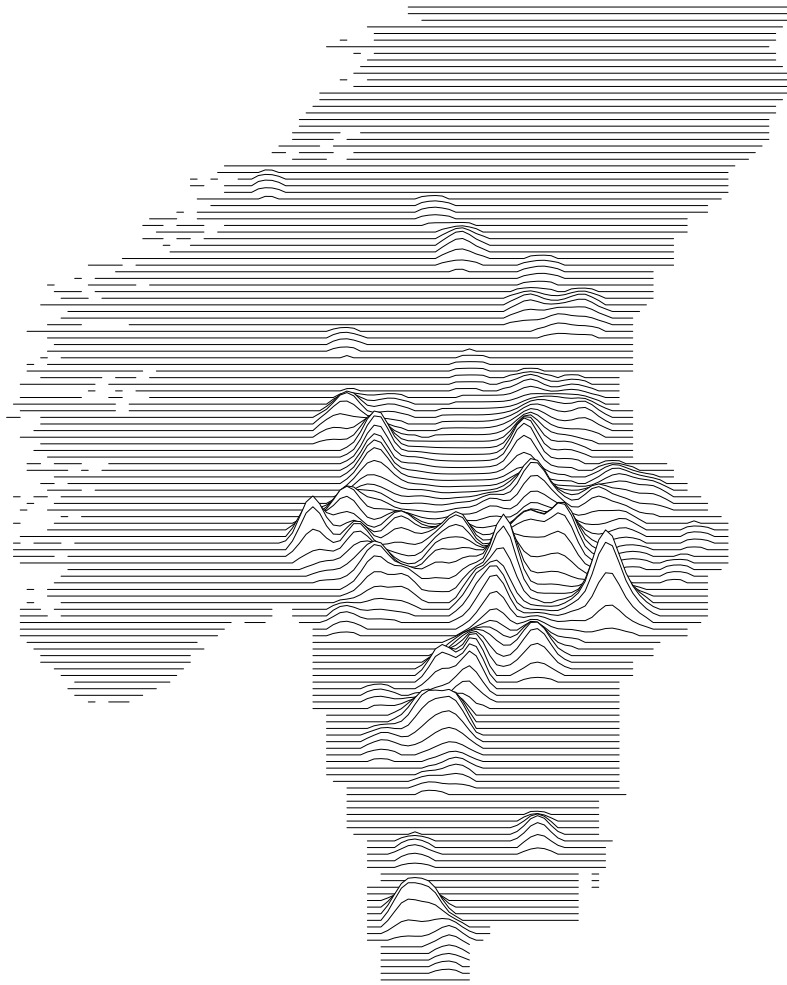**2024**

MINA fagrapport 97

Estimates of wolf density, abundance, and population dynamics in Scandinavia, 2014–2024

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Summary

Background The Scandinavian wolf (*Canis lupus*) population is being monitored annually using non-invasive genetic sampling (NGS) and recovery of dead individuals. DNA extracted from faeces, urine, hair, and tissue is used to identify the species, sex, and individual from which each sample originated. These data are compiled in the Scandinavian large carnivore database Rovbase 3.0.

Approach Using the Bayesian open-population spatial capture-recapture (OPSCR) model developed by RovQuant, we estimated annual density and vital rates of the Scandinavian wolf population for ten consecutive seasons from 2014/2015 to 2023/2024.

Results We generated annual density maps and estimated total and jurisdiction-specific population sizes for wolf from the winter 2014/2015 to 2023/2024 within the main population range. Based on the OPSCR model, the size of the Scandinavian wolf population was likely (95% credible interval) between 414 and 470 individuals in 2023/2024, with 353 to 403 individuals attributed to Sweden and 56 to 73 to Norway. In addition to annual density and jurisdiction-specific abundance estimates, we report annual estimates of cause-specific mortalities, recruitment, and detection probabilities.
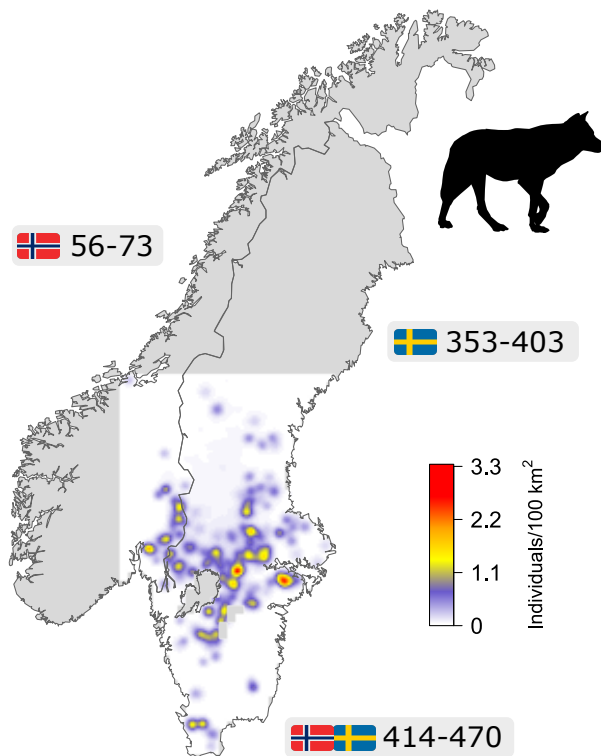
Density map and ranges of abundance
estimated for wolves in 2023/2024

