

Habitat selection of the raccoon dog (*Nyctereutes procyonoides*) during the breeding season of ground-nesting birds

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The raccoon dog is a highly invasive mammalian predator that threatens the nests of ground-nesting birds in Europe. In Finland, the raccoon dog is a more common nest visitor than any other native or invasive mammal species in the breeding habitats of waterbirds. Studying the habitat selection of the species is important to understand the nest predation risks caused by it. In my thesis, I studied the home ranges and habitat selection of the raccoon dog. My aims were to see if there were differences in the home ranges between three different Finnish landscape types and to investigate whether the spatial and temporal habitat preferences of raccoon dogs cause a particular risk for ground-nesting birds during the critical nesting period.

I used data from 26 GPS-collared raccoon dogs from three regions representing three landscape types: i) southern coastal region, ii) southern inland region and iii) Northern Finland. Both southern regions had seven collared individuals each and the northern region had 12 collared individuals. I estimated the home ranges of raccoon dogs using autocorrelated kernel density estimation (AKDE) and studied habitat selection using infinitely weighed logistic regression based resource selection functions (RSF). I compared home range sizes between the three regions. Habitat selection was studied during the breeding season of ground-nesting birds to get relevant information about the preferences when the risk for birds is highest. To study temporal differences in habitat selection, I compared the breeding season to the non-breeding season.

I found the home ranges to be the largest in Northern Finland. Raccoon dogs showed clear spatial and temporal preferences for wetlands as well as for peatlands. They also preferred the edge areas of agricultural fields, water bodies and forests more than the interior areas. Agricultural field edges were also one of the most used habitats in Northern Finland and in the southern coast. Raccoon dogs did not avoid any habitat in the coastal region. In the southern inland region, wooded peatlands, agricultural fields, built areas and roads were avoided. In Northern Finland, the most avoided habitat was open rock, while the riverbanks were among the most preferred. Raccoon dogs showed increased preferences for wetlands and peatland habitats during the breeding season when compared to the non-breeding season. Yet these habitats were not avoided during the non-breeding season either, they were just preferred less.

These findings support the hypothesis that the habitat preferences of the raccoon dog may influence the predation risk caused to wetland-associated ground-nesting birds. Since raccoon dogs prefer important bird nesting habitats during the breeding season, it increases the risk of encountering nests. The temporal preferences indicate that these habitats are especially preferred by raccoon dogs during the breeding season of birds. I conclude that while raccoon dogs are not specialists of water-associated habitats, they do use them more than expected by chance when available. In other words, the habitat preferences of raccoon dogs may cause a specific risk for ground-nesting birds in wetland and peatland habitats.

Keywords: habitat selection, habitat use, raccoon dog, home range, wetlands

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Supikoira on Euroopan alueella haitallinen vieraslaji, joka uhkaa maassa pesivien lintujen pesiä. Suomessa supikoira on yleisempi vesilintujen pesillä vieraileva nisäkäs kuin mikään muu alkuperäinen tai vierasperäinen nisäkäslaji. Tässä tutkielmassa tutkin supikoirien elinpiirejä ja habitaatin valintaa sekä niiden eroja kolmen suomalaisen maisema-alueen välillä. Tavoitteeni oli selvittää, suosivatko supikoirat juuri linnuille tärkeitä habitaatteja niiden pesimäkaudella.

Tutkielmani aineisto koostuu 26 GPS-pannoitetusta supikoirayksilöstä kolmelta eri alueelta, jotka edustavat kolmea eri maisema-aluetta: i) eteläinen rannikkoalue, ii) eteläinen sisämaa-alue ja iii) Pohjois-Suomi. Eteläisiltä alueilta aineistossa oli seitsemän supikoirayksilöä kummaltakin alueelta ja pohjoisesta 12 yksilöä. Estimoin elinpiirit käyttäen autokorreltoitunutta ydinestimointia (engl. autocorrelated kernel density estimation, AKDE), ja mallinsin habitaatinvalintaa käyttäen menetelmää ”infinitely weighed logistic regression”. Käytin elinpiirejä niiden kokojen vertailuun näiden kolmen maisema-alueen välillä sekä habitaatinvalinnan mallintamiseen. Tutkin habitaatinvalintaa lintujen pesimäkauden aikana ja vertasin sitä pesimäkauden ulkopuoliseen aikaan habitaatin ja kauden interaktiona.

Elinpiirit olivat suurimpia Pohjois-Suomessa. Supikoirat suosivat kosteikkoja ja turvemaita lintujen pesimäkauden aikana. Näitä kosteita habitaatteja suosittiin enemmän pesimäkauden aikana kuin sen ulkopuolella. Samoja habitaatteja suosittiin myös pesimäkauden ulkopuolella, mutta vähemmän kuin pesimäkaudella. Supikoirat suosivat peltojen, vesistöjen ja metsien reuna-alueita enemmän kuin niiden ydinalueita. Peltojen reuna-alueet olivat myös suosituimpia habitaatteja Pohjois-Suomessa ja eteläisellä rannikolla. Rannikkoalueella supikoirat eivät juuri vältäneet mitään habitaattia. Eteläisellä sisämaa-alueella ne välttivät puustoista turvemaata, peltoja, rakennettua aluetta ja teitä. Pohjois-Suomessa supikoirat välttivät eniten kalliomaata ja leveiden jokien avovesialueita, vaikkakin niiden rantoja suosittiin.

Nämä tulokset tukevat hypoteesia, jonka mukaan supikoirat suosivat linnuille tärkeitä pesimäympäristöjä, mikä lisää omalta osaltaan niiden aiheuttamaa pesäsaalistusiskä. Supikoirat siirtyivät myös käyttämään näitä tärkeitä pesimäympäristöjä juuri pesimäkaudella enemmän kuin sen ulkopuolella, mitä saattaa osittain selittää pesien lisäämä houkuttelevuus. Johtopäätöksinä voin todeta, että supikoirat ovat habitaattigeneralisteja, mutta käyttävät kosteita habitaatteja enemmän kuin voisi olettaa sattumalta, jos näitä habitaatteja on supikoirille saatavilla. Toisin sanoen, tutkielmani tulokset tukevat erityisesti kosteikkojen ja turvemaiden suhteen aikaisempia tutkimuksia, jotka ovat esittäneet supikoiran olevan riski maassa pesiville linnuille.

Avainsanat: habitaatinvalinta, habitaatinkäyttö, supikoira, elinpiiri, kosteikot

1 Introduction

1.1 Invasive predators as a threat to biodiversity

Humans influence the environment in many ways. One of them is the introduction of alien species to new locations where they have never been before. Sometimes these alien species become invasive, causing harm to the local populations that have not adapted to these new threats (Bondizio et al. 2019). Predation is one of the most direct ways invasive species can affect native species and invasive predators can have huge impacts on local populations (Doherty et al. 2016). This can be seen, for example, in Australia where invasive mammalian predators, such as feral cats (*Felis catus*) have caused serious harm to native marsupial species (Doherty et al. 2017). According to a recent report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), invasive species are the fifth largest driver of biodiversity loss, and the number of invasive species has increased by 70 % since 1970 in 21 countries where it could be estimated (Bondizio et al. 2019).

Not all alien species are harmful, but generalist predators are more likely to be invasive than specialists, and invasive mammalian predators have the biggest impact on native species (Pitt & Witmer 2007; Hurd 2008; Doherty et al. 2016). According to Doherty et al. (2016), globally 30 invasive mammalian predators have caused negative impacts on 596 threatened and 142 extinct species.

In Finland, there are only two invasive mammalian predators, the American mink (*Neovison vison*) and the common raccoon dog (*Nyctereutes procyonoides*, hereafter raccoon dog). Both are believed to cause harm to native waterbird species (e.g. Holopainen et al. 2020, 2021). According to the 2019 Red List of Finnish Species, alien species are one of the causes for the endangerment of 12 waterbird species and the biggest future threat to three endangered waterbird species (Hyvärinen et al. 2019).

1.2 Raccoon dog as an invasive predator

The most common invasive predator in Finland is the raccoon dog (Selonen et al. 2022). The raccoon dog spread to Europe from the Soviet Union where it was introduced from Eastern Asia. To Finland, they spread during the 1950s–60s (Finnish Biodiversity Information Facility 2020). Their European range consists of Eastern Europe, Finland, Germany and Denmark (Kauhala & Saeki 2016). Northern Finland and Sweden are part of their current invasion front.

According to a review conducted by Mulder (2012), the opportunistic diet of raccoon dogs varies by the landscape but consists mainly of plant material, invertebrates and rodents. In wet habitats, amphibians and fishes are noted as important food sources. Other significant food sources, when available, are birds, other small mammals and carrion. Birds eaten by raccoon dogs are mainly very young or were already dead. The raccoon dog is described as a slow and clumsy predator that cannot catch lagomorphs like a red fox (*Vulpes vulpes*, Mulder 2012).

There has been some debate about whether raccoon dogs eat bird eggs or not (e.g. Kauhala & Kowalczyk 2011; Dahl & Åhlén 2018) because this egg-eating behavior is not seen in stomach content analyses, as seen in the review by Mulder (2012). But new nest predation studies have challenged this idea. In their study, Dahl and Åhlén (2018) argue that the way raccoon dogs eat bird eggs does not generally leave visible evidence inside their stomachs or feces which is why bird eggs are likely a more common food source than previously thought. Raccoon dog is also a very common predator of artificial nests in duck breeding habitats (Dahl & Åhlén 2018; Holopainen et al. 2021) which gives support to this suggestion. To understand the role of the raccoon dog as a nest predator, we need to also understand its habitat selection, that is, what type of habitats it prefers to use.

1.3 Habitat selection, habitat use and preferences

Habitat selection, as defined by Johnson (1980), is the process in which animals make choices between habitats. The framework in which this process is studied is most often based on the use and availability of habitats. Johnson (1980) defined habitat usage as the quantity of utilization of the habitat in question during a fixed time period. The trickiest part of studying habitat selection is defining the habitats and their availability, which is scale dependent and most likely varies a lot between species.

Selective behavior produces preferences. When an animal uses a habitat disproportionately to its availability, the use is selective. Habitat preference then reflects the likelihood of a said habitat being used when available on an equal basis with other habitats (Johnson 1980). However, in habitat selection studies preference may as well be defined simply as the use of habitat relative to its availability, which is conditional to the availability of all habitats (Aarts et al. 2008).

Preferences can be shared within the species, but they also may differ between individuals. The selection of habitat may also be heavily influenced by temporal variation in the distribution of

resources (Roever et al. 2012). The factors and mechanisms behind the process of selection are the most difficult to study, and to my knowledge, are not studied that often.

1.4 Methodology in habitat selection studies

Studies of habitat use and selection have been usually based on radio telemetry, such as VHF-technology (radio frequency range 30–300 MHz). GPS tags used in satellite telemetry have become more common only recently when their prices have decreased. Radio telemetry is based on lower radio frequencies that are often received with hand-held devices while satellite telemetry is based on notably higher frequencies that are used in satellite communication.

