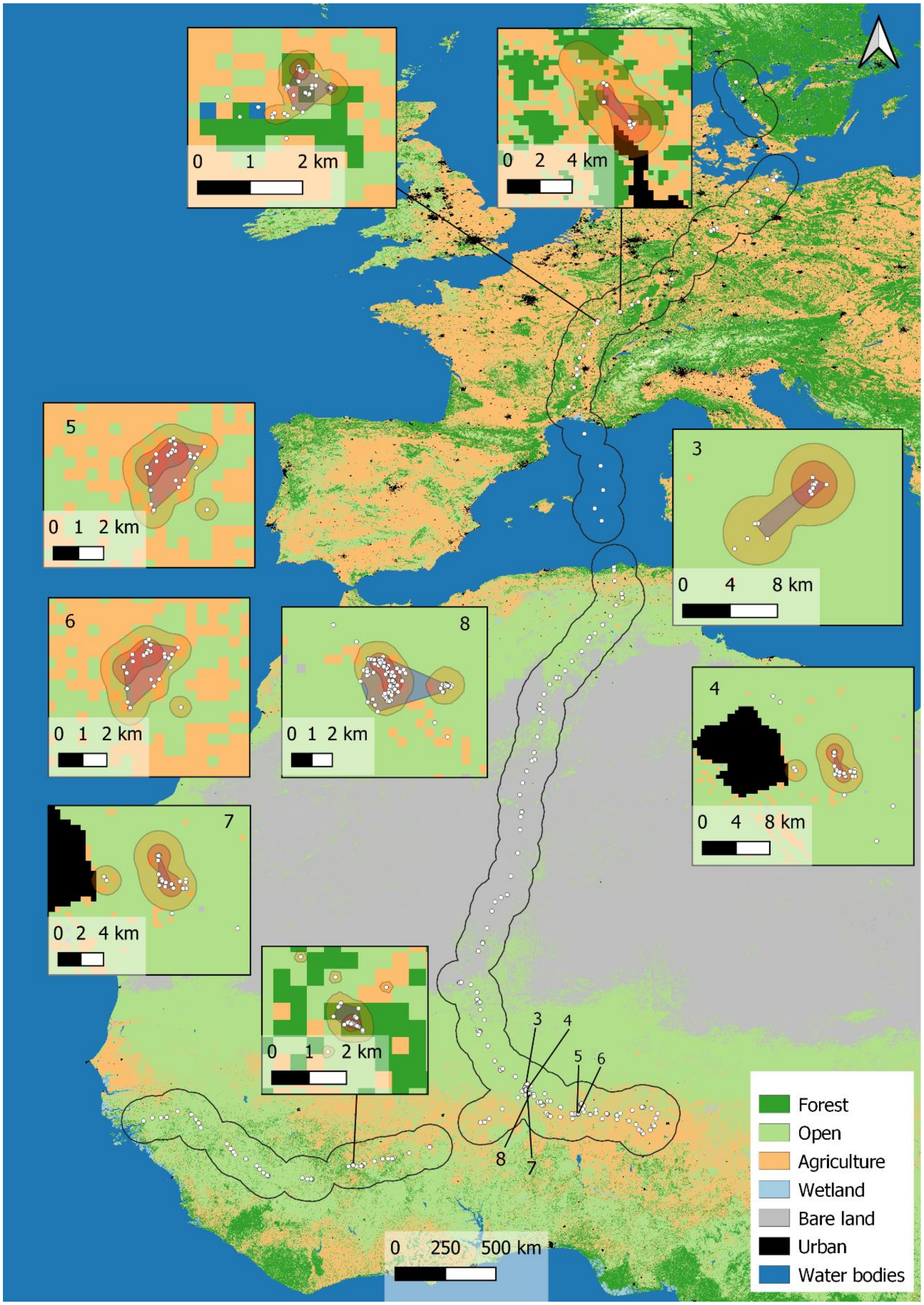
Map 49: Northward migration of Mrs. Søndre in 2016, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



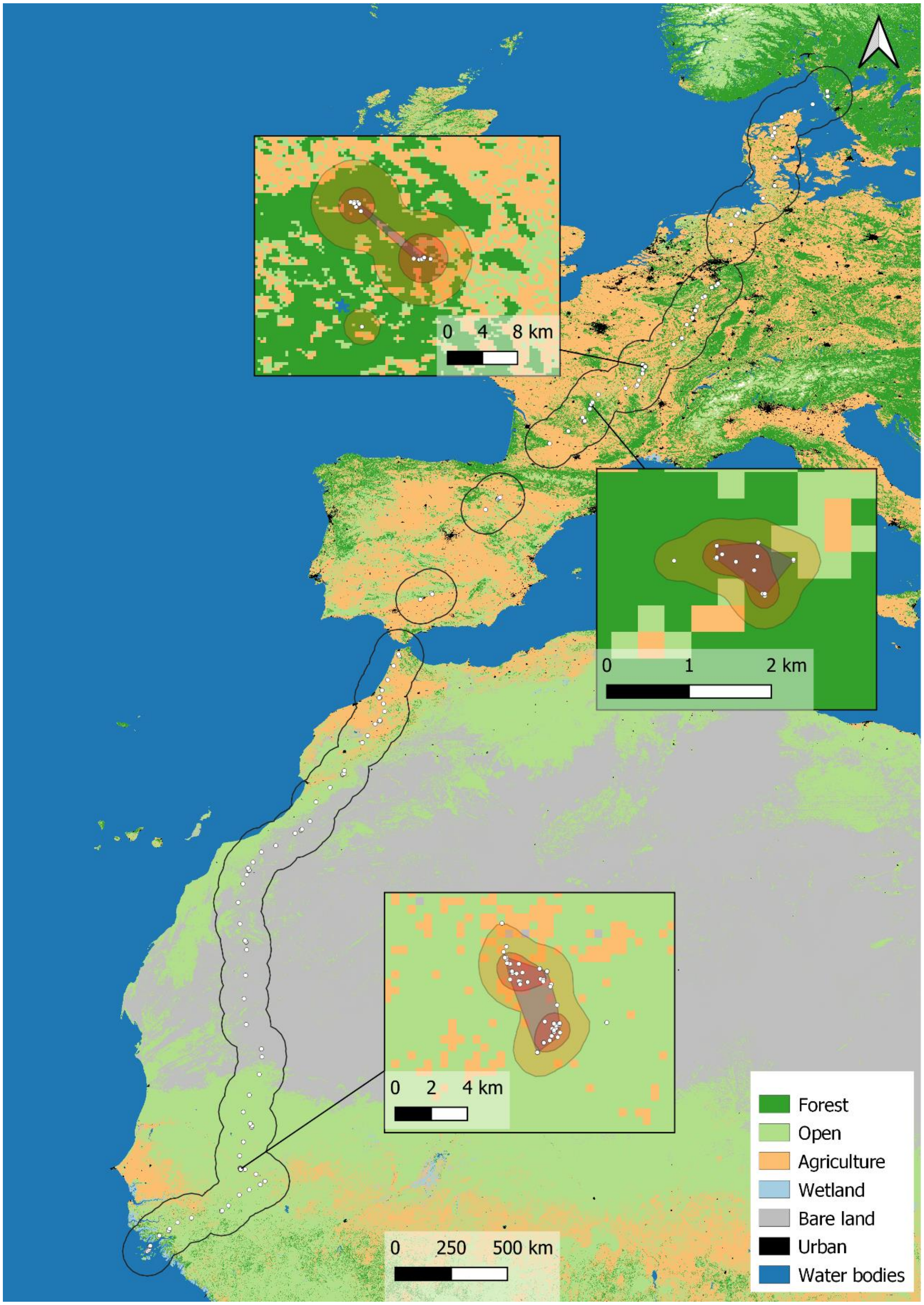
Map 50: Southward migration of Mrs. Søndre in 2016 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



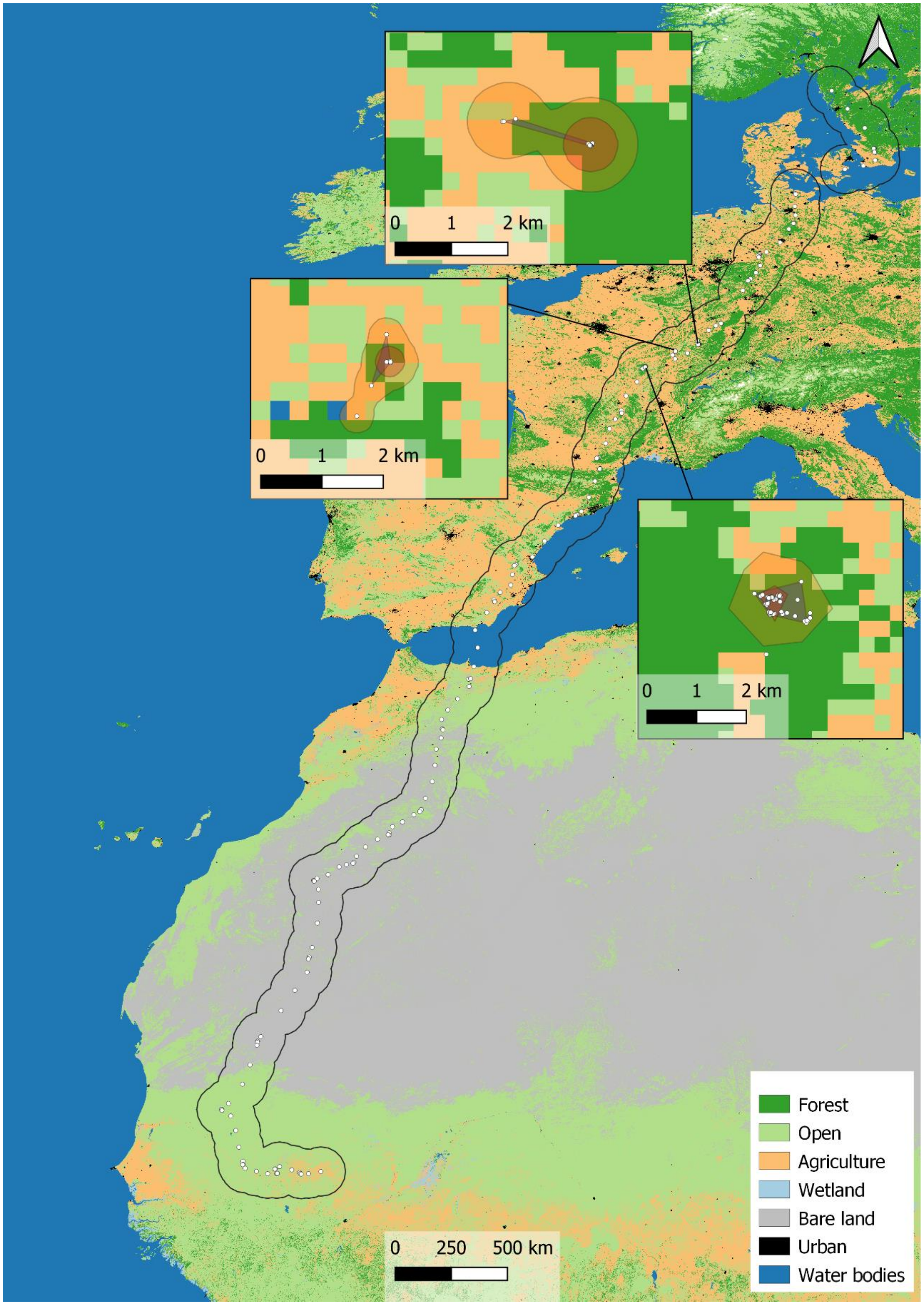
Map 51: Northward migration of Mrs. Søndre in 2017, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