Sammendrag

Bakgrunn Den skandinaviske ulvebestanden (Canis lupus) blir overvåket årlig ved bruk av ikke-invasiv genetisk prøveinnsamling (NGS) og gjenfunn av døde individer. DNA ekstrahert fra skit, urin, hår og vev brukes til å identifisere art, kjønn og individ for hver enkelt prøve. Denne informasjonen samles og ivaretas i den skandinaviske databasen for store rovdyr; Rovbase 3.0.

Tilnærming Ved bruk av en Bayesiansk åpen romlig fangst-gjenfangst populasjons modell (OPSCR), utviklet av RovQuant, estimerte vi årlige tettheter og demografiske rater i den skandinaviske ulvebestanden i ti sesonger fra 2014/2015 til 2023/2024.

Resultater Innenfor hovedutbredelsesområdet til ulvebestanden laget vi årlige kart over tettheten av ulv fra 2014/2015 til 2023/2024, som viser både total bestandsstørrelse og bestandsstørrels innenfor ulike administrative enheter. Basert på OPSCR modellen var den skandinaviske ulvebestanden mellom 414 og 470 individer i 2023/2024 (95% kredibelt intervall), med 353 til 403 individer i Sverige og 56 til 73 individer i Norge. I tillegg til årlige tettheter og områdespesifikke bestandsestimater, gir rapporten estimater på dødlighetsfaktorer, rekruttering og oppdagbarhet.
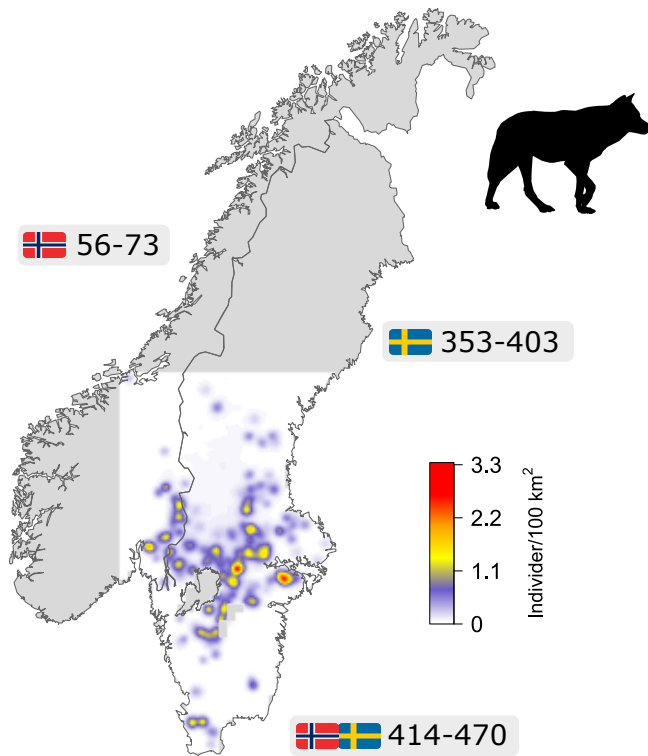
Kart som viser tetthet av ulv i 2023/2024 sammen
med intervaller for estimert antall ulv

Contents

1   Introduction

Non-invasive genetic sampling (NGS) and dead recoveries, are one of the centerpiece of national and regional large carnivore monitoring in Norway and Sweden. Both countries have accumulated an extensive individual-based data set for wolf (*Canis lupus*) and plan to continue such transnational monitoring in the future.

Since 2017, project RovQuant has been developing statistical methods that allow a comprehensive assessment of the status and dynamics of large carnivore populations using NGS data and other sources of information collected and stored in Rovbase (www.rovbase.se, www.rovbase.no) by the national monitoring programs in Sweden and Norway. At the core of the analytical framework developed by RovQuant (Bischof et al., 2019b, 2020) are Bayesian open-population spatial capture-recapture (OPSCR) models (Ergon and Gardner, 2014; Bischof et al., 2016; Chandler et al., 2018). These models use the spatial and temporal information contained in the repeated genetic detections of individuals to estimate various population parameters, including spatially-explicit abundance and vital rates. Importantly, the approach accounts for imperfect detection (i.e., the fact that some individuals are not detected at all) and animal movement (i.e., the fact that individuals may use and be detected in multiple management units or countries).