Radio telemetry has several pitfalls. To locate the tracked individuals, researchers must be on the field following them, which is time-consuming and problematic when following several individuals at the same time. Because of this, usually only one “focal animal” is followed at a time. Researchers might also influence the behavior of individuals while following them (Cagnacci et al. 2010). In radio telemetry, the probability of detecting location is also dependent on the observation effort of the researcher, which varies in time and space. Hence, the detection probability is not the same for every location unlike in satellite telemetry where observation effort is spatially and temporally constant. The biggest strengths of satellite telemetry are related to the ability to follow several individuals at the same time and the detection probability being independent of researchers. Most advanced GPS systems also let researchers to choose the temporal resolution of fixes (i.e. locations) and change it through the internet. Satellite telemetry enables collecting bigger sample sizes which is a huge benefit in spatial ecology.

Methods used in estimating home ranges and habitat selection have also taken big steps forward since the early 2000s. Previous home range estimation methods (e.g. kernel density estimation, minimum convex polygon) have failed to acknowledge the inevitable autocorrelation that comes with tracking successive movements. But now home ranges can also be estimated with autocorrelated kernel density estimation (AKDE) that takes autocorrelation into consideration (Fleming et al. 2015). In habitat selection studies there has been a shift from compositional analysis to resource selection functions (RSFs) that are usually done with logistic regression. The use of logistic regression in modeling habitat selection has also been criticized, which is why the method has been developed further by adding weights and defining the habitat availability with a heftier amount of sampling points (Fieberg et al. 2021). Habitat availability in logistic regression based RSFs is defined by

sampling randomized points. The distribution of these random points is then compared to the true GPS fixes. Results of logistic regression are often interpreted and visualized with odds ratios derived from the model's coefficients.

Resource selection functions can be any functions that are proportional to the probability of some habitat or resource unit being used (Manly et al. 2002). RSFs based on logistic regression are the most common, but also linear discriminant analysis (LDA) and log-linear models can be seen in the literature (Manly et al. 2002). Another family of function series seen in the literature are resource selection probability functions (RSPFs), which produce probability values. These function series are related in the sense that RSFs can be calculated from RSPFs by multiplying them with an arbitrary constant. In his article, McDonald (2013) argues that RSFs are more intuitive and useful than RSPFs and that they fit better with use-available -data (data where availability has been estimated with random points). Step-selection functions (SSFs) are functions derived from RSFs. They are an alternative way to study habitat selection without home range estimation and are used especially on dispersing or migrating individuals that have clear steps and linear movement.

1.5 Aims of the study

In this study, I will use GPS-tracked raccoon dog data and model it using an autocorrelated kernel density estimation to see whether there are any differences in the home range sizes between three different Finnish landscape types. I will then use logistic regression based RSFs to investigate whether raccoon dogs have any habitat preferences during the breeding season of ground-nesting birds. To further assess the risk to birds, I will study temporal preferences of habitats between the breeding season and the non-breeding season.

By using different landscapes with different habitat compositions, I can assess whether the habitat preferences remain constant or change when the availability of habitats change. These landscapes also represent the different breeding habitats of different ground-nesting bird species in areas where raccoon dogs may be a threat to them.

I predict the home range sizes to be larger in the northern region and smaller in the southern regions. In the case that raccoon dogs are a particular risk for waterbirds, I predict i) them to show preferences for wetlands, banks and shorelines, and ii) habitat preferences for aforementioned habitats to be stronger during the breeding season than the non-breeding season.

2 Material and methods

2.1 Study regions

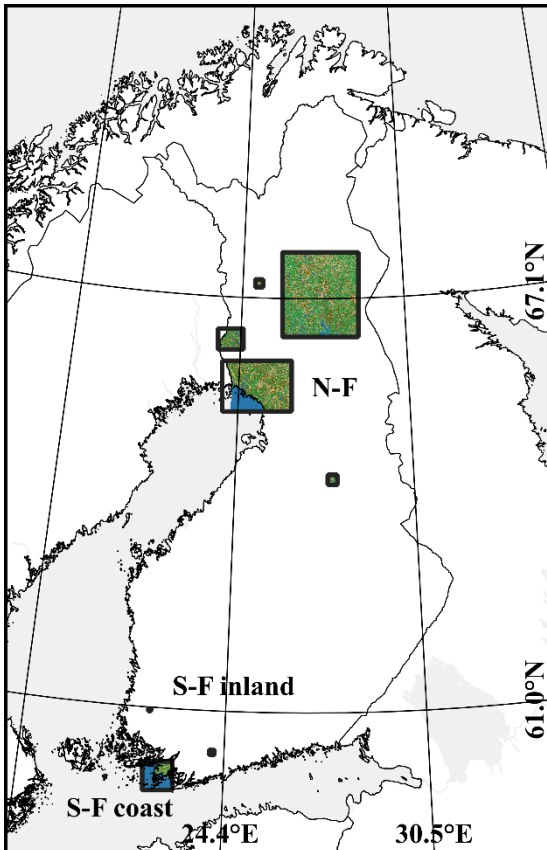


Figure 1. The three study regions and the areas representing them. Study regions are marked with text (N-F, S-F inland, S-F coast). N-F has five areas, S-F inland two areas and S-F coast has one area. Areas vary in size depending on the number of raccoon dogs in the area and their home range size. CRS: ETRS-TM35FIN (EPSG:3067)

This study has three different study regions representing three different landscape types (Fig. 1). One study region is in the coastal area in Southwestern Finland (S-F coast) around Kemiönsaari. The second region consists of one study area in the municipality of Lohja and another in the Saarenmäki in the municipality of Eura, representing inland regions of Southern Finland (S-F inland). The third study region is the largest of them all and contains different areas of Northern Finland (N-F) representing mainly inland regions of Northern Finland.

These study areas were selected mainly because of the availability of raccoon dog data in these regions. The size of the study area is defined by the number of raccoon dogs and the size of their estimated home ranges. The size of the study area does not influence the results because only the habitat data inside the home ranges were used.

2.2 Satellite tracking

Raccoon dogs were tracked with GPS collars from two different manufacturers (Followit and Arctic-iot). Both collars (Followit Ultra Light GSM/GPRS and Arctic-iot Naltio) weighed less than 5 % of the weight of the animal (211 g and 102 g, respectively). Data were obtained from two different sources: the Animal Ecology lab at the University of Turku and the Finnish Wildlife Agency. Because the data was already collected, I did not participate in the planning of data collection but instead took the opportunity to work with the data available to me.

The data did not have any precise, uniform tracking periods (Table 1). The data is influenced by the deaths of the raccoon dogs and the purpose of the tracking, which in the tracking by Finnish Wildlife Agency was to find out their nesting sites to remove the individual and their partner. The raccoon dogs followed by our research group in the southern inland region were tracked mainly from March to May in 2021 and 2022 for research purposes. However, also in this region, there was extensive hunting of raccoon dogs (with the exception that it had been agreed with local hunters that the tracked individuals were aimed not to be killed). All the raccoon dogs were set to be followed mainly during nighttime, but also daytime locations were taken to locate the nesting sites of the individuals. However, daytime locations were least likely to return coordinates, probably due to poor connection inside underground nests. The mean tracking interval was 3.5 hours in Southern Finland's inland region, 6.9 hours in Southern Finland's coastal region and 8.4 hours in Northern Finland. AKDE takes tracking intervals into consideration, but these differences between regions might have some effect on size differences because shorter intervals produce more locations closer together.

I only used data from raccoon dogs that were followed during the months of April, March, May, June or July. Data were filtered by the number of satellites used, with four or more satellites being acceptable. The estimated error given by the most inaccurate collars was around 20 meters, which is partly covered by the resolution of the habitat rasters. Some of the tracked individuals were partners and because partners move together and use the habitat in a very similar manner, only the partner with the most fixes was used to avoid pseudoreplication. After filtering, I had 16918 locations from 26 individuals (14 males, 12 females) that I used in the analysis (see Table 1).

To compare the habitat selection between the breeding season and the non-breeding season, I divided the locations into two seasonal categories. One included the locations from the breeding season (S-F: April-July, N-F: May-July) and the other included the remaining locations (S-F: August-March, N-F: August-April). I decided on these periods because they match the breeding season of most ground-nesting birds (Aleksi Lehikoinen, personal communications, 25.9.2022). For temporal preference models, I only used the individuals that had locations in both seasonal categories.

Table 1. Basic information about the raccoon dogs used in the study. Animal ID is the unique ID assigned to the individual. Sex is the sex assigned to the individual. The region is the study region where the individual was tracked (S-F coast = Southern Finland coastal region, S-F inland = Southern Finland inland region and N-F = Northern Finland). The tracking start date is the date of the first GPS fix and the tracking end date is the date of the last GPS fix. Number of fixes is the number of GPS fixes from the individual used in the analyses. In parentheses is the number of fixes during the breeding season of ground-nesting birds (dd.mm.yyyy – dd.mm.yyyy). Partner removals is the number of partners that were removed from the individual.

Animal ID	Sex	Region	Tracking start date	Tracking end date	Number of fixes (breeding season)	Partner removals
103	Male	S-F coast	28.9.2020	15.7.2021	832 (375)	2
105	Male	S-F coast	12.2.2020	12.11.2021	1010 (376)	1
107	Male	S-F coast	29.10.2020	30.12.2021	1184 (445)	3
108	Female	S-F coast	14.2.2020	19.8.2020	701 (444)	0
109	Female	S-F coast	30.8.2019	28.5.2020	918 (163)	0
110	Male	S-F coast	9.1.2021	7.10.2021	1370 (576)	1
111	Male	S-F coast	5.4.2022	15.7.2022	355 (355)	1
202	Female	S-F inland	13.3.2022	12.4.2022	283 (94)	0
203	Female	S-F inland	14.1.2022	14.4.2022	348 (156)	0
205	Female	S-F inland	20.2.2022	28.6.2022	615 (587)	0
206	Female	S-F inland	17.3.2022	28.6.2022	989 (913)	0
207	Female	S-F inland	19.3.2021	9.6.2021	438 (411)	0
208	Male	S-F inland	12.3.2021	18.5.2021	173 (137)	0
211	Female	S-F inland	29.4.2021	13.6.2021	447 (447)	0
301	Female	N-F	24.5.2017	12.10.2017	438 (247)	NA
302	Male	N-F	30.6.2017	6.11.2017	610 (119)	NA
303	Female	N-F	23.5.2017	8.11.2017	562 (195)	NA
304	Male	N-F	27.10.2017	7.8.2018	853 (464)	1
306	Male	N-F	28.9.2017	21.8.2019	2134 (636)	2
307	Female	N-F	12.5.2019	7.10.2019	537 (297)	0
308	Male	N-F	20.5.2020	14.9.2020	398 (237)	0
309	Male	N-F	20.2.2020	4.8.2020	111 (111)	1
310	Female	N-F	4.6.2021	15.10.2021	506 (219)	1
311	Male	N-F	18.6.2021	16.10.2021	463 (168)	0
312	Male	N-F	14.12.2021	16.8.2022	392 (281)	0
313	Male	N-F	5.10.2021	13.8.2022	251 (251)	1

2.3 Habitat classification

To define habitat classes for habitat selection analysis, I created habitat rasters combining several public environmental datasets. This was done using both QGIS (v. 3.16.16) and the raster package's (v. 3.6-3, Hijmans 2022) merging and focal-window tools in R (R Core Team 2022). When creating habitat rasters for the raccoon dogs, I treated them as groups. These groups consisted of raccoon dogs from the same area with the same tracking year. This was necessary because the landscape in some areas changed heavily between the tracking years because of intensive logging activity.