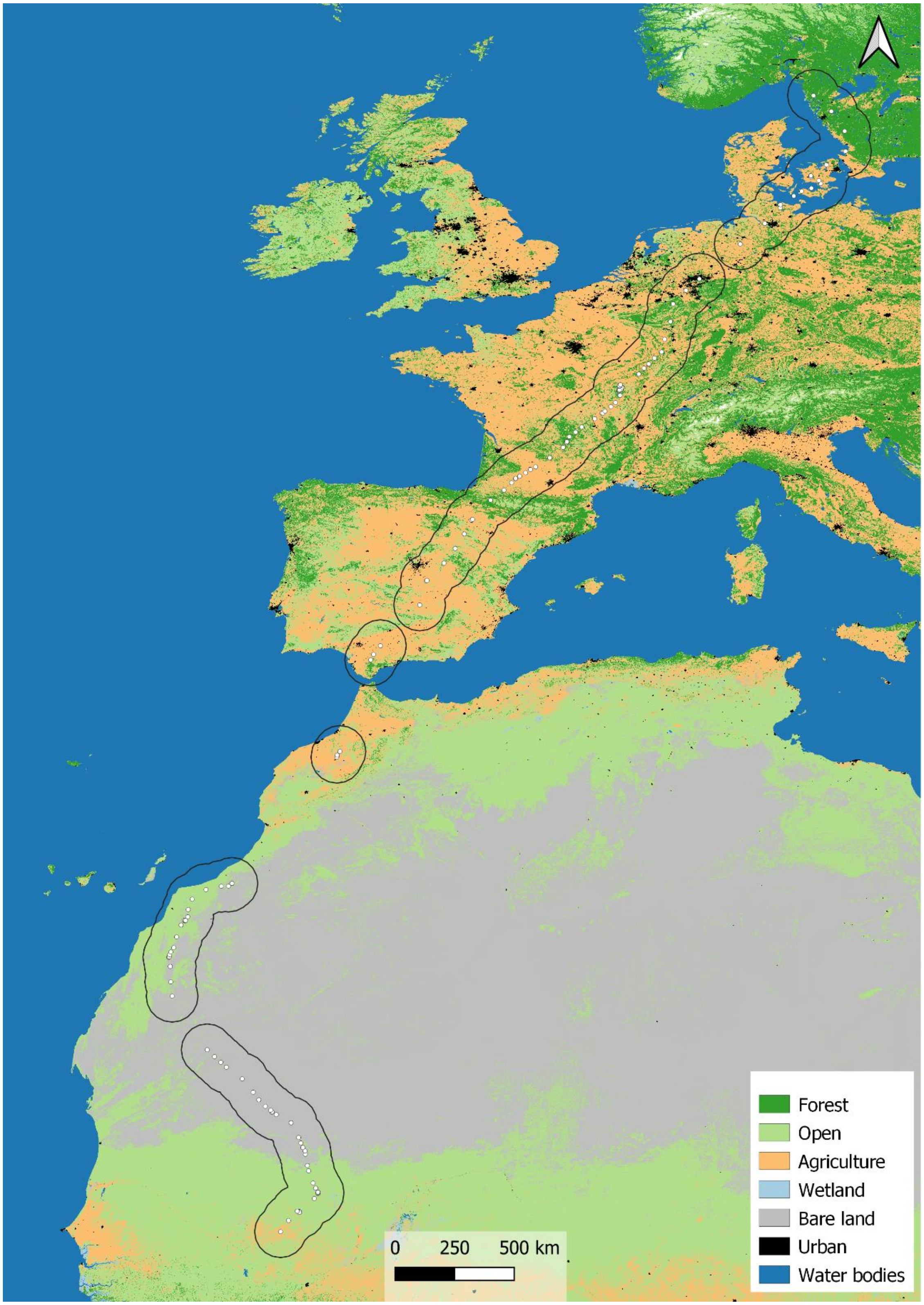
Map 52: Southward migration of Mrs. Søndre in 2017 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



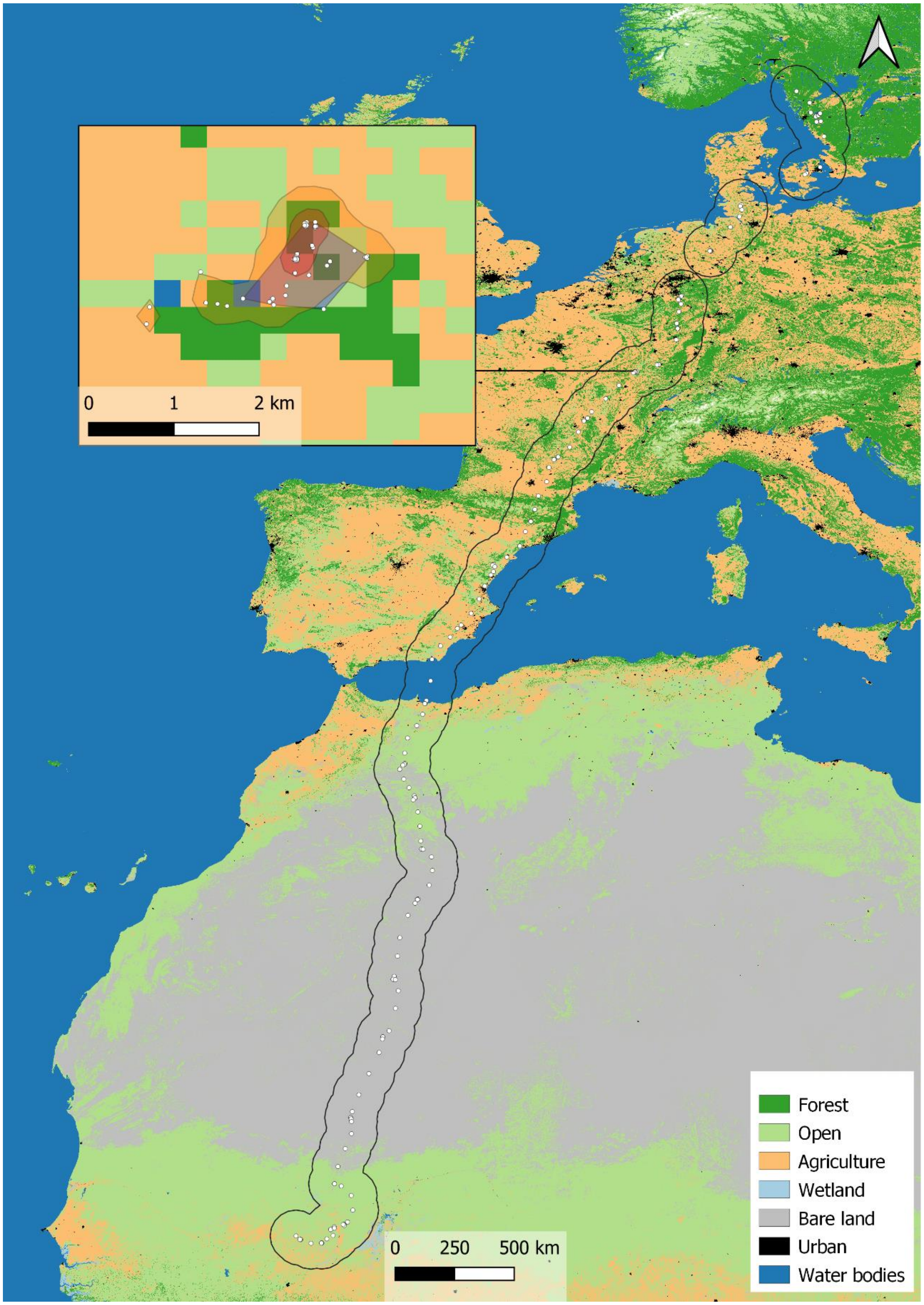
Map 53: Northward migration of Mrs. Søndre in 2018, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



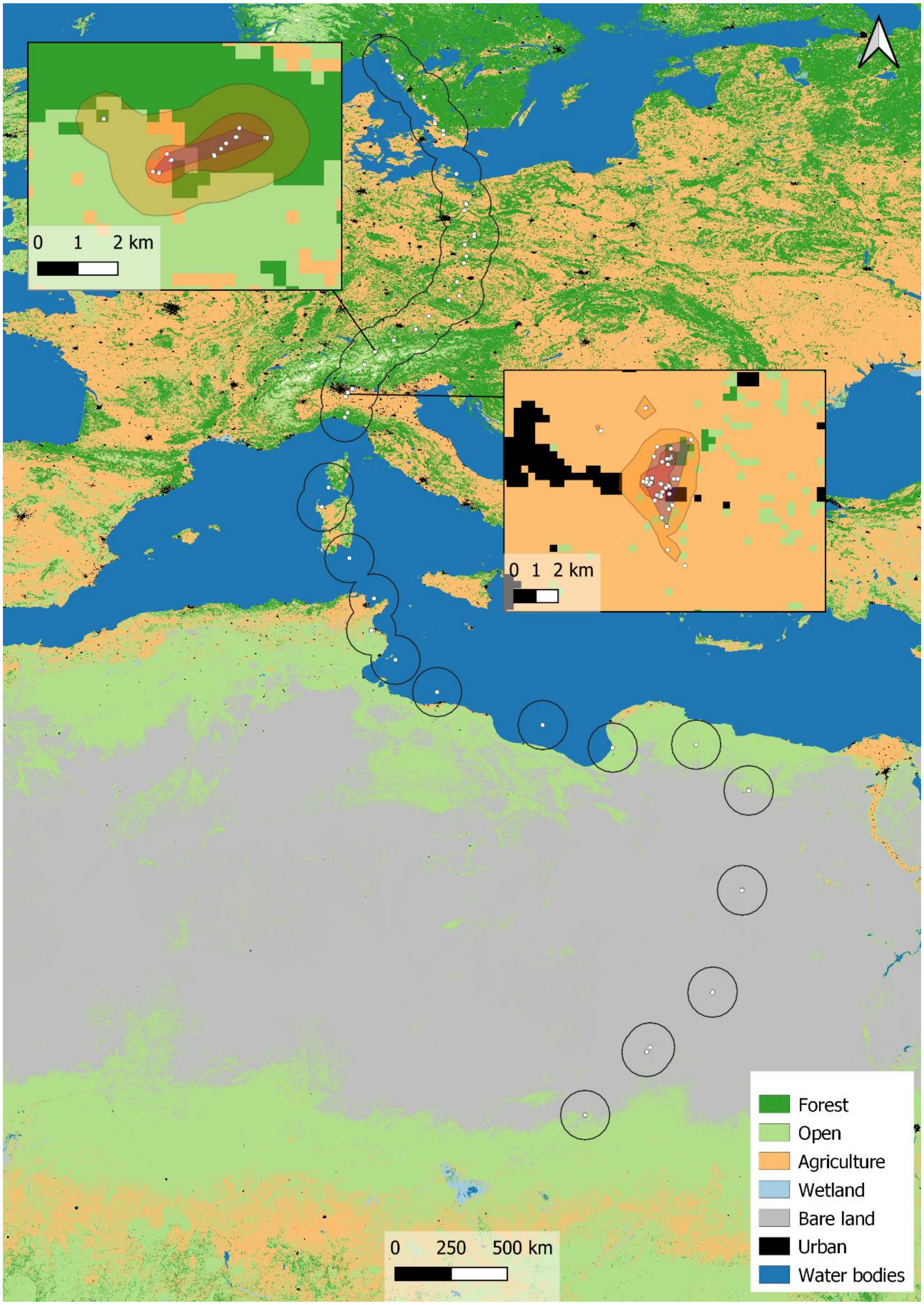
Map 54: Southward migration of Mrs. Søndre in 2018 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