The conventional approach for wolf population size estimation in Scandinavia since 2014/2015 entails the use of a static conversion factor to calculate the size of the wolf population from the number of observed reproductions (Wabakken et al., 2024). The conversion factor approach assumes that the relationship between total population size and the number of observed reproductions remains unchanged over time and between regions, which has led to criticism of the method (Chapron et al., 2016; Bischof et al., 2019a). Aside from relaxing this and several other assumptions (Bischof et al., 2019a), the OPSCR method brings along several advantages. These include the ability to map density, derive jurisdiction-specific abundance, estimate survival and recruitment (which are needed for making population projections), and yield tractable measures of uncertainty (Bischof et al., 2019a, 2020).

RovQuant reported its first results for wolves in 2019 (Bischof et al., 2019a,b, 2020) and on an annual basis since 2021 (Milleret et al., 2021, 2022c, 2023). In the present report we summarize the analysis of a 10-year time series (2014/2015–2023/2024) using the latest available wolf monitoring data and the most recent version of the OPSCR model. We provide the following information:

- Annual estimates of the number of wolves within the main population range (with credible intervals) for Sweden, Norway, and both countries combined, as well as estimates by county in Sweden and by large carnivore management region in both countries.

- Annual maps of wolf density throughout the species' primary range in Scandinavia.

- Annual estimates of survival, cause-specific mortality, recruitment, and population growth rate (with credible intervals).

- Estimated proportion of individuals detected through non-invasive genetic sampling (with credible intervals).

Box 1: Terms and acronyms used

AC: Activity center. Model-based equivalent to the center of an individual's home range during the monitoring period. "AC location" refers to the spatial coordinates of an individual AC in a given year, and "AC movement" to the movement of an individual AC between consecutive years.

CrI: 95% credible interval associated with a posterior sample distribution.

Detectors: Potential detection locations in the spatial capture-recapture framework. These can refer to fixed locations (e.g., camera-trap locations) or to areas searched (e.g., habitat grid cells where searches for genetic samples were conducted; used in this project).

Statsforvalteren: Norwegian state's representative in the county, responsible for following up decisions, goals, and guidelines from the legislature and the government.

Habitat buffer: Buffer surrounding the searched area that is considered suitable habitat but was not searched.

Legal culling: Lethal removal of individuals by legal means including licensed recreational hunting, management removals, defense of life and property.

Länsstyrelserna: Swedish County Administrative Boards, in charge of the monitoring of large carnivores at the county level.

MCMC: Markov Chain Monte Carlo.

NGS: Non-invasive genetic sampling.

OPSCR: Open-population spatial capture-recapture.

p0: Baseline detection probability; probability of detecting an individual at a given detector, if the individual's AC is located exactly at the detector location.

σ: Scale parameter of the detection function; related to the size of the circular home-range.

SCR: Spatial capture-recapture.

SNO: Statens naturoppsyn (Norwegian Nature Inspectorate) is the operative field branch of the Norwegian Environment Directorate (Miljødirektoratet).

2   Methods

2.1   Data

We included data from multiple sources, the primary one being the Scandinavian large carnivore database Rovbase 3.0 (rovbase.se and rovbase.no; last extraction: 2024-04-30). This database is used jointly by Norway and Sweden to record detailed information associated with large carnivore monitoring, including, but not limited to, non-invasive genetic sampling (NGS) data, dead recoveries, and GPS search tracks. In the following sections, we describe the various types of data used in the analysis. We used data collected during winters 2014/2015 to 2023/2024.

Non-invasive genetic sampling Swedish and Norwegian management authorities, SNO (Norway) and Länsstyrelserna (Sweden) conduct annual searches for sources of DNA (primarily scats and urine) throughout the Scandinavian wolf range (Svensson et al., 2023). Although samples may be collected throughout the year, the official survey period starting with the 2014/2015 season has been Oct 1 – Mar 31. About one third (30%) of DNA samples originated from opportunistic searches (without associated information on search effort) conducted by hunters or other members of the public (see Liberg et al. 2012 and Bischof et al. 2019a for further details about the data collection procedure). For individual identification, at least 17 microsatellite markers were amplified with PCR throughout the study period. Samples were amplified four times to account for the occurrence of allelic dropout and false alleles (Taberlet et al., 1996). Consensus genotypes were constructed from the replicated PCR runs using the threshold rule that the same alleles had to appear at least twice for a heterozygous genotype and three times for a homozygous genotype (Åkesson et al., 2016). Since 2017/2018, 90 single nucleotide polymorphisms (SNPs) were used for individual identification, in addition to microsatellites. Samples were amplified and genotypes visualized twice using nanofluid arrays (Fluidigm Inc.). Consensus SNP genotypes consisted of the markers with the same allele composition from the two amplifications (Åkesson et al., 2018).