The datasets used were the Topographic Database produced by the National Land Survey of Finland (NLS, downloaded 7/2022), 2017 and 2019 MS-NFI canopy cover and land class datasets produced by Natural Resources Institute Finland (Luke), land use declarations produced by Forest Centre, and Land Cover on Wetlands 2017 and Corine Landcover 2018 both produced by Finnish Environment Institute (SYKE). Satellite images produced by the ESA Sentinel-2 MSI satellite and orthophotos from 2021 produced by NLS were used as supporting datasets for confirming habitat classification. For the satellite images, I chose a sensing period that matched the midway of the tracking period of each raccoon dog group. Small rivers and streams were digitized by hand using these supporting datasets, and bigger ones in Northern Finland were obtained from the Topographic Database. To include forestry-caused open forest areas in Southern Finland, I digitized all the regenerative logging events for each home range in each raccoon dog group using the land use declaration dataset. To achieve this, I confirmed each logging event, most being clearcuts, manually using mentioned supporting datasets, and did some fixes when needed. In Northern Finland, I couldn't confirm logging events because no satellite data or orthophotos were available for all the years and areas, so open forest areas were classified by the canopy cover given by the MS-NFI 2017 and 2019 datasets, with less than 35 % being classified as open. This was done in the coastal region as well in addition to confirming logging events because coastal landscapes have lots of naturally open forest areas which would not show in any other dataset.

Finally, I defined two-pixel-wide edges (16 meters straight to both sides of the edge) for agricultural fields and forest patches, and water bodies using a method described by Metzger and Muller (1996). For this method, I used a cross-shaped 3x3 focal window and produced the final versions of habitat rasters for each area and year. I only used the aforementioned edge classes because they were deemed relevant and producing edges for all of the habitat classes would produce too many habitat classes and therefore risk skewing the results. As an outcome, the final rasters consist of 13-14 habitat classes (Table 2) and their final resolution is 16x16 meters.

To compare the habitat selection during the breeding season and the non-breeding season of ground-nesting birds (temporal analysis), I made simpler habitat rasters. I removed the classes representing forest edges and open forest areas because these classes may change between years and even months. One individual may visit one area that was a mature forest during the breeding season but clear-cut during the non-breeding season. In this case, both visits would have been registered as mature forests. Forest edges were also removed from the temporal analysis because the open forest areas produced a big part of them. These pixels were replaced by either forest pixels or other land-class pixels that the edges originally overlaid. In the end, I was mainly interested in the temporal preferences of wetland and peatland habitats. Simpler rasters served this goal well enough and reduced the amount of work needed.

Table 2. Values and legends for the habitat classes used. Class value is the raster value assigned to each habitat class. The habitat column includes the English names of the habitats. The last three columns include the proportions calculated from 2022 habitat rasters for each of the three regions. The proportion of class 16 (open forest area) is underestimated for S-F inland and S-F coast because only loggings done inside the home ranges of animals were considered.

Class value	Habitat	% (S-F inland)	% (S-F coast)	% (N-F)
1	Built area	5.73	1.93	0.76
2	Roads	5.58	0.79	1.04
4	Agricultural fields	20.40	3.20	1.75
5	Field edges	7.19	1.52	0.69
8	Forests	37.75	11.45	33.95
9	Forest edges	4.20	9.81	13.06
16	Open forest area	2.12	2.64	5.84
32	Lakes and sea	8.85	63.11	10.28
33	Banks and shoreline	1.65	3.42	1.11
64	Wooded peatland	2.07	0.28	14.64
128	Treeless peatland	0.49	0.08	15.61
256	Rivers and streams	1.02	0	0.79
512	Wetlands	2.95	0.64	0.27
1024	Open rock	0	1.14	0.21

2.4 Home ranges

I estimated the home ranges of the raccoon dogs in R using autocorrelated kernel density estimation (AKDE, Fleming et al. 2015) using `ctmm` (v. 0.6.2, Fleming & Calabrese 2022) and related packages. Estimation was done on two utilization levels: 95 % and 50 %, the latter being the estimation for core areas. Utilization levels define which intensity of spatial use the home ranges are estimated on, with 95 % being a standard for general home ranges and 50 % for core areas.

To compare the home range sizes between the regions, I used a linear model with home range size as the dependent response variable and the region as the main independent explanatory variable. I also included the proportion of water-associated habitats inside the home range as an independent variable to see whether they would be negatively correlated. This would be expected if the raccoon dogs focused heavily on these habitats, hence decreasing the size of the home ranges. Water-associated habitats include treeless peatland, banks and shorelines and wetlands. To conform with the assumptions, I removed clear outliers (>15 000 ha) and transformed the area to a logarithmic scale. In addition, I made another linear model to study the effect of partner removals on the size of the home range since they can increase activity and activate partner-seeking behavior. Only the individuals that had data about partner removals were included (see Table 1), and only the partner removals executed during the breeding season were counted. The effect of sex was not tested because earlier studies have shown that raccoon dogs do not have sexually dimorphic differences in how they use their environment (Drygala et al. 2007; Saeki et al. 2007; Melis et al. 2015; Herfindal et al. 2016). Home range sizes were calculated using the *sf* (v. 1.0-7, Pebesma 2018) and related packages. All the analyses were done using R, but habitat proportions were calculated in QGIS.

Finally, Jacobs' index (Jacobs 1974) was calculated to assess the differences in habitat proportions between the home range and the core area. Jacob's index is a common way to compare how different habitats are used in relation to their availability (Monterroso et al. 2011). In this study, the purpose of the index is to offer supporting information for the interpretation of habitat selection results.

2.5 Habitat selection

I studied the habitat selection of raccoon dogs using resource selection functions (RSFs). The parameters were estimated using infinitely weighted logistic regression as described by Fieberg et al. (2021).

I used previously estimated home ranges (95 % utilization level) to assess the availability of habitat classes by simulating random points 35 times the number of fixes inside the individual home ranges. The number of random points was decided by assessing the change in parameter values when increasing the number of random points from five to 100 times the number of fixes as described by Fieberg et al. (2021). Each fix and random point were assigned the value of the habitat class it landed on, and this made up the main independent explanatory variable for the models. I also calculated the distance to the nearest water body, house and agricultural field for each GPS fix and random point. I

did not include the proximity to the nearest agricultural field in the southern coastal region because not every raccoon dog had agricultural fields in their home range and the closest ones were situated across the sea. These variables are hereafter referred to as proximity variables.

To study the habitat selection of raccoon dogs during the breeding season, I made one model for each of the three regions because the landscapes differ in their habitat composition (S-F inland $n = 7$, S-F coast $n = 7$, N-F $n = 12$). The binary response variable had a value of 0 if it was a random point and 1 if it was an actual GPS fix. Independent explanatory variables used were the habitat class and the proximity variables. Models also included raccoon dog identities as a random effect. I compared the models including the proximity variables to simpler alternative models that did not include them or all of them, but they all had higher AIC values than the models with all the variables selected. AIC (Akaike Information Criteria) values are used to compare model fit and prediction error. Lower AIC values are preferred when selecting models.

In addition, I made one more model for each region to study the difference between the bird breeding season and the non-breeding season. These models were done using the data from raccoon dog individuals that were followed during both the breeding season and the non-breeding season (S-F inland $n = 6$, S-F coast $n = 6$, N-F $n = 10$). In these models, the temporal preference was modeled using a binary season variable and its interactions with the habitat classes as explanatory variables.

Finally, I decided to remove the lakes and sea category completely from all of the models, because the raccoon dogs did not use these habitats at all (except short swims between islands), so they were deemed not to be available to them. This decreased the number of random points by 483 to 29 455 post hoc but did not affect the model coefficients in any remarkable way. The number of removed random points was highest in the coastal region where the home ranges included lots of water even though the raccoon dogs did not use those areas of the home ranges.

I created all these models by assigning weights of 5000 to the random points representing availability, as suggested by Fieberg et al. (2021). According to Fieberg et al. (2021), the point of weights is to facilitate the interpretation of the model parameters. All models were implemented with the lme4 (v. 1.1-30, Bates et al. 2015) package and all the calculations were done using R.

Categorical variables in logistic regression require one level to be set as the reference level which is used as a reference for the other levels. I chose the forest class to be the reference level because to raccoon dogs it represents a neutral matrix of the landscape (odds ratio value very close to zero). A neutral matrix means that the raccoon dog doesn't prefer or avoid it. The odds ratios are calculated in reference to this level. When the odds ratio of habitat is over one, that habitat would be used more

likely than the forest matrix if their coverage were equal. Using the neutral matrix as a reference level lets us interpret the odds ratio results as preference and avoidance. Habitats that were selected less than the neutral matrix can be interpreted as habitats that the raccoon dogs avoided, and the habitats that were selected more than the neutral matrix can be interpreted as habitats that were preferred.

3 Results

3.1 Home ranges

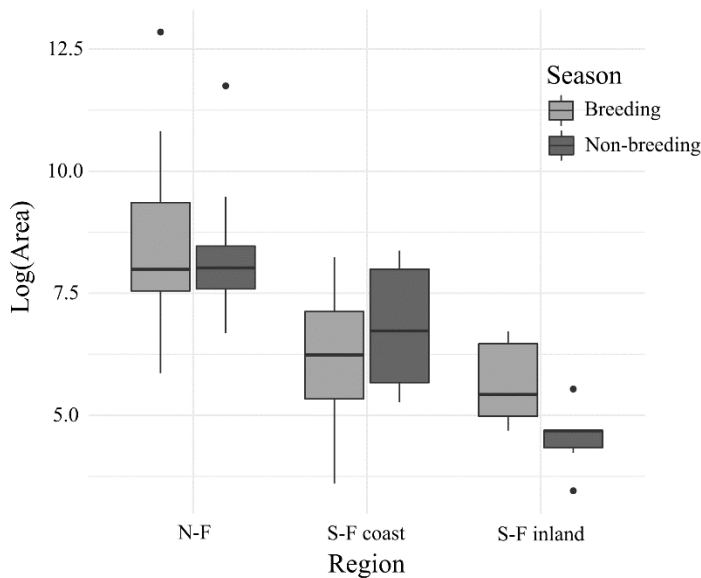


Figure 2. Home range sizes during the breeding and non-breeding season in Northern Finland (N-F), southern Finland coastal region (S-F coast) and southern Finland inland region (S-F inland). Area is transformed into logarithmic scale because the northern home ranges would have dwarfed the southern ones. The breeding season consists of months of April to July in southern Finland and May to July in Northern Finland. The non-breeding season consists of months of August to March in Southern Finland and August to April in Northern Finland. N-F n = 12, S-F coast n = 7, S-F inland n = 7.