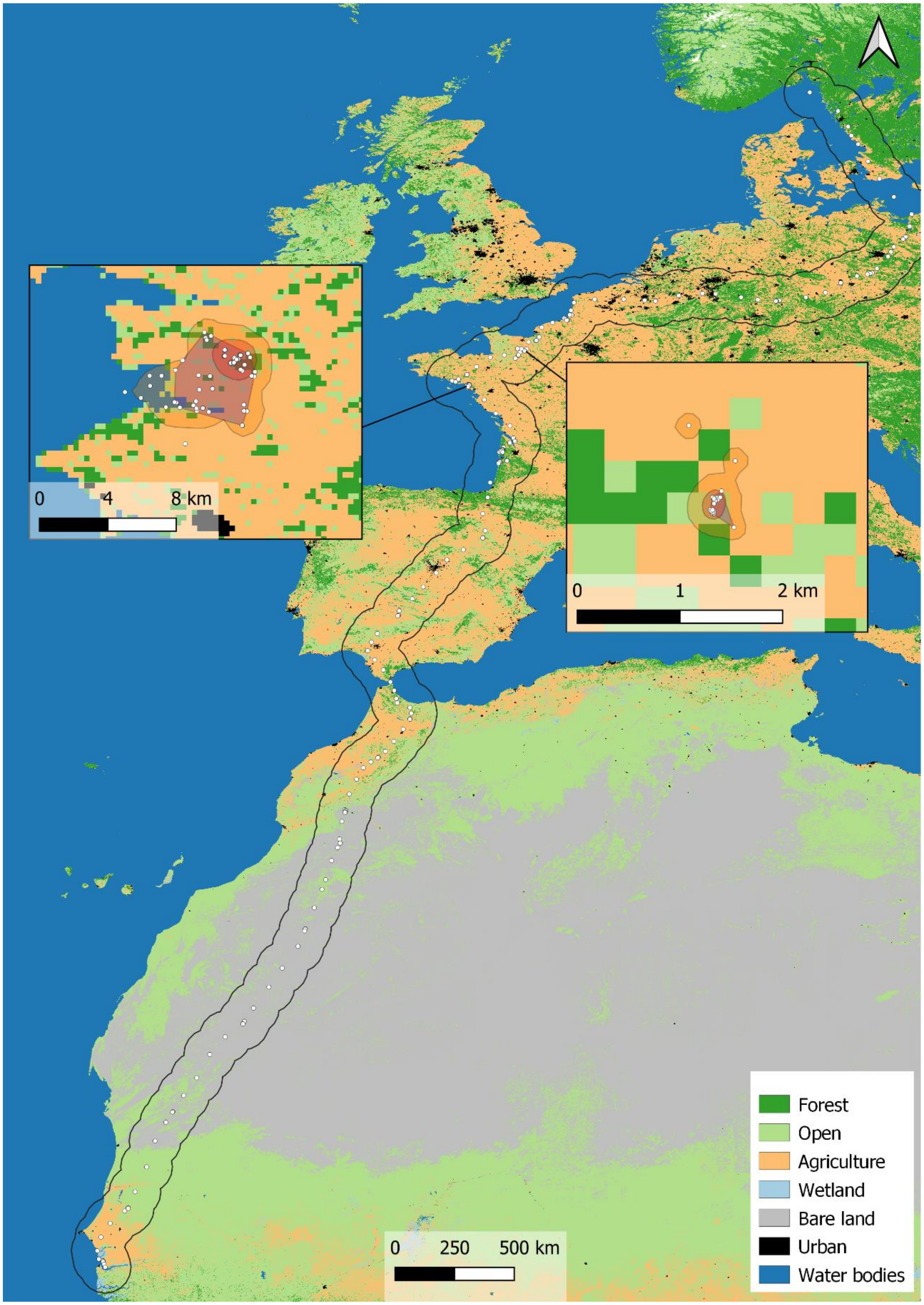
Map 55: Northward migration of Mrs. Søndre in 2019, with observed points in white and the buffer. No stopovers were made during this migration.



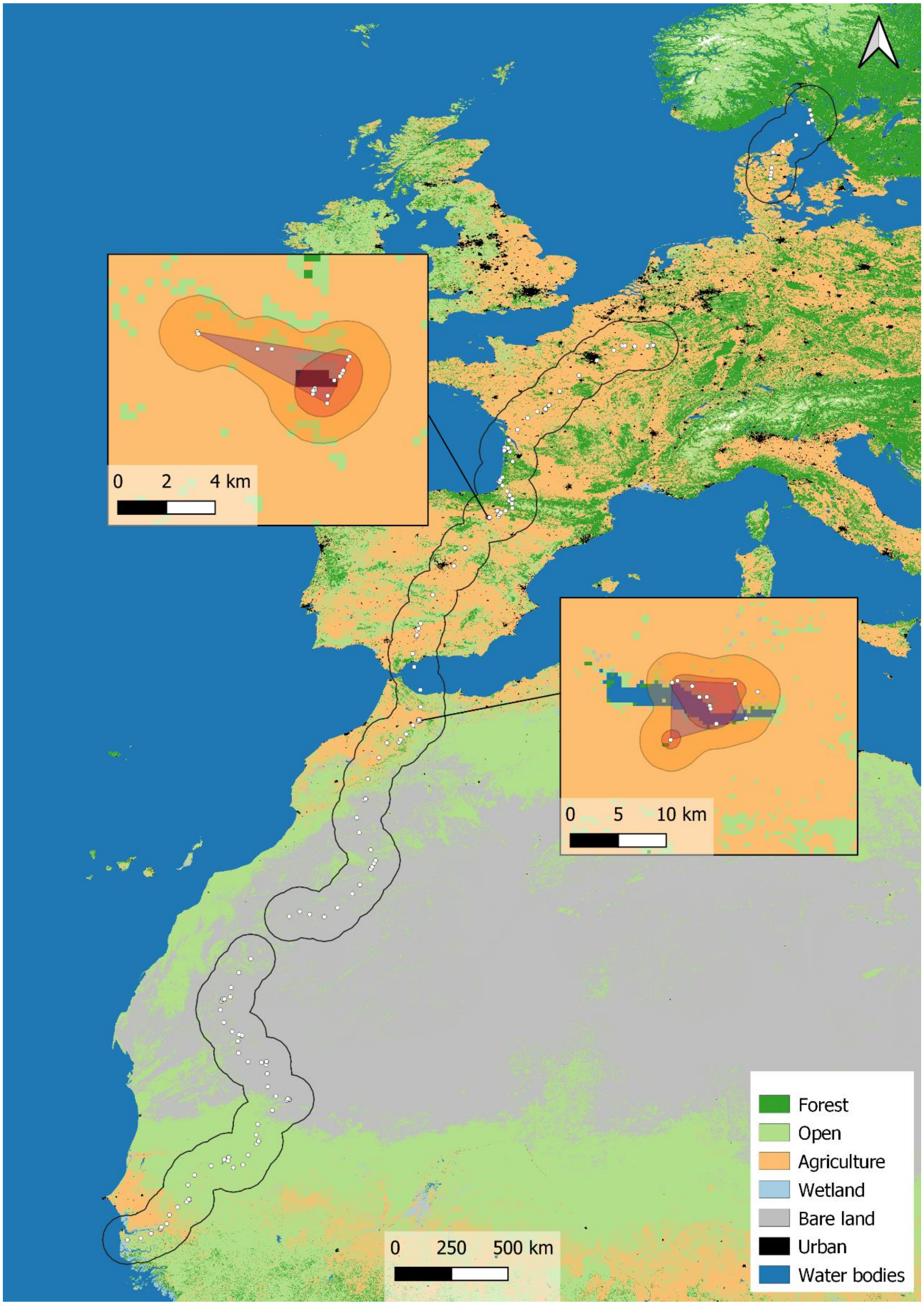
Map 56: Southward migration of Mrs. Søndre in 2019 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