Dead recoveries In Scandinavia, all dead large carnivores killed legally (e.g., legal hunting, management kills, defense of life and property) have to be reported to the state authorities (Statsforvalteren or SNO in Norway and Länsstyrelserna or the police in Sweden). All wolves found dead due to other reasons (e.g., natural deaths, vehicle and train collisions, illegal hunting) also have to be reported, but an unknown proportion remains undetected. Tissue is collected from all reported dead carnivores for DNA extraction and analysis. DNA from dead carnivores, if genotyped, can be linked with NGS data via individual IDs and provide definite information about the fate of individuals. Dead recoveries associated with GPS-coordinates also provide additional information for the estimation of individual locations, especially valuable for individuals with few or no NGS detections (Dupont et al., 2021).

GPS search tracks Government employees involved in systematic searches for wolf DNA along roads and following wolf tracks (e.g., via snowmobiles, skis, snowshoes) documented their effort with GPS track logs which were registered in Rovbase 3.0. GPS search tracks were included in the OPSCR model to account for spatial and temporal variation in search effort.

Observation reports in Skandobs We used all observation records available from Skandobs (skandobs.se; skandobs.no) that were recorded during the wolf monitoring seasons since Oct 1, 2014, (last extraction: 2024-04-08). Skandobs is a web application that allows anyone to anonymously register observations (e.g., visual, tracks, faeces) of bears, lynx, wolves, and wolverines in Scandinavia. This data consists of more than 65 000 records of possible large carnivore observations. Although most observations are not verified, they offer the best available proxy for spatio-temporal variation in opportunistic search effort.

Parentage analysis and social status assignation Each year, field observations, genetic sampling data, dead recoveries, and parentage analysis (which resulted in a near-complete pedigree of the Scandinavian wolf population) are used to establish counts of pairs, packs, and reproductions (Svensson et al., 2014, 2015, 2017, 2019, 2021, 2023; Wabakken et al., 2016, 2018, 2020, 2022, 2024). The social status (adult scent-marking member in a pack/pair, or subadult member of a pack and vagrant individuals) was determined on a yearly basis for genetically identified individuals using the pedigree and tracking information from the monitoring (Åkesson et al., 2022). The identity of known adult scent-marking individuals was reported in the yearly monitoring reports (Svensson et al., 2014, 2015, 2017, 2019, 2021, 2023; Wabakken et al., 2016, 2018, 2020, 2022, 2024) and a detailed description of the method used for parental assignment was provided in Åkesson et al. (2016). We assigned individuals to two different states depending on whether the individual had been identified as an adult scent-marking member of a pair or a pack ("adult scent-marking") or not ("other"). See Bischof et al. (2019a) for further details.

Study area Although wolves can be occasionally present within the entire Scandinavian range, we restricted the analysis to the core area (Figure 1). Following the recent wolf range expansion towards the south of Sweden, the Swedish Environmental Protection Agency requested an expansion of the study area (Milleret et al., 2022c, 2023). Since 2022, the RovQuant models therefore included an additional $68\,400$ km^2 in the study area (total= $322\,400$ km^2), compared to the previous analyses of the Scandinavian monitoring wolf data by RovQuant (Bischof et al., 2019b, 2020; Milleret et al., 2021).

2.2 Open-population spatial capture-recapture model

We analysed the data using a Bayesian open-population spatial capture-recapture (OPSCR) model (Bischof et al., 2019b), which addresses three challenges associated with population-level wildlife inventories:

1. Detection is imperfect and sampling effort heterogeneous in space and time: not all individuals present in the study area are detected (Kéry and Schaub, 2012).
2. Individuals that reside primarily outside the surveyed area may be detected within it. Without an explicit link between the population size parameter and geographic space or area, density cannot be estimated and population size is ill-defined (Efford, 2004).
3. Non-spatial population dynamic models usually estimate "apparent" survival and recruitment, as these parameters include the probability of permanent emigration and immigration, respectively. By explicitly modelling movement of individuals between years, the OPSCR model can help return unbiased estimates of demographic parameters (Ergon and Gardner, 2014; Schaub and Royle, 2014; Gardner et al., 2018; Efford and Schofield, 2022).

The OPSCR model (Ergon and Gardner, 2014; Bischof et al., 2016; Chandler et al., 2018) is composed of three sub-models:

1. A model for population dynamics and population size.
2. A model for density and movements.
3. A model for detections during DNA searches.

Population dynamics and population size sub-model We used a multi-state formulation (Lebreton and Pradel, 2002) where each individual life history is represented by a succession of up to five discrete states $z_{i,t}$: 1) "unborn" if the individual has not been recruited in the population (state "unborn" is required for the data augmentation procedure, see below); 2) "alive other" if it is alive and not assigned as an "adult scent-marking" individual; 3) "alive adult scent-marking" if it is alive and assigned as an "adult scent-marking" individual; 4) "culled" if it was

culled and therefore recovered dead between the start of the previous and current monitoring season; or 5) "dead": if it has died but was not recovered dead. We then modelled the transition between states from one monitoring season to the next (t to $t + 1$) to estimate vital rates (recruitment and mortality). More details are available in Bischof et al. (2019b), and Bischof et al. (2020). We used data augmentation (Royle and Dorazio, 2012), whereby additional, undetected individuals are available for inclusion in the population at each time step.