Home range sizes were different in the three regions with the smallest ones being in the inland region of Southern Finland and the biggest ones in Northern Finland (Fig. 2, Table 4). Home range sizes were approximately the same between the breeding and the non-breeding season of ground-nesting birds in all the regions. An exception to this is the inland region, but it is very likely explained by the low amount of GPS fixes during the non-breeding season.

The mean home range sizes (95% utilization level) during the breeding season can be seen in Table 3. Without the clear outliers, the mean home range size in

Northern Finland during the breeding season would be 4349 ± 4316 ha (n = 10) and still larger than in Southern Finland.

Table 3. Home range sizes during the breeding season of ground-nesting birds (April to July). The proportion of water-associated habitat includes banks and shorelines, treeless peatlands and wetlands. Outliers increase the mean size of home ranges in Northern Finland.

Region	Mean \pm SD (ha)	n	Water-associated habitat \pm SD (%)
S-F inland	396.45 \pm 313.87	7	12.05 \pm 11.64
S-F coast	1098 \pm 1394	7	9.69 \pm 6.31
N-F	39 510 \pm 108 309	12	12.38 \pm 6.91

Table 4. Model estimates for the comparison of home ranges sizes between regions. WAH means the proportion of water-associated habitats inside the home range. Water-associated habitats include banks and shorelines, treeless peatlands and wetlands. Intercept includes the home range size of Northern Finland. Intercept includes the N-F region. Outliers were removed from the data before fitting the models. N-F n = 10, S-F coast n = 7, S-F inland n = 7.

	Estimate	SE	t-value	Adj. R ²	P
(Intercept)	8.458	0.487	17.368	0.444	<0.001
WAH (%)	-5.049	3.070	-1.644		0.115
S-F coast	-1.825	0.564	-3.237		0.004
S-F inland	-2.174	0.565	-3.850		0.001

The habitat composition of home ranges is presented in Fig. 3. Common habitats of the landscape were the most abundant in the home ranges, reflecting a generalist use of landscape (Fig. 3).

Partner removals did not have a significant effect on the home range size (DF = 21, t = 1.93, p = 0.07).

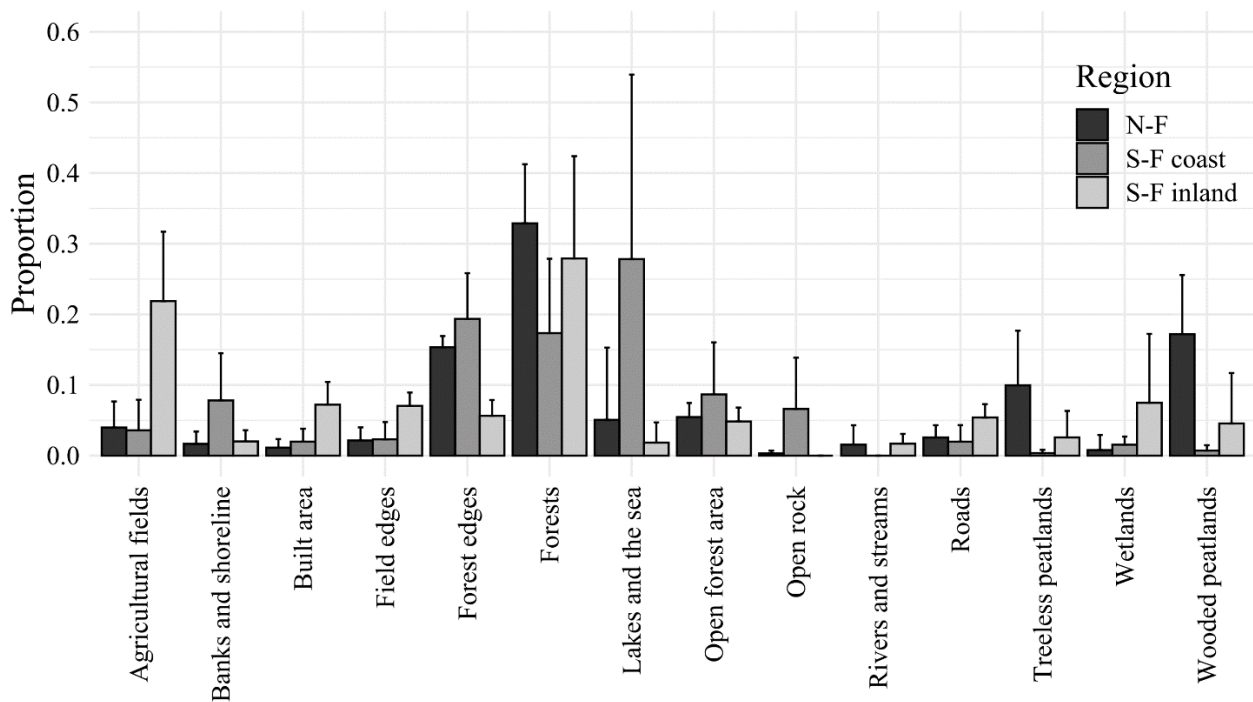


Figure 3. Composition of different habitats on home ranges (95 % utilization level). The bars denote the mean proportion and the whiskers the standard deviation.

The mean core areas (50% utilization level) during the breeding season can be seen in Table 5. Core areas were on average 21 % of the size of the home ranges. The proportion of water-associated habitats did not differ between the home ranges and core areas (Table 3, 4, 5). According to Jacob's index, there were fewer lakes and sea in the core areas than in the whole home ranges (Fig. 4). Other

results varied between regions with treeless peatlands and wetlands having the highest relative abundance in the core areas in Southern Finland.

Table 5. Core area sizes during the breeding season of ground-nesting birds (April to July in Southern Finland and May to July in Northern Finland). The proportion of water-associated habitat includes banks and shorelines, treeless peatlands and wetlands. Outliers (see text) increase the mean size and variation of home ranges in Northern Finland.

Region	Mean \pm SD (ha)	n	Water-associated habitat \pm SD (%)
S-F inland	73.53 \pm 63.29	7	25.25 \pm 38.72
S-F coast	256.58 \pm 316.97	7	9.30 \pm 5.01
N-F	9436 \pm 26900	12	11.64 \pm 7.56

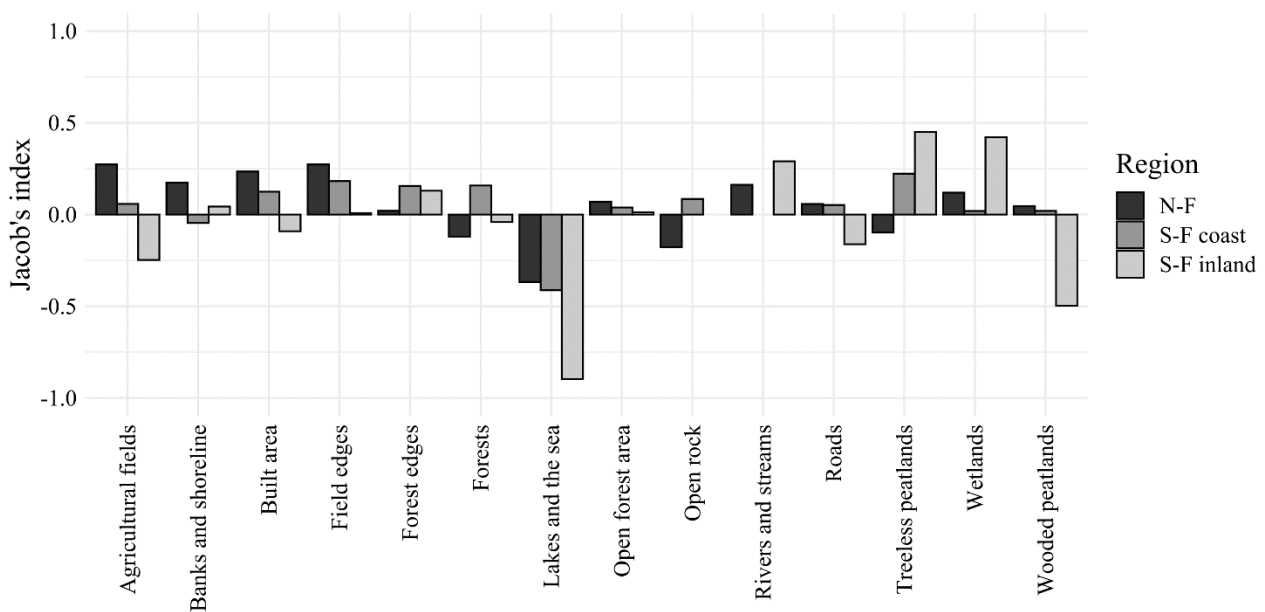


Figure 4. Jacob's selection index. Habitat proportions of the core area are compared to the proportions of the whole home range. Index values above zero mean that the habitat is proportionally more abundant in the core area than the whole home range. Values below zero mean that those habitats are proportionally less abundant in the core area than the whole home range. The index is calculated from the habitat proportion averages. Habitats are on the horizontal axis.