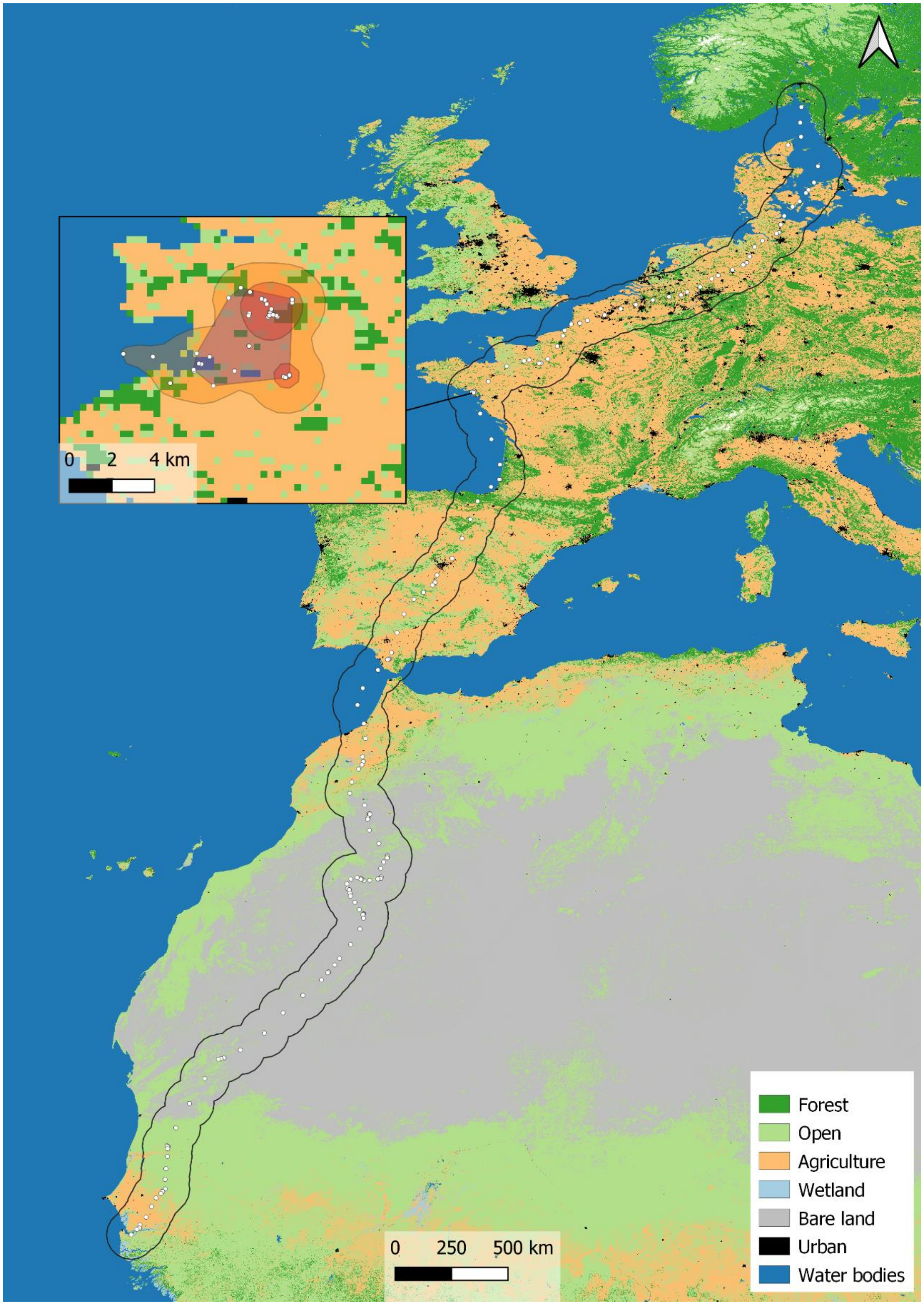
Map 57: Southward migration of Mr. Bjørnlandsevja (juvenile) in 2013, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



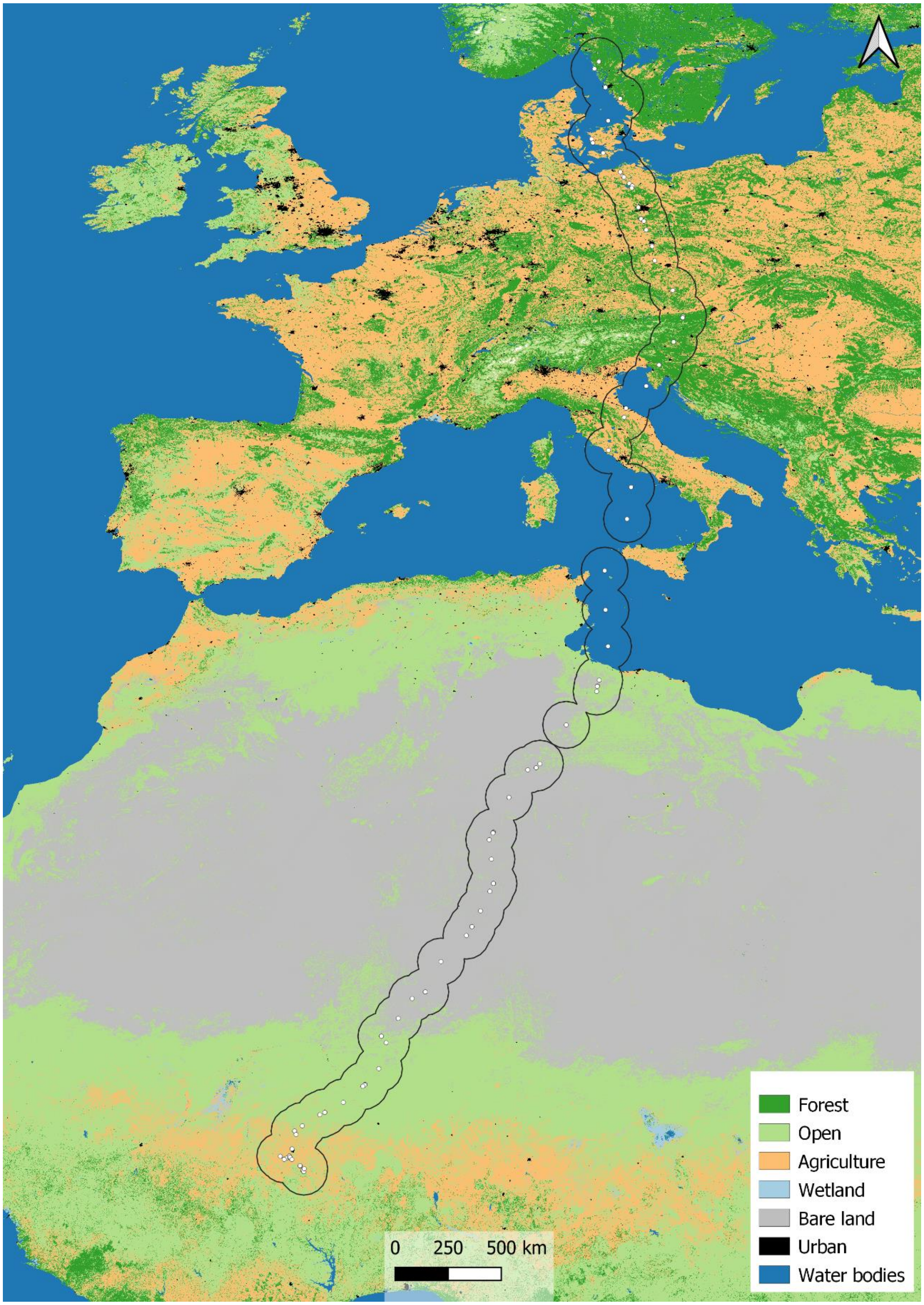
Map 58: Southward migration of Mr. Huseby in 2019 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



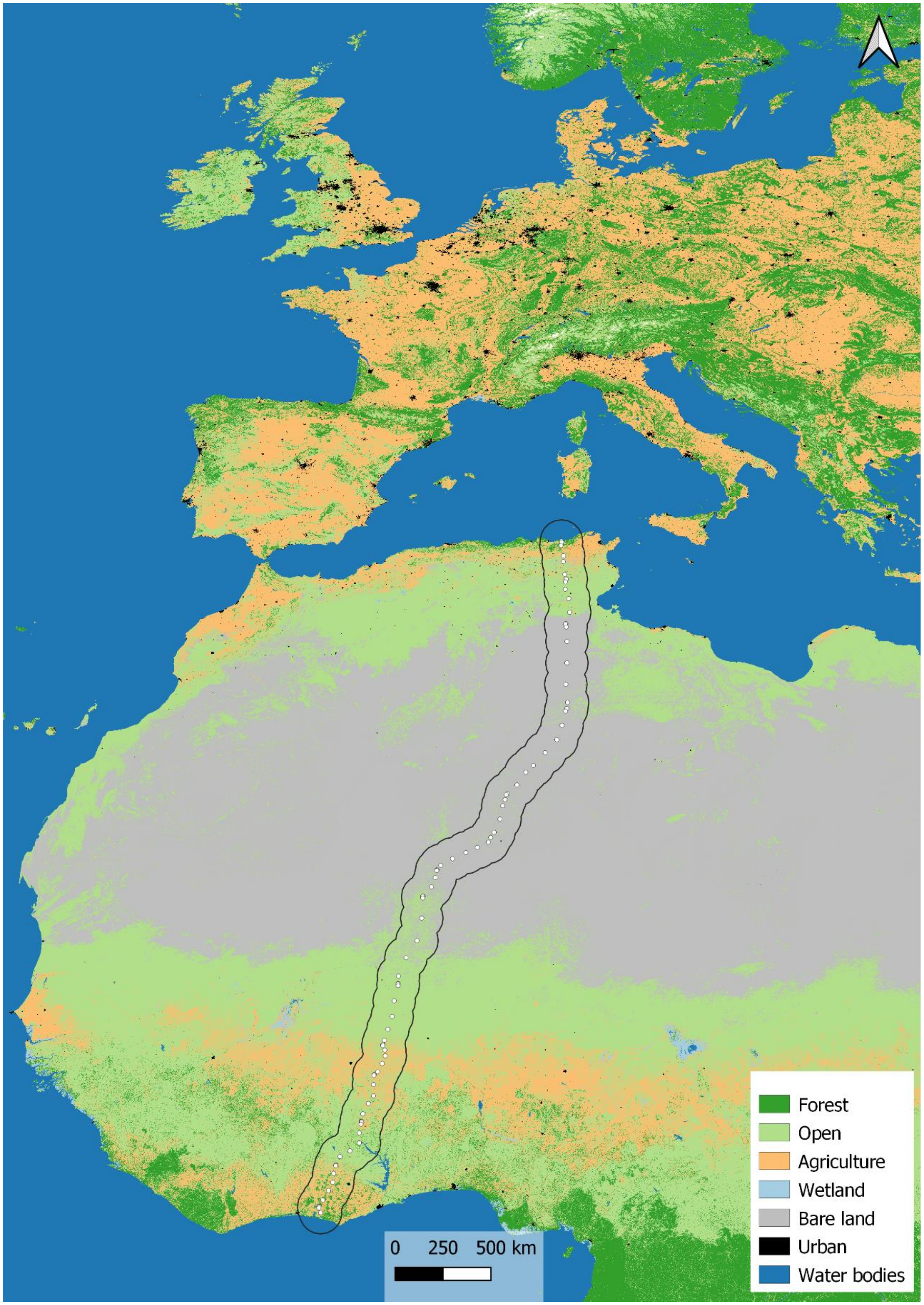
Map 59: Northward migration of Mr. Huseby in 2020, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