Density and movement sub-model We used a Bernoulli point process to model the distribution of individual activity centers. In the first year, individuals were located according to an intensity surface, which was a function of the locations of known packs at time $t - 1$ (see Bischof et al., 2019b and Bischof et al., 2020 for more details). For all subsequent years ($t > 1$), the location of individual activity centers was a function of the distance from previous activity centers (at time $t - 1$), as well as a function of the locations of known packs (at time $t - 1$). As in previous analyses (Milleret et al., 2022c, 2023), we used an exponential model to describe the movement of individuals between years, as it better accommodates distributions with long tails (i.e., a few individuals that make exceptionally long dispersal movements).

Detection sub-model SCR models take into account the spatial-variation in individual detection probability based on the distance between activity center locations (estimated by the density sub-model) and a given detector. A half-normal function was used to express the declining probability of detection with increasing distance between the activity center and the detector.

In Scandinavia, DNA material from live wolves are collected following two main processes. First, authorities collect genetic samples and record the corresponding search effort during official searches ("structured sampling" thereafter). Second, DNA material can be collected by any member of the public (e.g., hunters) or by the authorities in a more or less opportunistic manner and associated search effort is not directly available ("unstructured" sampling thereafter). Currently, it is not possible to unambiguously distinguish between samples collected by the authorities during the structured or unstructured sampling in Rovbase. We therefore assigned each sample to structured or unstructured sampling based on whether a given sample matched in time and space with recorded search tracks: a sample was assigned to the "structured" sampling if it was collected by the authorities (marked as collected by "Statsforvalteren" or "SNO" in Rovbase) and if it was located within 500 m from a search track recorded on the same day. All remaining samples were assigned to the unstructured sampling.

We assumed that both sampling processes could in theory occur within the entire study area and therefore used the same 10 km detector grid for both observation processes. Samples were then assigned to the closest detector (see details in Bischof et al., 2019b, and Bischof et al., 2020). However, spatial and temporal variation in the probability to detect a sample during the structured or unstructured sampling were assumed to be driven by different processes.

We accounted for spatio-temporal heterogeneity in detectability during ***structured sampling*** using:

- Spatial-temporal variation in effort using the length of GPS search tracks in each detector grid cell.

- Spatio-temporal variation in snow cover.

- Spatio-temporal variation in monitoring regimes between jurisdictions (groups of counties in Sweden, monitoring regions in Norway).

- Individual variation linked with the state of the individual (i.e., adult scent-marking individuals, other individuals).

- Individual variation linked with a previous detection that could be expected to positively or negatively influence the probability of being detected at subsequent occasions, depending on the state of knowledge in the territory or neighboring territories.

We accounted for spatio-temporal heterogeneity in detectability during **_unstructured sampling_** using:

- Spatio-temporal variation in unstructured sampling or carnivore observations (Figure A.1). For each detector grid cell and during each monitoring season (Oct 1 – Mar 31), we identified whether a) any carnivore sample had been registered in Rovbase (excluding successfully genotyped wolf samples already used in the OPSCR analysis) or b) any observation of carnivores had been registered in Skandobs. Roughly, the variable distinguishes areas with very low detection probability from those with some reasonable probability that carnivore DNA samples, if present in a detector grid cell, could have been detected and submitted for genetic analysis (Figure A.1).

- Spatio-temporal variation in snow cover.

- Spatial variation in accessibility measured as the average distance to the nearest road.

- Spatio-temporal variation between countries.

- Individual and temporal variation linked with the state of the individual (i.e., adult scent-marking individuals, other individuals).

- Individual and temporal variation linked with a previous detection that could be expected to positively influence the probability of being detected at subsequent occasions.

The different model components and data sources for covariates are described in detail in Bischof et al. (2019a), Bischof et al. (2019b), and Bischof et al. (2020).

Model fitting We fitted sex-specific Bayesian OPSCR models using Markov chain Monte Carlo (MCMC) simulation with NIMBLE version 0.12.2 (Turek et al., 2021; de Valpine et al., 2017; de Valpine et al., 2022) and nimbleSCR (Bischof et al., 2021) in R version 4.1.0 (R Core Team, 2021). We ran 4 chains each with 30 000 iterations, including a 10 000-iterations burn-in period. Due to the computing challenge associated with post-processing large amounts of data, we thinned chains by a factor of 10 from which abundance estimates were derived. We considered models as converged when the Gelman-Rubin diagnostics (Rhat, Gelman and Rubin, 1992) was ≤1.1 for all parameters and by visually inspecting the trace plots.