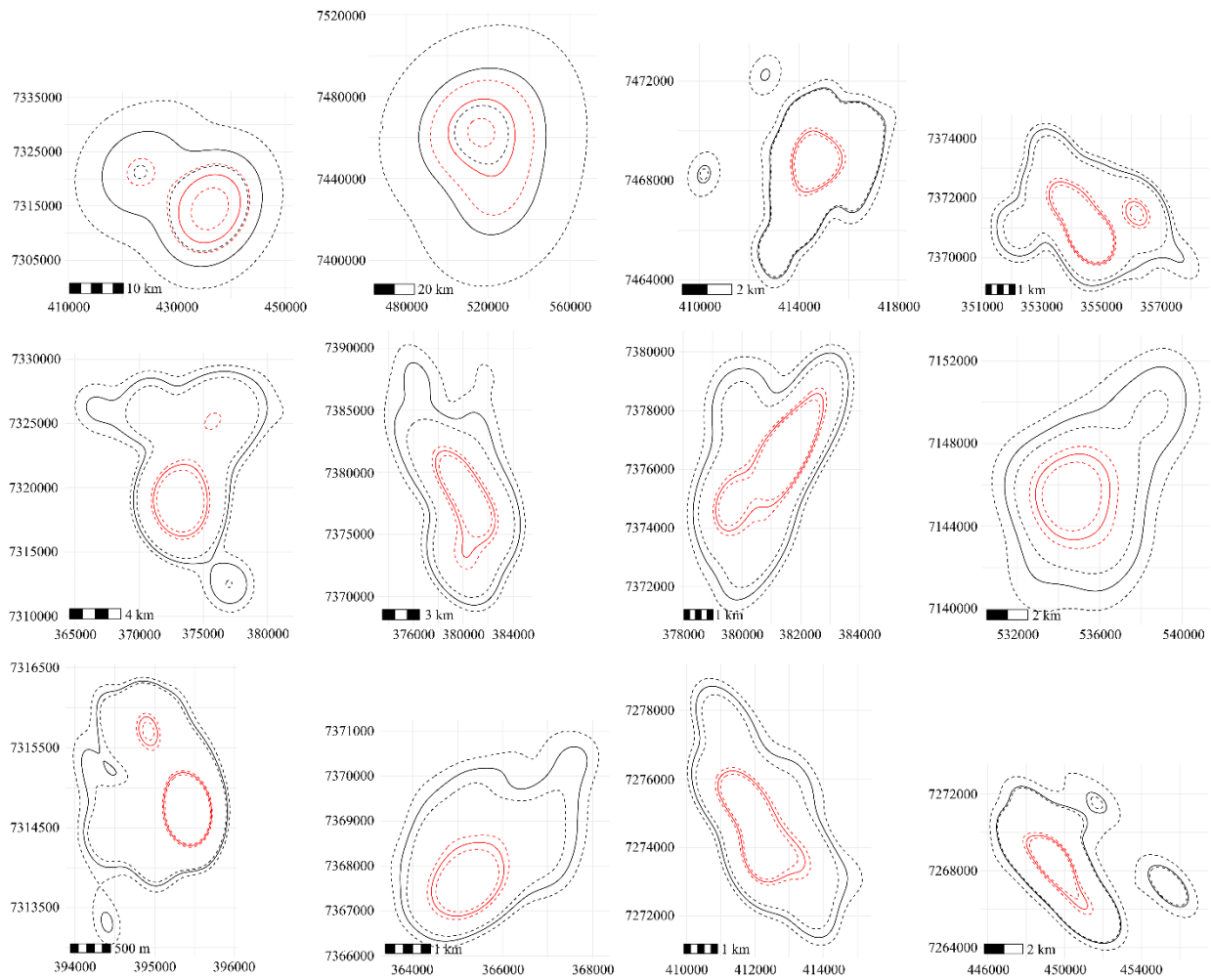
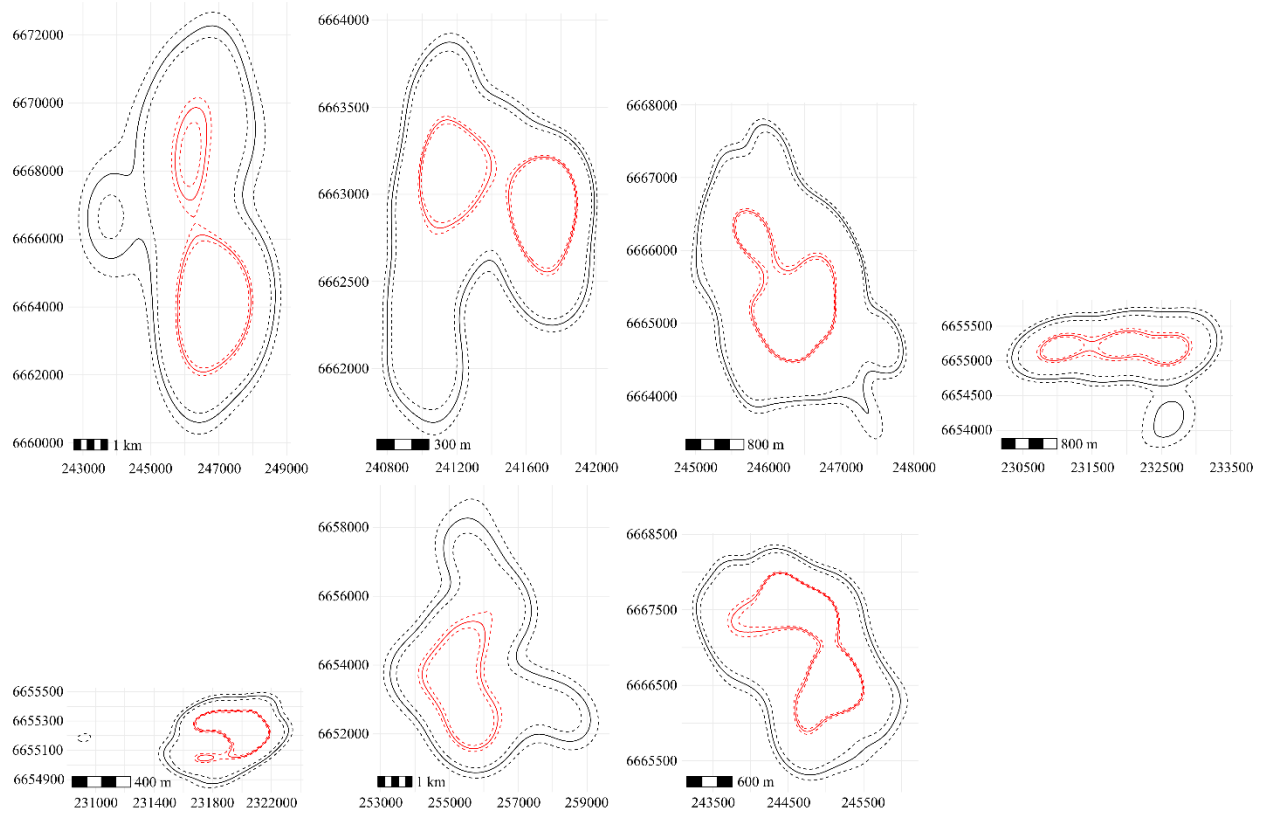


Figure 5. Home ranges (95 % utilization level, black) and their core areas (50 % utilization level, red/lighter color) of different individuals in Northern Finland during the breeding season (May to July). Dashed lines represent 95% confidence intervals. N-coordinates are on the vertical axis and E-coordinates are on the horizontal axis. Note that the panels have different axes. The first two home ranges from the top left were considered outliers because of their enormous size and circular shape that fitted GPS fixes loosely. CRS: ETRS-TM35FIN (EPSG:3067)

S-F coast



S-F inland

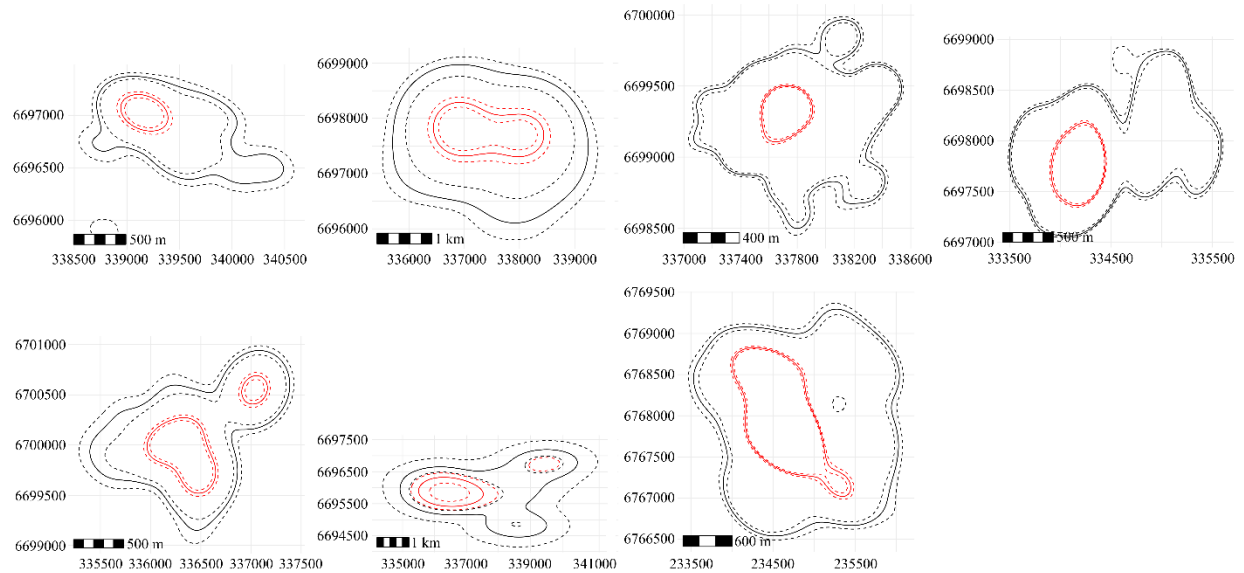


Figure 6. Home ranges (95 % utilization level, black) and their core areas (50 % utilization level, red/lighter color) in the southern coastal region (S-F coast, upper) and the southern inland region (S-F inland, lower) during the breeding season (April to July). Dashed lines represent 95% confidence intervals. N-coordinates are on the vertical axis and E-coordinates are on the horizontal axis. Note that the panels have different axes. CRS: ETRS-TM35FIN (EPSG:3067).

3.2 Habitat use

GPS tracking data reflected the generalist nature of the raccoon dog. Habitats that were used the most were mostly the dominant habitats in those regions. In all regions, forests and forest edges were the most used habitats (Fig. 7). These habitats together contained almost half of the GPS fixes. Regionally, wooded peatlands were the second most used habitat in the northern region, open forest areas were the third most used habitat in the southern coastal region, and treeless peatlands were the second most used habitat in the southern inland region. Wetlands were used the most in the southern inland region where they also were the third most used habitat (Fig. 7).