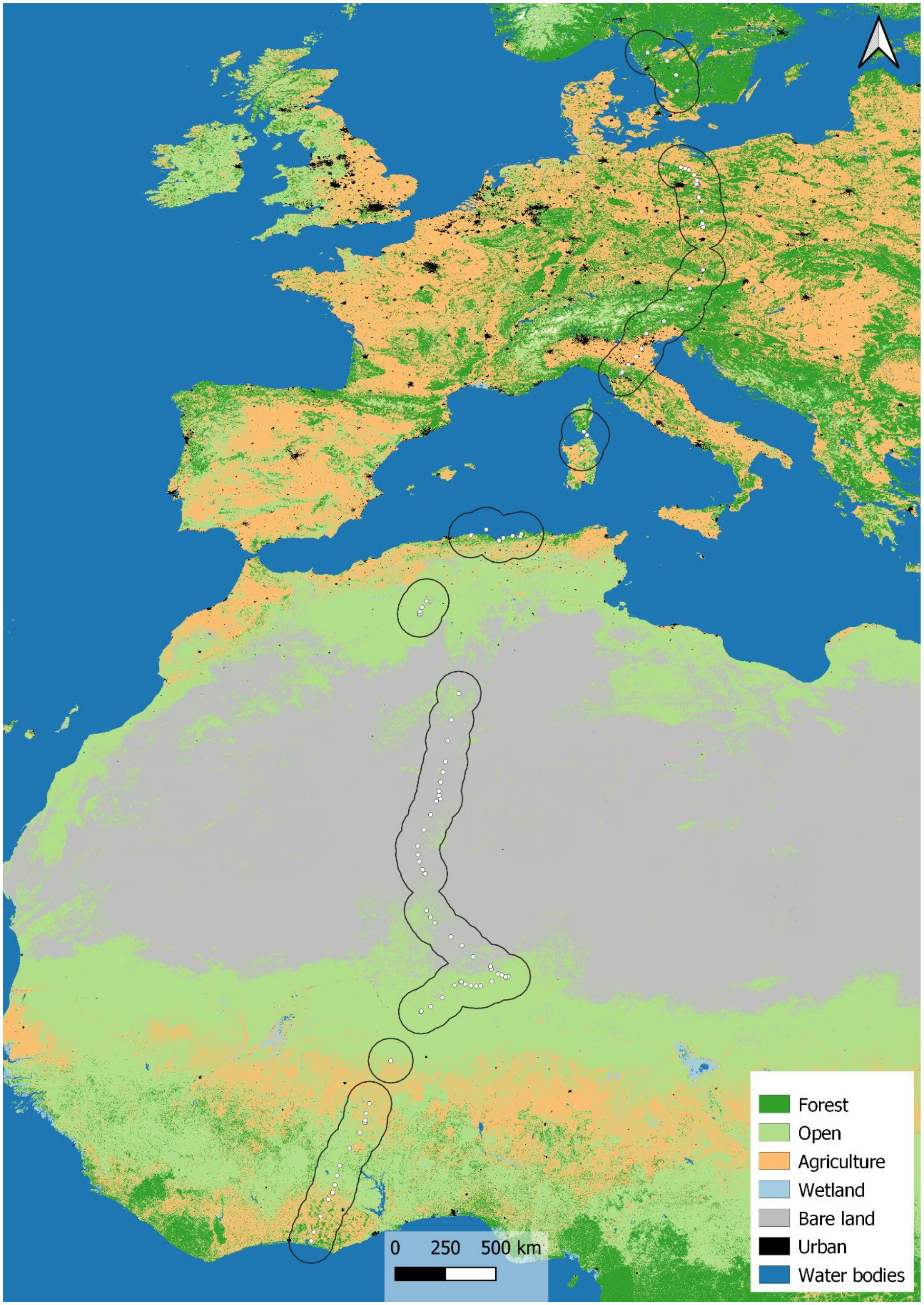
Map 60: Southward migration of Mr. Huseby in 2020 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



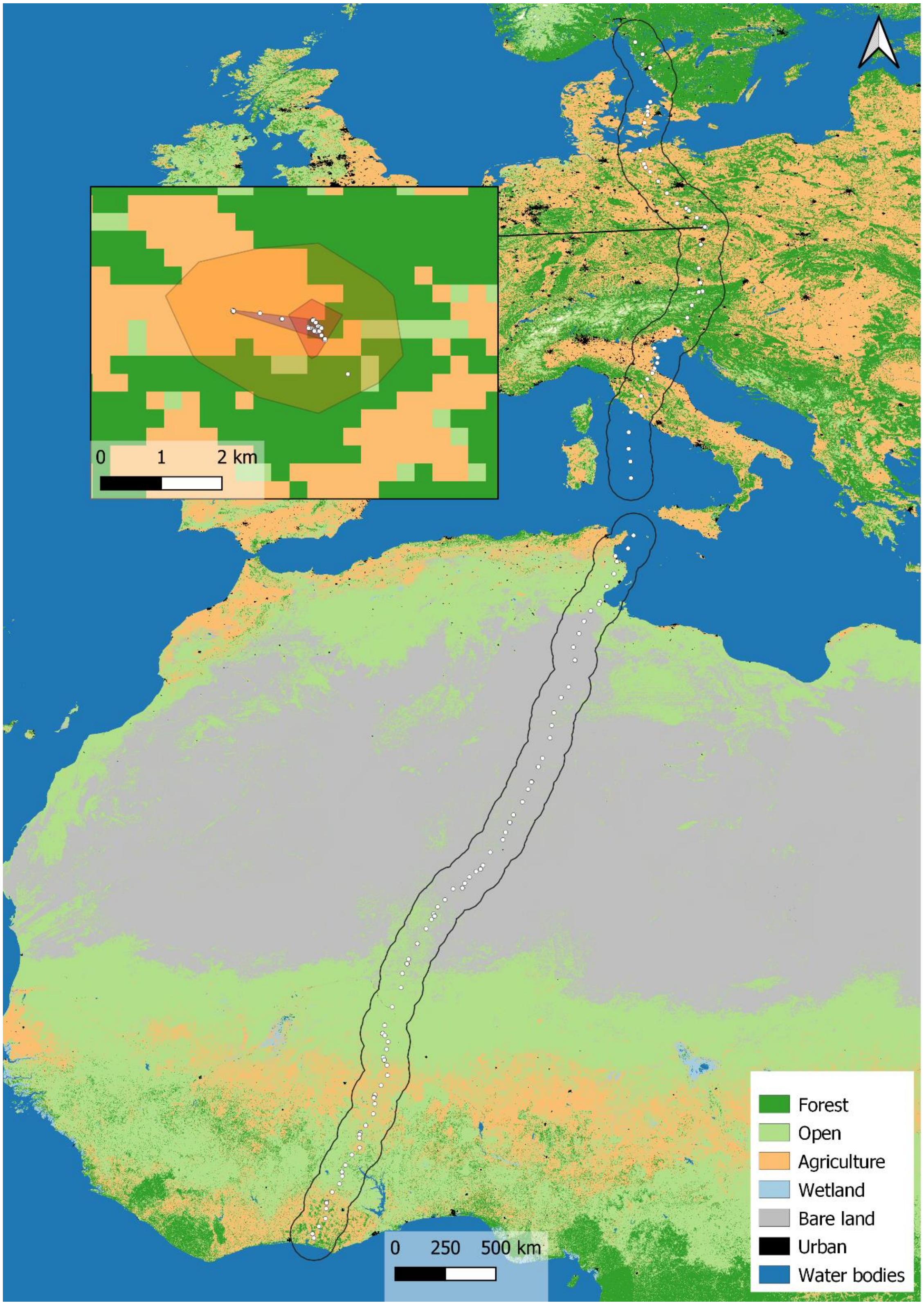
Map 61: Southward migration of Mr. Ise (juvenile) in 2013, with observed points in white and the buffer. No stopovers were made during this migration.



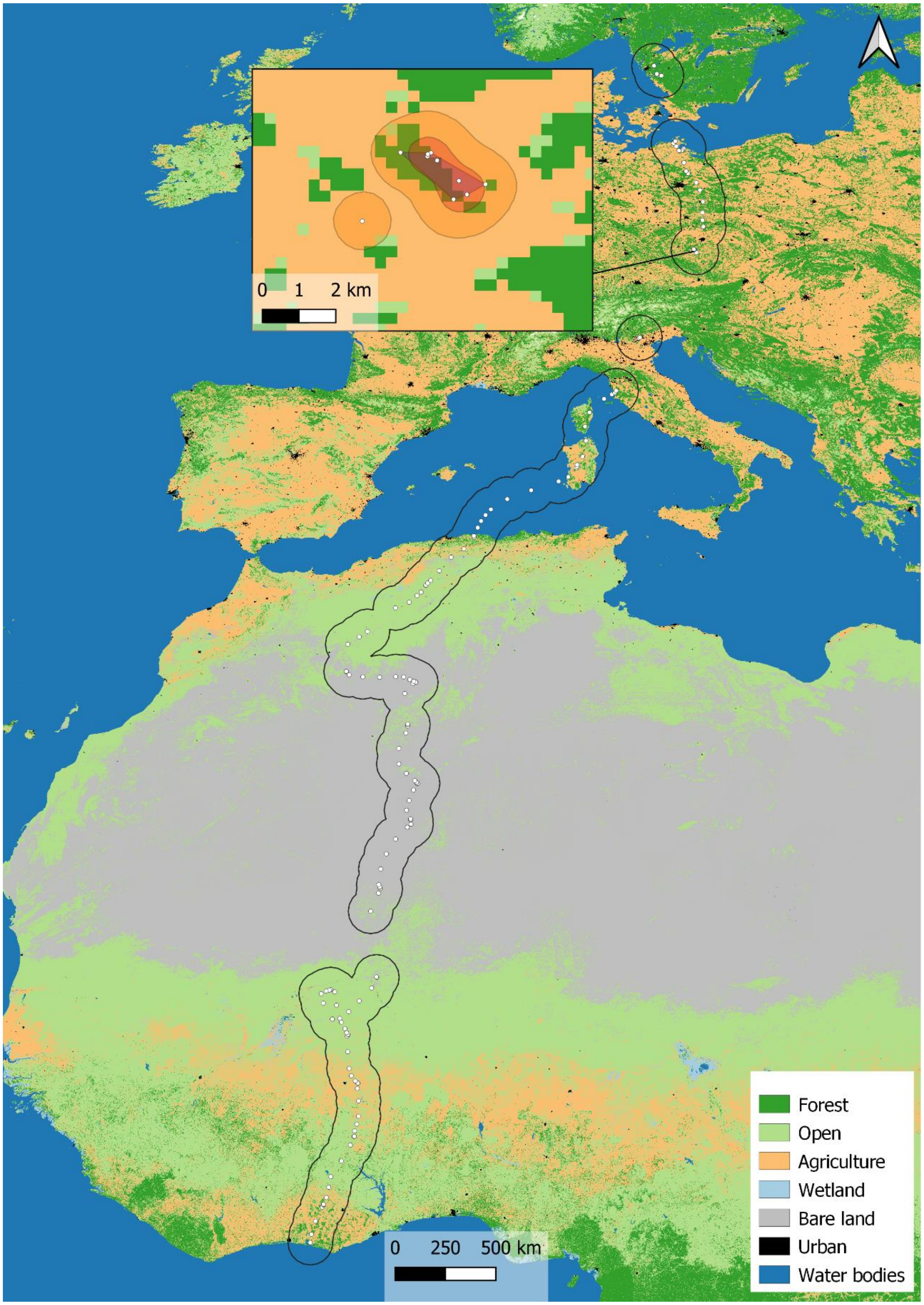
Map 62: Southward migration of Mr. Søndre in 2015 (breeding year), with observed points in white and the buffer. No stopovers were made during this part of the migration.