Abundance estimates To obtain an estimate of abundance for any given area, we summed the number of predicted AC locations (live individuals) that fell within that area for each iteration of the MCMC chains, thus generating a posterior distribution of abundance for that area. In this fashion, abundance estimates and the associated uncertainty can be extracted for any spatial unit, including countries or counties (Figure A.2). Individuals detected near a border can have their model-predicted AC placed on different sides of that border in different model iterations (even if detections are only made on one side of the border). As a result, the probability of designating such individuals to either side of the border can be integrated into jurisdiction-specific abundance estimates. This is especially relevant for wolves detected along the Swedish and Norwegian border ("cross-boundary wolves", Wabakken et al., 2022); individual wolves can be partially designated to both countries (Bischof et al., 2016).
To ensure that abundance estimates for spatial sub-units (jurisdictions) add up to the overall abundance estimate, we used the mean and associated 95% credible interval limits to summarize posterior distributions of abundance. Combined (female/male) parameter estimates were

obtained by merging posterior samples from the sex-specific models.

Density maps We used both the distribution of model-estimated AC positions and the scale parameter (σ) of the detection function to construct density maps based on individual utilization distributions. These maps are not only based on the position of the center of an individual's home range, but also take into account the area over which that individual's activity is spread, i.e., its space use (Bischof et al., 2020). To do so, we constructed raster maps (5 km resolution) of individual utilization distributions, scaled values in each raster to sum to one, and then summed rasters across individuals to create a single population-level raster map for each iteration. An overall density map was derived by calculating the mean across iterations in each cell (Bischof et al., 2020).

Other derived parameters The average proportion of individuals detected and the associated uncertainty were obtained by dividing the number of individuals detected through NGS sampling (Table A.3) by the abundance estimates and their associated credible intervals, respectively. We derived the proportion of females in the population and the associated uncertainty by dividing the posterior distribution representing the number of females by the combined abundance estimate for males and females (Table A.3). Yearly population growth rates were calculated as $\lambda_t = N_{t+1}/N_t$ (Table A.6).

Focus on uncertainty Although we reported median (or mean for abundance; see above) estimates for all parameters in the tables, we intentionally focused the main results of this report on the 95% credible interval limits of the estimates. We did so with the aim of drawing the reader's attention to the uncertainty around population size estimates, rather than a single point estimate (Milleret et al., 2022b).

3 Results

## 3.1 Non-invasive genetic samples and dead recoveries

A total of 20 171 (8 828 female; 11 343 male) genotyped wolf genetic samples were included in the analysis, of which 76% originated from Sweden. These samples were associated with 1 838 (846 female; 992 male) individuals. We did not include individuals with unknown sex in this analysis. Among all genotyped samples, 8 803 (3660 female; 5143 male) were assigned to the structured sampling and 11 368 (5168 female; 6200 male) to the unstructured sampling. We also used 721 (324 female; 397 male) dead recoveries of wolves in the OPSCR model, of which 601 (267 female; 334 male) were due to legal culling and 120 (57 female; 63 male) due to other causes of mortality. The majority of dead recoveries (68%) originated from Sweden. Annual total and country-specific tallies of NGS samples and associated individuals, as well as dead recoveries included in the analysis are provided in the Appendices (NGS samples: Table A.2 and Table A.1, NGS individuals: Table A.3, dead recoveries: Table A.4)

3.2 Density and abundance

Wolf abundance for the entire study area (322 400 km^2, excluding the buffer area) was likely (95% credible interval) between 414 and 470 individuals in 2023/2024 (Table 1, Figure 1). Estimates refer to the status of the population at the start of the annual sampling period (Oct. 1). The proportion of females in the Scandinavian wolf population was likely between 48% and 54% in 2023/2024. Based on the model-predicted location of ACs, we estimated that in 2023/2024, between 353 to 403 individuals could be attributed to Sweden and 56 to 73 to Norway (Table 1). See Table 1 for total and sex-specific abundance estimates for each country and management area. See Table A.5 for annual wolf abundance estimates for all of Scandinavia and by region between 2014/2015 and 2023/2024. During the past three years, the wolf population experienced a steady decrease from 494-525 in 2021/2022 to 414-470 in 2023/2024 (Figure 2, Table A.5) . Note that estimates for different years (Figure 2) shown here differ slightly from those provided in Bischof et al. (2020), Milleret et al. (2021), Milleret et al. (2022c), and Milleret et al. (2023). This is due to the use of an updated OPSCR model and the inclusion of additional years of data. The analysis yielded annual density maps, which illustrate changes in the distribution of wolves over time (Figure A.3).