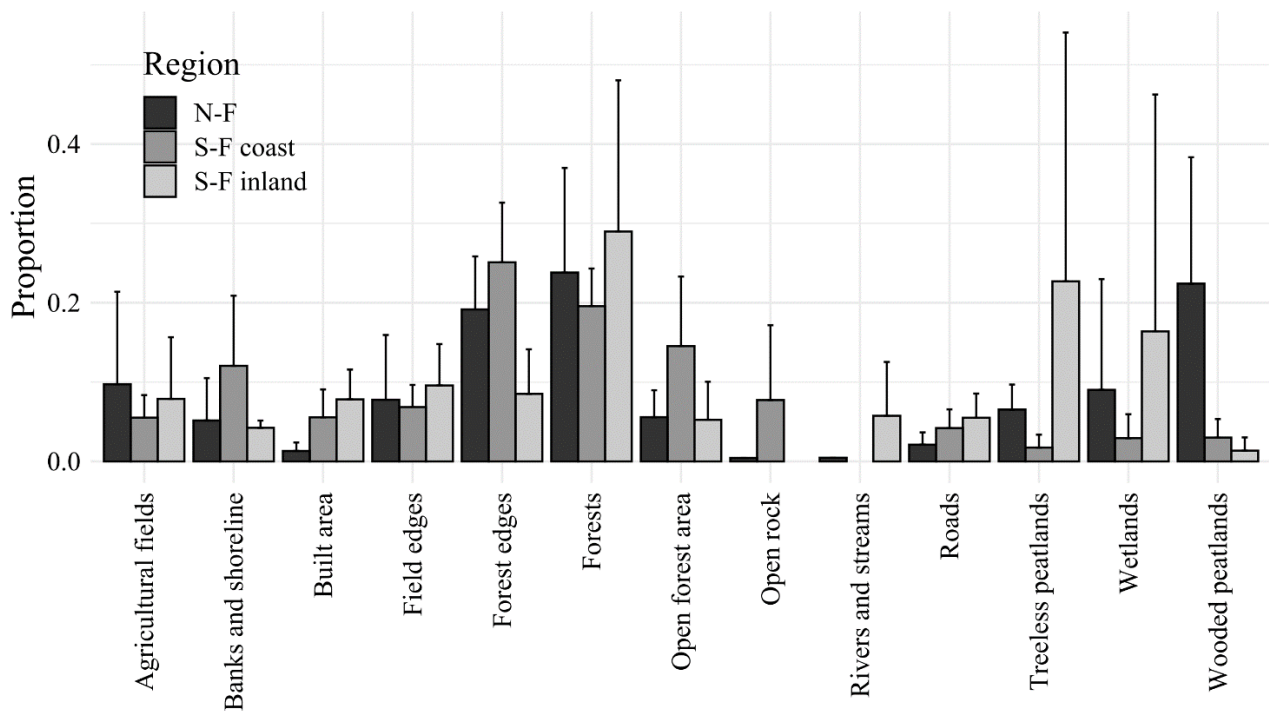


Figure 7. Mean (+SD) proportion of GPS fixes in each habitat by region. The graph illustrates the habitat use of the raccoon dog. Habitats are on the horizontal axis.

There were no clear habitats standing out uniformly as the least used habitat, but open rock and rivers were clearly the least used habitats in Northern Finland (Fig. 7) and wooded peatlands were clearly avoided by individuals in the southern inland region (Fig. 7).

A comparison of the distance of GPS fixes to the closest water body shows that there are no differences between the breeding season and the non-breeding season (Table 6).

Table 6. Mean distance from GPS fixes to closest water bodies during and outside the breeding season of ground-nesting birds. There is no difference between the seasons. The region is the region from which the GPS fixes are part of. Season lengths are defined in the methods section.

Region	Breeding season		Non-breeding season	
	Mean (m)	SD (m)	Mean (m)	SD (m)
S-F inland	727.40	429.48	605.45	351.37
S-F coast	295.06	321.33	331.06	321.11
N-F	990.46	783.54	1067.28	817.34

3.3 Habitat selection

Raccoon dogs showed clear preferences for wetlands in all three regions and for treeless peatlands, field edges and wooded peatlands in two of the regions. There was no clear universal avoidance of any other habitat than open rock areas (Fig. 8, Table 7), which were only present in Northern Finland and the southern coastal region. Wooded peatlands, agricultural fields, built area and roads were avoided by the individuals in the southern inland region while treeless peatlands, wetlands, forest edges, open forest areas, and rivers and streams were preferred (Fig. 8). Individuals in the southern coastal region did not show avoidance of any habitat but open rock, and showed the greatest preference for field edges, peatlands and wetlands. Individuals in the northern region preferred wetlands, field edges and banks and shorelines the most, and strongly avoided rivers and streams (Fig. 8). It is important to note that in the northern region, a big part of the banks and shoreline class was riverbanks, so the raccoon dogs avoided open water of the rivers but strongly preferred their banks.

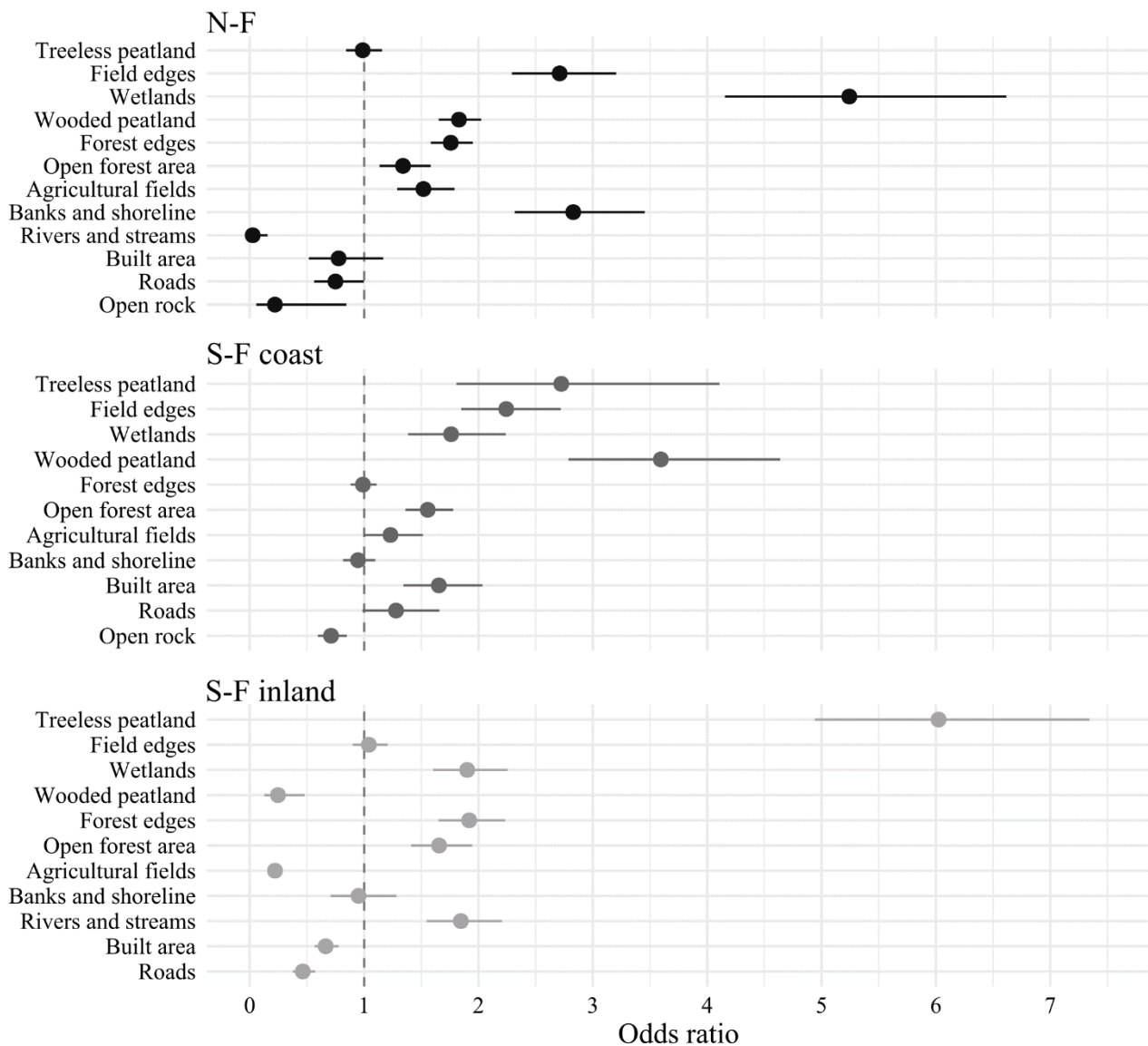


Figure 8. Habitat preferences in the three different regions. The use of every habitat is compared to the forest class, which is used by raccoon dogs with no preference in any direction. Odds ratios close to zero indicate dispreference in proportion to that value (when compared to the use of forests). Odds ratios greater than one are preferred by the raccoon dogs in that region. Lines indicate 95 % confidence intervals. N-F n = 12, S-F coast n = 7, S-F inland n = 7.

Regarding the selection of habitat edges, raccoon dogs preferred field edges more than interior areas in all three regions, implicating that the use of agricultural fields is mostly focused on the edges (Fig. 8). Preference for banks and shorelines is also much higher than open water areas in all three regions because raccoon dogs avoid open water in their normal, non-migratory habitat use. Open water was removed from the models because of such a high avoidance. Forest edges are preferred more than interior forest areas in the southern inland region and Northern Finland, but not in the southern coastal region (Fig. 8).

Table 7. The results of logistic regression models for the three regions. The variable column includes the habitat classes. Intercept contains the reference level which is the forest class. Asterisks denote the statistical significance of the coefficient. Odds ratios were conducted by exponentiating the coefficients shown in the table.

Variable	S-F inland model	S-F coast model	N-F model
	Estimate (\pm SE)	Estimate (\pm SE)	Estimate (\pm SE)
Intercept	-12.059* (\pm 0.105)	-11.717* (\pm 0.284)	-12.373* (\pm 0.050)
Built area	-0.409* (\pm 0.080)	0.514* (\pm 0.106)	-0.252 (\pm 0.208)
Roads	-0.767* (\pm 0.107)	0.254 (\pm 0.133)	-0.288* (\pm 0.146)
Agricultural fields	-1.509* (\pm 0.082)	0.215* (\pm 0.106)	0.418* (\pm 0.084)
Field edges	0.041 (\pm 0.074)	0.815* (\pm 0.099)	0.997* (\pm 0.086)
Forest edges	0.652* (\pm 0.077)	-0.013* (\pm 0.059)	0.564* (\pm 0.053)
Open forest area	0.505* (\pm 0.081)	0.440* (\pm 0.068)	0.293* (\pm 0.085)
Banks and shoreline	-0.049 (\pm 0.152)	-0.063 (\pm 0.076)	1.040* (\pm 0.102)
Wooded peatland	-1.399* (\pm 0.338)	1.279* (\pm 0.130)	0.604* (\pm 0.052)
Treeless peatland	1.800* (\pm 0.101)	1.002* (\pm 0.210)	-0.012 (\pm 0.081)
Rivers and streams	0.613* (\pm 0.090)		-3.641* (\pm 0.991)
Wetlands	0.643* (\pm 0.087)	0.570* (\pm 0.123)	1.657* (\pm 0.119)
Open rock		-0.353* (\pm 0.090)	-1.511* (\pm 0.708)
Proximity to field	-0.206* (\pm 0.029)		-0.044 (\pm 0.027)
Proximity to water	-0.238* (\pm 0.036)	0.172* (\pm 0.029)	-0.011 (\pm 0.022)
Proximity to house	-0.165* (\pm 0.025)	-0.139* (\pm 0.028)	-0.163* (\pm 0.029)

Proximity to houses is preferred in all three regions, but only slightly. Otherwise, the preference for proximity varies between regions with proximity to water being preferred in the southern inland region while distance is kept in the coastal region abundant in sea area (Fig. 9). Some level of proximity to agricultural fields seems to be preferred in Southern Finland, where fields were abundant but also avoided or neutral habitats. But as said, the selection of fields seems to be more focused on the edges than the interiors.