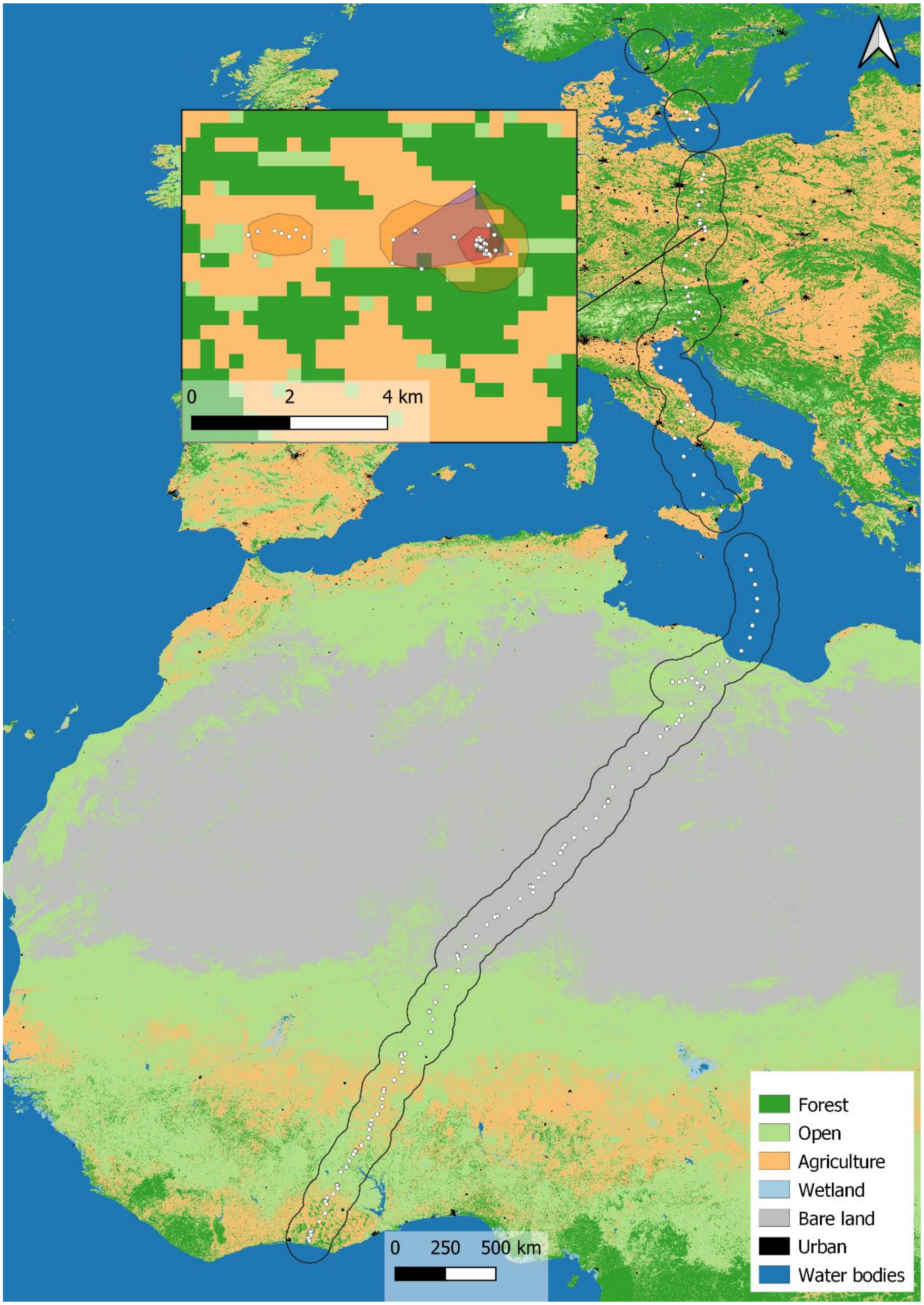
Map 63: Northward migration of Mr. Søndre in 2016, with observed points in white and the buffer. No stopovers were made during this migration.



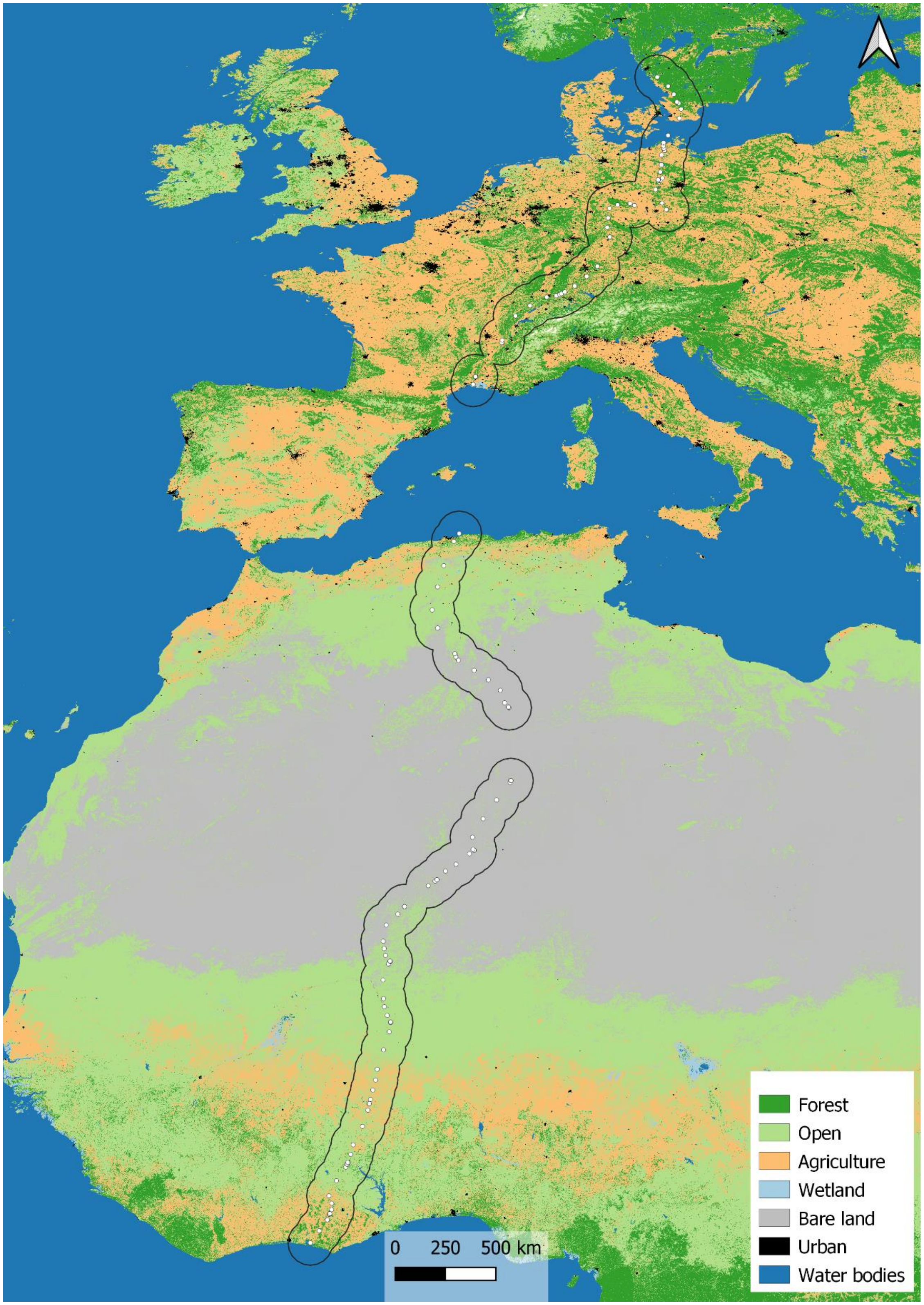
Map 64: Southward migration of Mr. Søndre in 2016 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



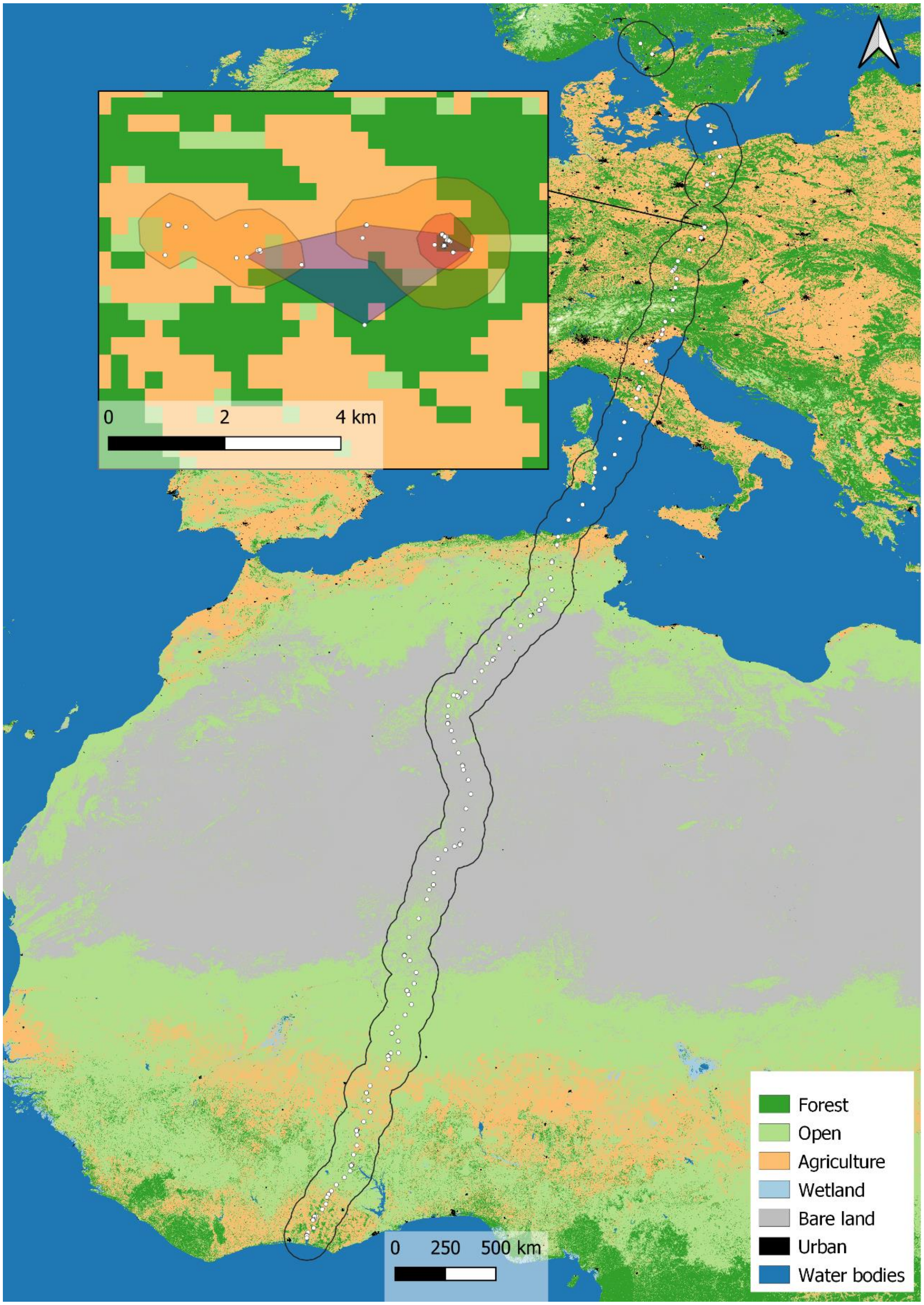
Map 65: Northward migration of Mr. Søndre in 2017, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