Table 1: Wolf population size estimates in 2023/2024 within the study area by sex at several spatial scales: the entire study area, by country, by management unit (carnivore management regions in Norway and "Rovdjursförvaltningsområden" in Sweden), and counties ("Län" in Sweden); see also Figure A.2. Only counties and management units that are within or that intersect the study area are included in the table. Readers should focus on the 95% credible interval provided in parentheses, as these - unlike mean values - convey uncertainty inherent in abundance estimates. Numbers are based on estimated activity center locations of wolves. Combined female-male estimates were obtained by joining sex-specific posterior distributions. Rounding may result in small deviations between total estimates and the sum of the estimates for constituent regions. Note that the numbers reported here are predictions from a statistical model which always represents an oversimplification of reality and is based on available data (NGS and dead recoveries). As a consequence, especially at the local scale, the model-estimated number of wolves based on DNA sampling can deviate from the number of wolves inferred from ancillary observations (e.g., camera traps).

	Females	Males	Total
TOTAL	224.6 (205-249)	214.9 (201-232)	439.5 (414-470)
NORWAY	28.6 (24-35)	35 (29-42)	63.6 (56-73)
Region 2	0.2 (0-1)	0.4 (0-2)	0.6 (0-3)
Region 3	0.8 (0-3)	0.8 (0-3)	1.5 (0-5)
Region 4	9.4 (8-12)	11.2 (9-14)	20.7 (17-24)
Region 5	16.3 (13-21)	21.8 (18-27)	38.1 (33-45)
Region 6	1.8 (1-4)	0.8 (0-3)	2.7 (1-6)
SWEDEN	195.9 (178-218)	179.9 (167-195)	375.8 (353-403)
Norra	12.8 (7-21)	9.7 (5-16)	22.4 (14-32)
Jämtland	9.3 (4-16)	6.2 (3-11)	15.5 (9-23)
Västerbotten	0 (0-1)	0 (0-0)	0 (0-1)
Västernorrland	3.5 (0-8)	3.4 (1-7)	6.9 (3-12)
Mellersta	150.7 (137-167)	131 (121-143)	281.7 (264-302)