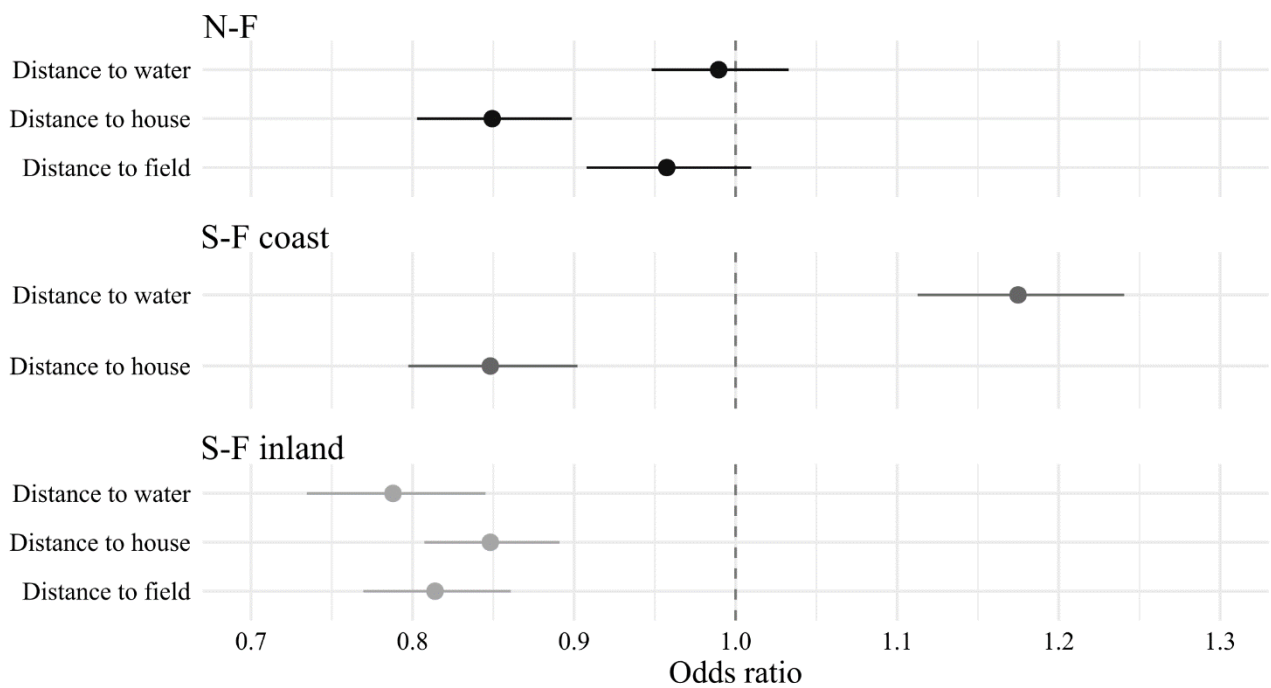


Figure 9. Proximity preferences as odds ratios. Values closer to zero mean preference for proximity and values equal to one (dashed line) mean no preference. Lines indicate 95 % confidence intervals. N-F n = 12, S-F coast n = 7, S-F inland n = 7.

The raccoon dogs preferred wetlands and wooded peatlands more in all three regions during the breeding season than the non-breeding season (Fig. 10). This was also true with treeless peatland in the southern inland region and Northern Finland. Banks and shorelines were preferred less during the breeding season in the southern inland region and Northern Finland, even though they were preferred more in the southern coastal region, where raccoon dogs can cause serious harm to birds nesting on the shorelines. Higher preference during the breeding season can also be seen in agricultural fields and field edges in Northern Finland (Fig. 10).

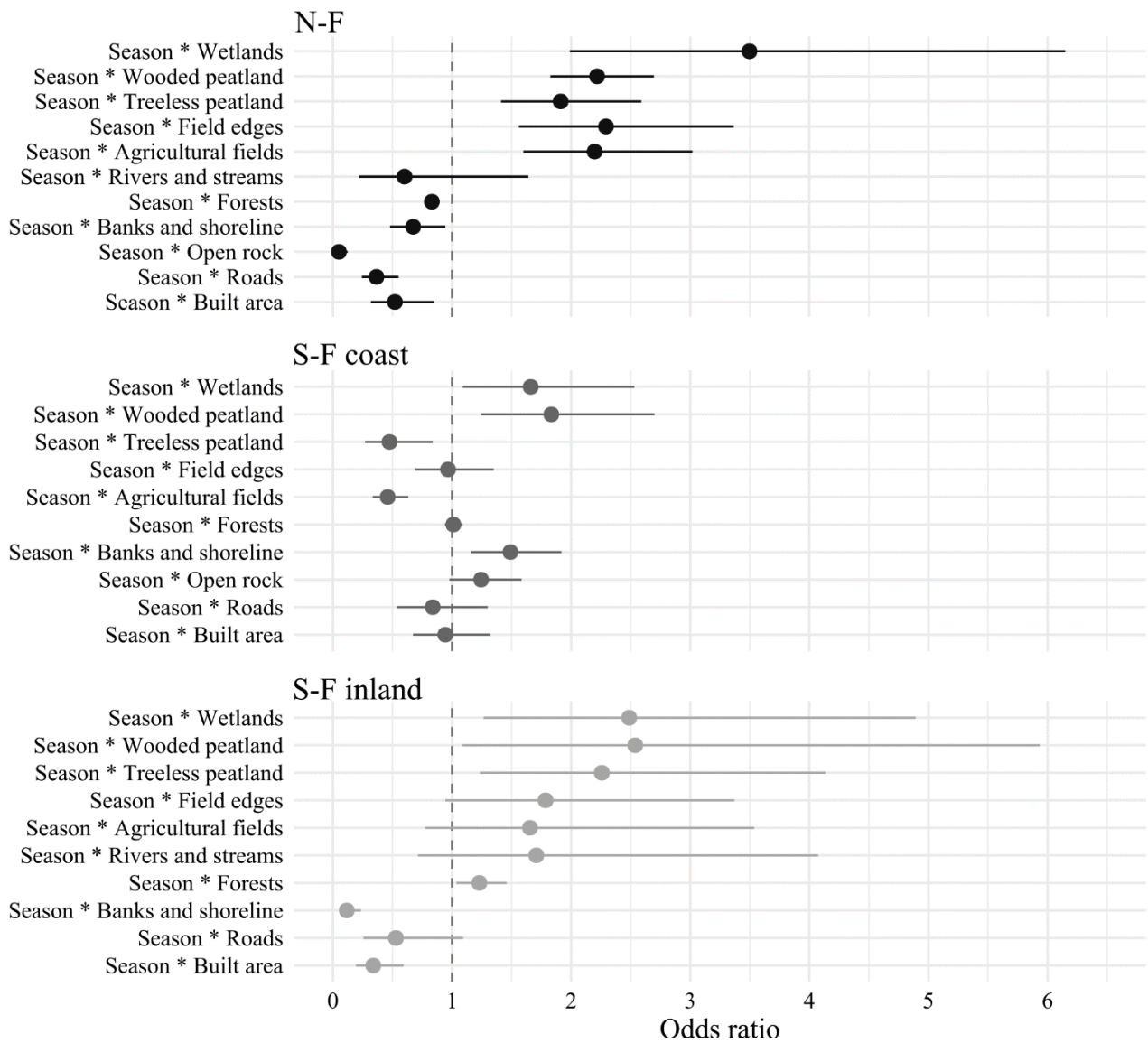


Figure 10. Temporal preferences as odds ratios. Values equal to one mean equal preference during the breeding and non-breeding season. Values above one mean stronger preference during the breeding season and values below one mean stronger preference during the non-breeding season. Lines indicate 95 % confidence intervals. N-F n = 10, S-F coast = 6, S-F inland n = 6.

4 Discussion

I studied the temporal and spatial habitat selection and home range sizes of GPS-collared raccoon dogs in three different landscapes in Finland. Spatial habitat selection was studied within the home ranges of raccoon dogs and temporal selection was studied by comparing the habitat selection during the breeding season and the non-breeding season of ground-nesting birds. I found home range sizes to be larger in Northern Finland than in Southern Finland and raccoon dogs to prefer wet habitats, such as wetlands and peatlands in their habitat selection, particularly during the breeding season of waterbirds. These preferences may cause a specific risk for nesting birds and their eggs as discussed in detail below. The risk is especially concerning in wetlands and coastal areas where waterbirds are abundant and other predation pressure occurs.

4.1 Home ranges

Home ranges were the largest in the northern region of this study. This is in line with a somewhat common pattern seen in other mammal species where the home range size increases with the decrease of productivity associated with, for example, a colder climate and higher latitudes and altitudes (Harestad & Bunnell 1979; Damuth 1981; Dahle & Swenson 2003; Dahle et al. 2006; Rautio et al. 2013). Northern home ranges remained the largest even after excluding the two clear outliers that increased the mean size. These outliers can be explained by the used autocorrelated kernel density estimation (AKDE) which utilizes movement models. It is likely that these two raccoon dogs were not stationary according to the movement models used in the estimation, even though they did not seem to be migratory by eye (migratory individuals were aimed to be omitted from the current analysis).

My results differ from other studies done on raccoon dogs, but so do the estimation methods and other specifications. My results are from the most active period of raccoon dogs, data was collected via GPS tracking and home ranges were estimated using AKDE, which is known to estimate larger home ranges than kernel density estimation (KDE) or minimum convex polygon (MCP) (Fleming et al. 2015). Thus, e.g. earlier home range estimates by Kauhala et al. (2010) and Herfindal et al. (2016) may at some level be underestimated due to the used methods (KDE, MCP). The home ranges have quite big standard deviations both in this study and in earlier studies, indicating high individual variation.

I found the home range sizes (95 % utilization level) to be 396 ± 314 ha in the southern inland region, 1098 ± 1394 ha in the southern coastal region and 4349 ± 4316 ha in Northern Finland. Earlier, Kauhala et al. (1993) estimated the maximum home ranges (using the harmonic mean method) in Southern Finland to be 950 ha and core areas with 85 % utilization level to be 340 ha. The mean home range sizes estimated in a newer study by Kauhala et al. (2010) using kernel density estimation (KDE, 95 % utilization level) were between 90 to 261 ha in Southern Finland. A study done in Northern Sweden reported a mean home range size of 1084 ha estimated with minimum convex polygon (MCP, 95 % utilization level) 50 days after capture and release (Herfindal et al. 2016). A study in north-eastern Germany found the mean home range sizes to be between 239 to 313 ha (Drygala et al. 2007). Another study done in Germany found the mean annual home range size to be 183 ha (Sutor & Schwarz 2013). Both German studies used kernel density estimation. In addition, many of these studies used VHF-based radiotracking instead of satellite tracking (Kauhala et al. 1993, 2010; Drygala et al. 2007; Sutor & Schwarz 2013). These methodological differences cause problems when trying to compare my results with other studies.