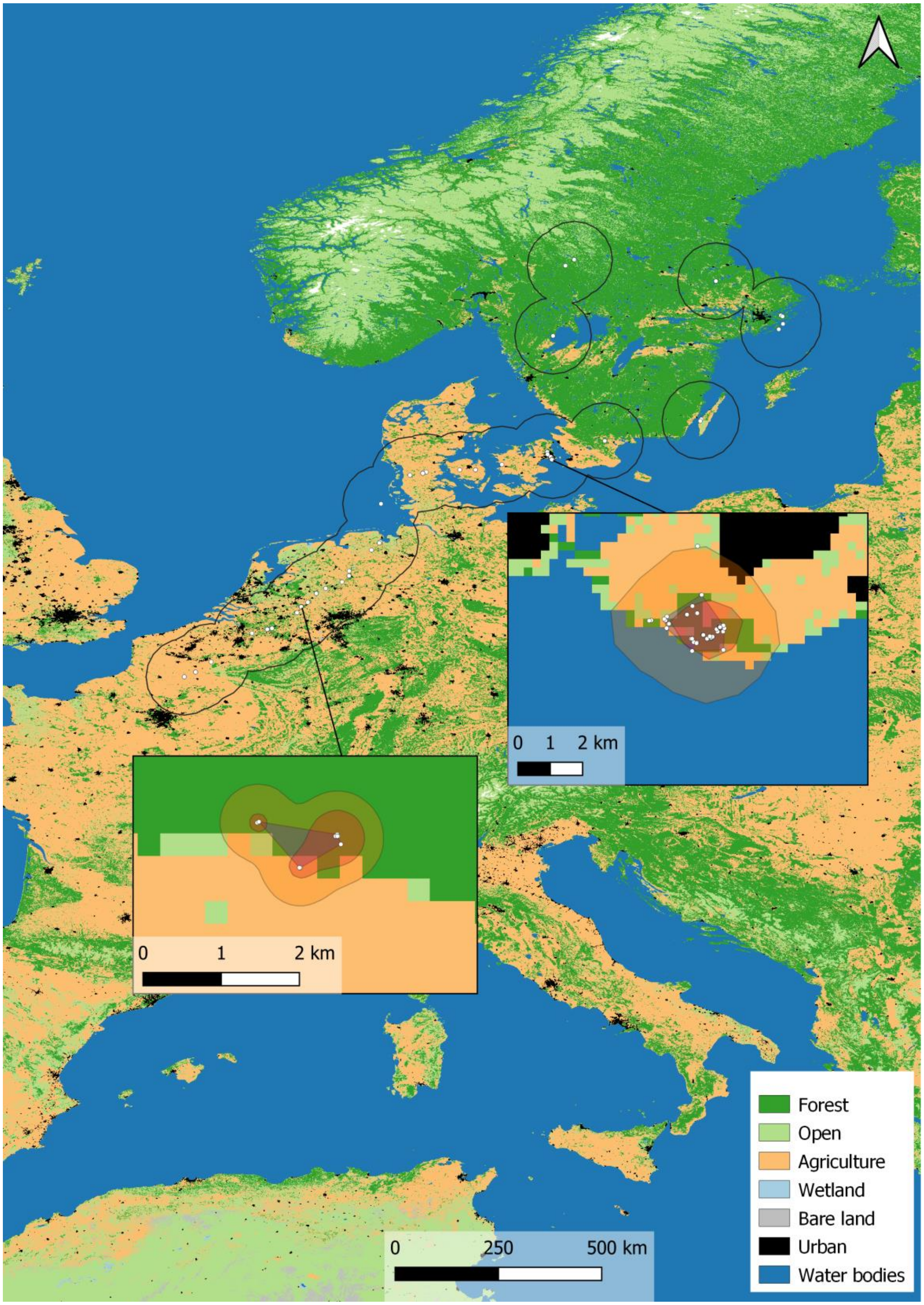
Map 66: Southward migration of Mr. Søndre in 2017 (non-breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



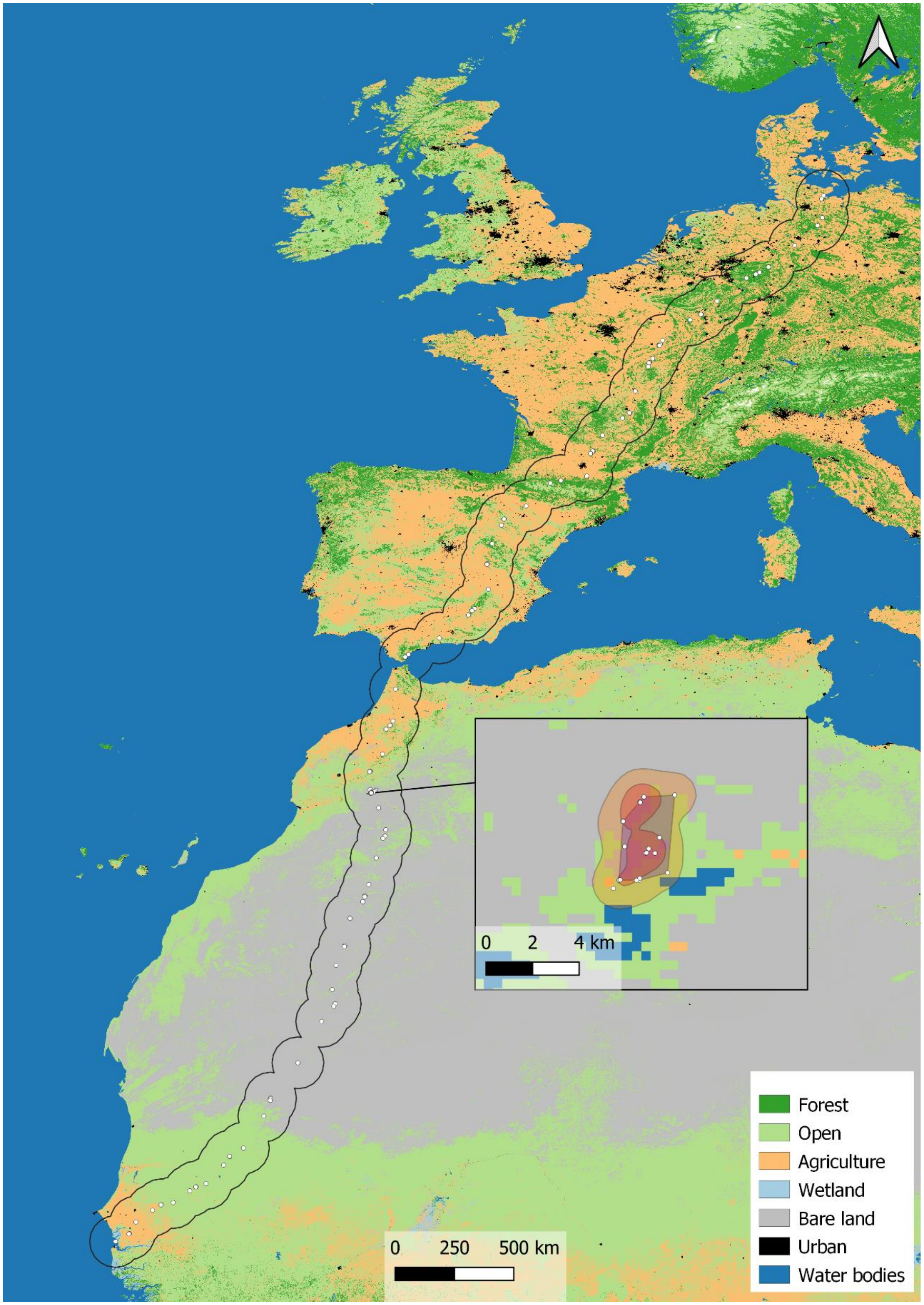
Map 67: Northward migration of Mr. Søndre in 2018, with observed points in white and the buffer. No stopovers were made during this migration.