In conclusion, the northern home ranges in my study are notably larger than the southern home ranges and any home ranges estimated in other studies. But the southern home ranges of my study are in the same size category as those in Kauhala et al. (1993), Drygala et al. (2007) and Kauhala et al. (2010) (85 % utilization level). My northern home range estimates have only one Northern European study to compare to, which reported remarkably smaller sizes (Herfindal et al. 2016).

4.2 Habitat selection of the raccoon dog

Generalist predators have a versatile way of using habitats and may not exhibit almost any true selection, at least in the scale we humans are used to. Habitat use of generalists is heavily influenced by the mere availability of habitats, and this makes studying their selection hard (Roever et al. 2012). Generalist species are particularly challenging and successful when they become invasive, because of their ability to utilize a wide variety of habitats (Hurd 2008). The raccoon dog is an addition to the generalist predators in Europe feeding on bird eggs and other vulnerable species, such as frogs (Mulder 2012).

To summarize the results of my study, raccoon dogs showed a great spatial preference for wet habitats, such as wetlands and peatlands, with wetlands being consistently preferred in all three regions. They also showed more preference for these wet habitats during the breeding season of

ground-nesting birds than outside the breeding season. In addition, the raccoon dogs selected the edge areas of agricultural fields, water bodies and forests more than the interior areas, with field edges also being one of the most preferred habitats in the southern coastal region and Northern Finland. In Northern Finland, banks and shorelines were strongly preferred by raccoon dogs, mainly because of the use of riverbanks of wide rivers which influence the movement of raccoon dogs.

The definition of some habitat classes may vary between regions. Wooded peatland is a particularly difficult class to classify because of the extensive ditching of peatlands in Finland. Many of the areas classified into this class are peatlands turned into commercial forests. The proportion of wooded peatland, ditched or not, is higher in Northern Finland than in Southern Finland. This might explain the variation in results between the regional models. Another class inhibiting lots of variation between the models is the class of treeless peatlands. This might be because of a high proportion of treeless peatlands in Northern Finland and the fact that in the study sites of the southern inland region treeless peatlands were formed inside lakes as a result of overgrown vegetation. Maybe the preference of habitats is area-dependent, with more common habitats turning into a neutral matrix. This is also called a functional response in habitat selection studies (Myrsterud & Ims 1998). Or maybe this is explained by the different conditions that make these overgrown lake bogs in the southern region more preferable for raccoon dogs than the abundant conventional mires of Northern Finland.

Other studies done on the habitat selection of raccoon dogs show avoidance or the least preference for agricultural fields (Drygala et al. 2007; Kauhala & Auttila 2010; Sutor & Schwarz 2013), standing water and built area (Drygala et al. 2007; Sutor & Schwarz 2013). The use of forests varies, but so do the methods to classify them. Coniferous forests were preferred or neutral in German studies (Drygala et al. 2007; Sutor & Schwarz 2013) while deciduous forests were avoided (Sutor & Schwarz 2013). In Northern and Eastern European studies, coniferous forests were avoided (Kauhala & Auttila 2010; Melis et al. 2015), while mixed forests were preferred (Kauhala & Auttila 2010). Studies that included wetlands and other wet habitats showed a preference for them (Melis et al. 2015; Schwemmer et al. 2021). Most of these studies have been done with an older compositional analysis method (Drygala et al. 2007; Kauhala & Auttila 2010; Sutor & Schwarz 2013) which, in my opinion, measures second-order selection (home range selection inside a landscape) more than third-order selection (individual behavior inside a home range), which is what I am studying. Melis et al. (2015) studied migratory raccoon dogs with different availability sampling method and a much coarser scale than I did, so the results might not be directly comparable, but they are nonetheless in line regarding the strong preference for wetlands and agricultural fields (edges) and avoidance of open natural areas (open rock in my study). Melis et al. (2015) found preferences for both wetlands and proximity to

water, but I did not find a preference for proximity to water in either breeding season or non-breeding season despite preferences found for riverbanks and wetlands which are habitats close to water. This might be explained by the mean available proximity of water bodies since all the study areas had several water bodies in them. Maybe the home ranges did not have much of space where the available distance to the closest water body would be calculated high enough to change the results, and raccoon dogs seemed to stay at the same locations during the breeding season and non-breeding season explaining no seasonal variability.

My study also offers more insight into the selection of agricultural and forest areas by introducing the idea of edge selection by raccoon dogs, an aspect that was previously left out of studies. There are some studies showing the importance of habitat edges to mammalian predators (e.g. Šálek et al. 2010, 2014; Sonerud 2022). These habitat edges and their importance should be studied more with mammalian generalists because they might as well be very important to their foraging and movement patterns.

The biggest source of errors in my study comes from asymmetric data when the number of fixes is not equal or close to equal between the breeding season and the non-breeding season. This is especially true in the southern inland region where the raccoon dogs were followed outside the breeding season for only a very short period. This uncertainty is also recorded in the long confidence intervals in the temporal preference model. As briefly discussed before, the classification of habitats also comes with a fair amount of uncertainty since the datasets are not always up to date and land cover classes can include a set of variation. However, modeling the habitat selection of generalist species does not require as much detail as some specialist species that are dependent on more specific resources inside a habitat.

Overall, the preferences found and methods used in my study differ from other studies. But my results support some of the trends found in other studies, mainly those showing less preference or direct avoidance for built area, water and open natural areas and more preference for wet habitats.

4.3 Implications for potential prey

The findings of this study support the idea that invasive species, in this case the raccoon dog, may cause problems for native species. According to one meta-analysis, alien predators had double the impact of native predators on vertebrate prey (Salo et al. 2007). In the case of the raccoon dog, the

effect may be caused by lowering the breeding success of ground-nesting birds via an increase in nest predation pressure (Dahl & Åhlén 2018; Holopainen et al. 2021).

The preferences found in my study imply potential harm especially to waterbirds, but also to birds nesting in peatland habitats. This finding is quite new since previous studies have not included peatland habitats in habitat selection analyses (e.g. Drygala et al. 2007; Kauhala & Auttila 2010; Melis et al. 2015). But still, the generalist use of habitat is maintained by raccoon dogs, so practically no habitat is left unused. According to nest predation studies, raccoon dogs increase the nest-predation rate of artificial nests on shorelines (Dahl & Åhlén 2018; Holopainen et al. 2020, 2021), forests (70 meters from the shoreline) and wetland habitats (Holopainen et al. 2020, 2021). Raccoon dogs are also the most common mammalian predator of artificial nests in Finland in forests, wetlands and shorelines (Holopainen et al. 2021). While my results do not show a preference for forests, forests were, along with the edges, the most used habitats in all three regions. Edges of forests were used almost as much as forests, but they were also preferred more than forests, indicating their potential importance for this mammalian mesopredator.

Banks and shorelines in addition to wetlands provide links to water habitats usually avoided by raccoon dogs. While raccoon dogs are not a particular risk for adult waterbirds (Mulder 2012) they may also be a threat to nesting females (Öst et al. 2018; Jaatinen et al. 2022), which is why they only need to forage on shorelines and banks. Banks and shorelines are part of the neutral matrix in the southern regions, which means that they do use them, but there is no clear spatial preference for them. There is a temporal preference in the coastal region during the breeding season, meaning that the raccoon dogs start preferring them almost up to two times more likely during the breeding season than outside of it.

While raccoon dogs in Northern Finland do not prefer treeless peatland as much as in southern parts of the country, they do prefer wetlands, which is mainly seen in the coastal region of Northern Finland which is abundant in wetland classified habitat. There are not that much of wetlands in other northern areas. Because of the low availability of wetlands in other home ranges in the northern region, the coastal individual has a disproportionately large impact on the results. When this fact is considered, we can say that, realistically, the most preferred habitats in the northern region are riverbanks and field edges, since the availability of wetlands is poor.

Overall, the most threat is caused where the raccoon dogs spend the most time. While wetlands are preferred habitats, they only make up a small part of the home ranges of raccoon dogs and some

individuals do not have wetlands in their home ranges at all. Most often the most used habitats are the most common habitats of the landscape. This means that forests are also utilized while not preferred. The coastal region is a great example where raccoon dogs did not avoid almost any habitat, which is indeed bad news for many waterbirds. Because of this generalist nature, it is tempting to think that the threat caused to ground-nesting birds would be more coincidental. But the evidence showing a 1.5 to up to 5 times more likely preference for important nesting habitats during the breeding season cannot be completely ignored. While the raccoon dogs do not move closer to water bodies between these seasons, they shift to prefer these water-associated habitats more during the breeding season. I can conclude that while raccoon dogs are most definitely not specialists of water-associated habitats, they may use them disproportionately when available. In other words, the habitat preferences of raccoon dogs may cause a specific risk for ground-nesting birds in wetland and peatland habitats as well as in the whole of the coastal region.

4.4 Recommendations

To further study the behavior of raccoon dogs, it would be interesting to focus on their olfactory skills. Selonen et al. (2022) studied how chemical camouflage treatment and conditioned food aversion would influence the nest predation rate of raccoon dogs and red foxes in wetlands. They found that while both treatments decreased the nest predation by red foxes, they did not affect the nest predation by raccoon dogs. The visitations to wetlands did not decrease in either case, but the red foxes probably could not find the nests or just stopped eating the eggs. These results would imply that raccoon dogs do not rely on their olfactory senses as much as similar-sized red foxes, so their nest predation would be coincidental rather than consequential. To further investigate this connection, more research on how raccoon dogs sense their environment and make their decisions is needed. I could not find any research on how olfactory-oriented raccoon dogs are in their predation.

To mitigate the negative impacts of raccoon dogs, I would recommend putting most of the effort into the removal of raccoon dogs in wetlands and other important nesting habitats. Raccoon dogs are most expected to be found in the most common habitats of the region, so the best trapping and hunting results are expected to be achieved in those habitats. This is not surprising since the generalist nature of raccoon dogs is long known. The biggest problems are caused in regions where wetland habitats are most abundant since raccoon dogs show a preference for these habitats which is even magnified during the breeding season of ground-nesting birds. In the coastal region, raccoon dogs utilize all

sorts of habitats with no clear avoidance of any habitat but open rock, so they are practically a threat everywhere where the birds can imagine laying their eggs.

As we have seen from the results of my study, the invasive raccoon dog spends time in bird nesting habitats and this way poses a very potential risk for nesting waterbirds and their eggs. To mitigate this, I would recommend continuing the removal of raccoon dogs from these areas. This is especially important in those wetlands and coastal areas where native species, such as the pine marten (*Martes martes*) and the fox, already pose a risk to nesting success.

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