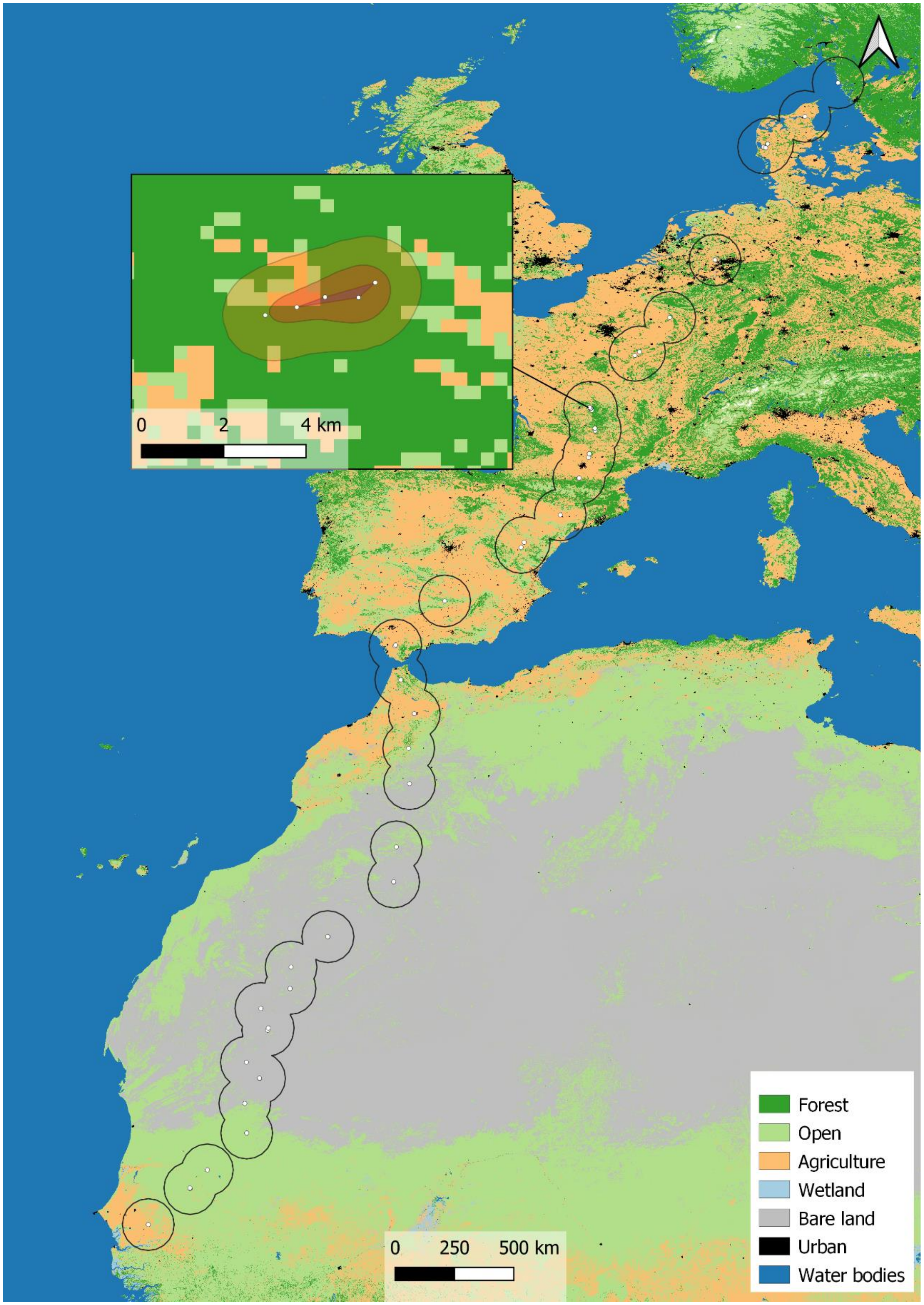
Map 68: Southward migration of Mr. Søndre in 2018 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



Map 69: Southward migration of Huse (juvenile) in 2013, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

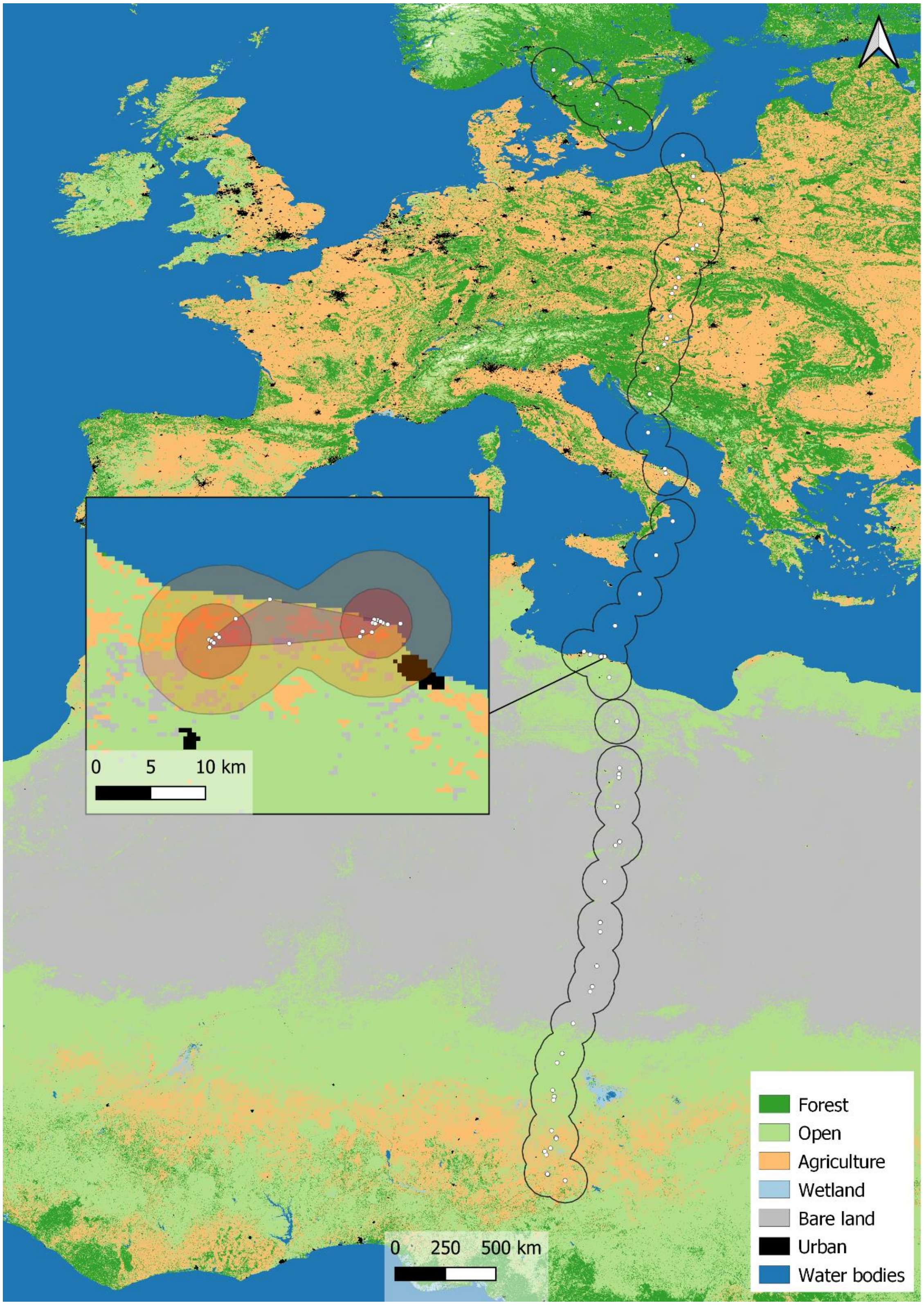


Map 70: Southward migration of Lotta in 2011 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

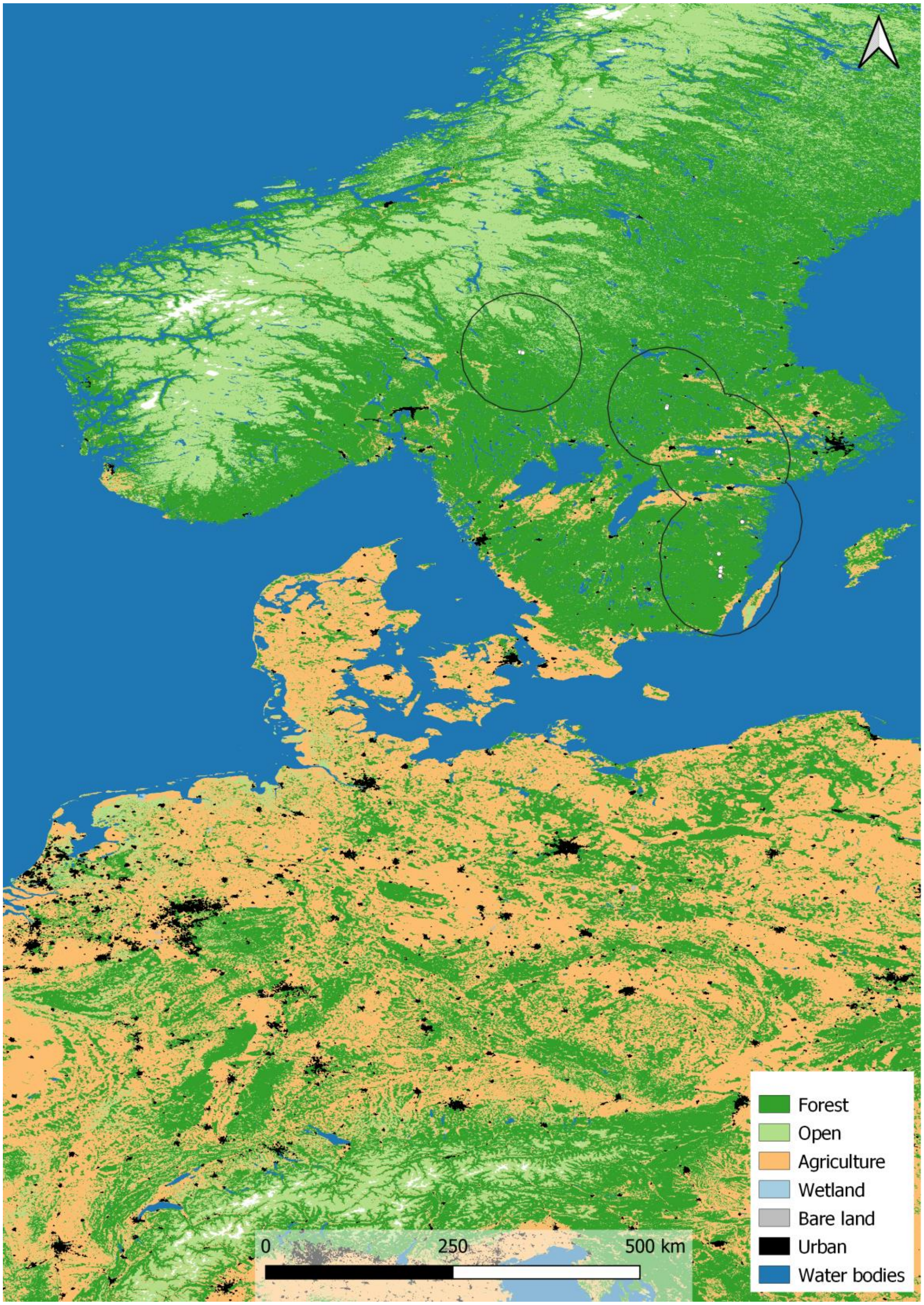


Map 71: Northward migration of Lotta in 2012, with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.

Map 72: Southward migration of Lotta in 2012 (non-breeding year), with observed points in white and the buffer. No stopovers were made during this migration.



Map 73: Southward migration of Mikael in 2011 (breeding year), with buffer. With observed points in white, and stopovers MCP (95%) in blue, kernel core use area (95%) in orange, and kernel core use area (50%) in red.



Map 74: Attempted southward migration of Signe (juvenile) in 2011, with observed points in white and the buffer. No stopovers were made during this migration.

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