Dalarna	31.3 (24-40)	25 (20-32)	56.2 (47-67)
Gävleborg	14 (10-19)	7.4 (4-11)	21.4 (16-28)
Örebro	26.4 (22-32)	29.3 (26-33)	55.7 (50-62)
Stockholm	2.1 (1-4)	2.3 (2-4)	4.5 (3-7)
Uppsala	3.8 (2-6)	5.6 (4-7)	9.4 (7-12)
Värmland	34.2 (29-41)	33 (28-39)	67.3 (60-76)
Västmanland	11.8 (9-15)	11.2 (9-14)	23 (20-27)
VästraGötaland	27 (24-31)	17.2 (14-21)	44.2 (39-49)
Södra	32.5 (28-38)	39.2 (35-44)	71.7 (66-79)
Blekinge	0.1 (0-1)	0.1 (0-1)	0.3 (0-2)
Halland	1.9 (1-3)	0.3 (0-2)	2.2 (1-4)
Jönköping	4.5 (2-7)	4.4 (2-7)	8.9 (6-13)
Kalmar	0.7 (0-3)	0.6 (0-2)	1.2 (0-4)
Kronoberg	1.7 (0-4)	3.2 (2-5)	4.9 (3-8)
Östergötland	6 (5-8)	4.4 (3-7)	10.4 (8-14)
Skåne	6.4 (6-8)	11.4 (11-13)	17.8 (17-20)
Södermanland	11.2 (10-14)	14.8 (13-17)	26 (24-29)
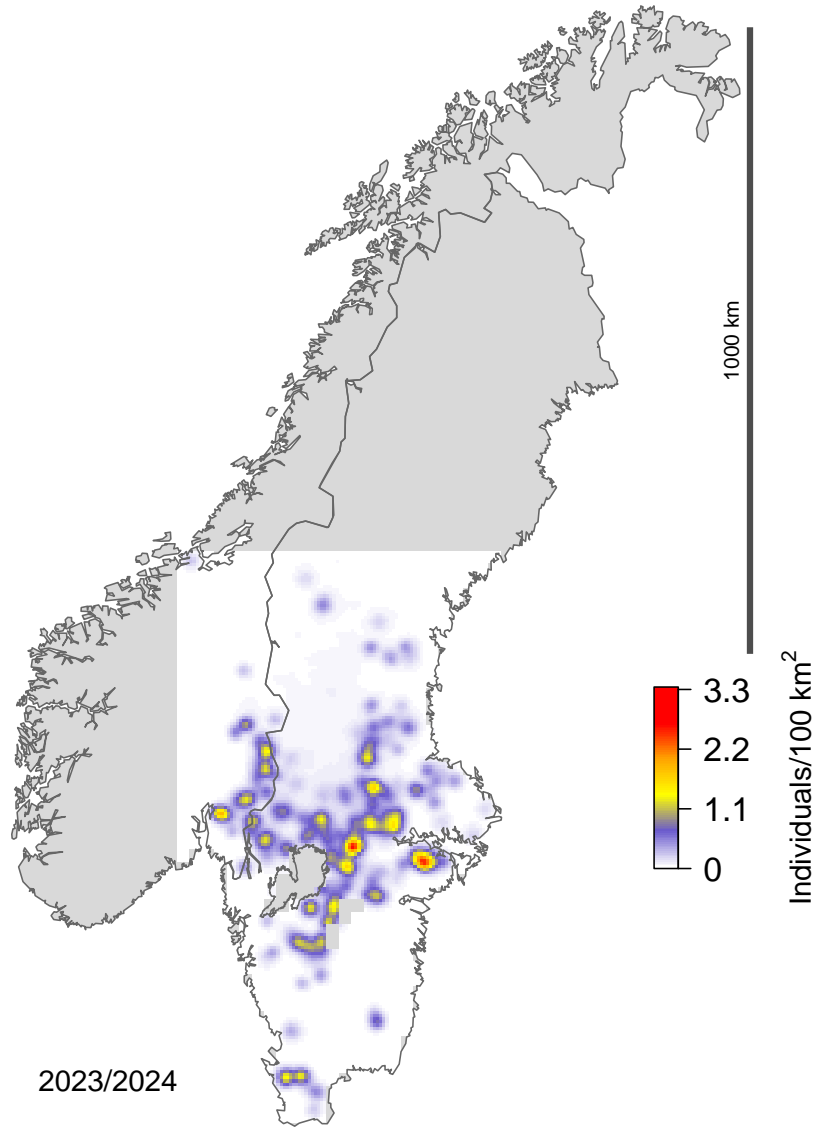
Figure 1: Wolf density based on individual utilization distributions throughout the study area (white background) in Scandinavia in 2023/2024. This map is freely available as a geo-referenced raster file at https://github.com/richbi/RovQuantPublic
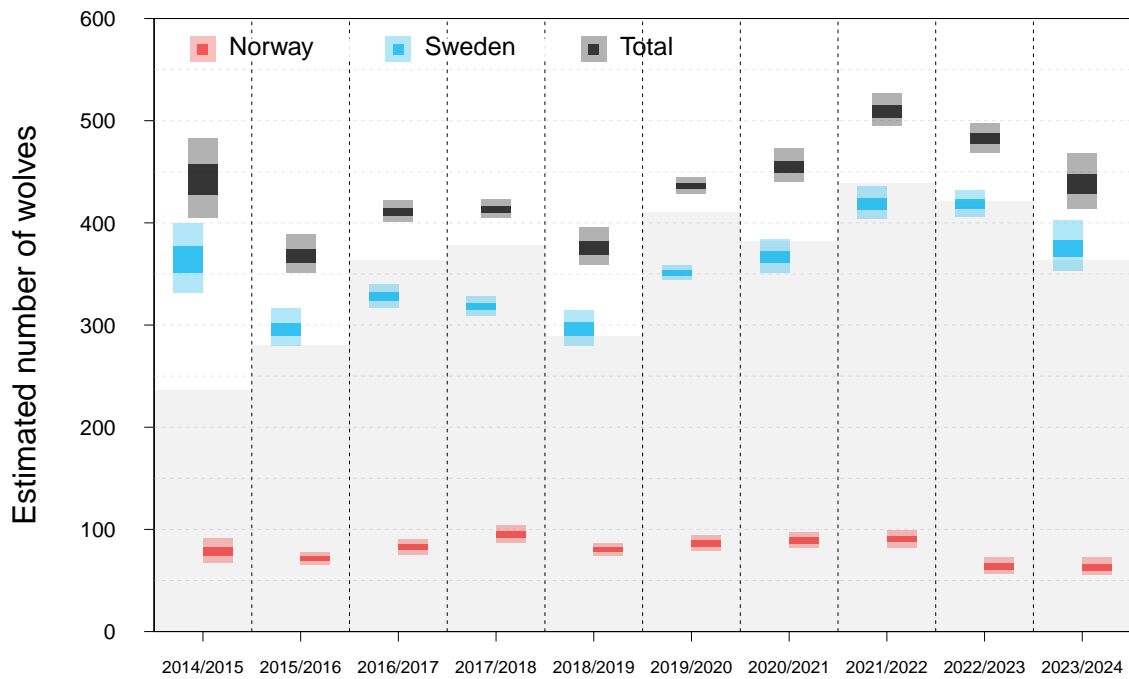
Figure 2: Wolf population size estimates within the study area by country (blue: Sweden, red: Norway), and total (black) between 2014/2015 and 2023/2024. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Credible intervals indicate uncertainty in estimates given the model and data used to generate the estimates. Light grey bars in the background show the total number of individuals detected within the entire study area. Changes in the model and the data can result in different estimates and associated uncertainty compared with estimates provided in previous reports by RovQuant. Note the higher precision (lower uncertainty) in the three monitoring seasons (2016/17, 2017/18, 2019/20) with higher sampling intensity in Sweden.

3.3 Vital rates

The OPSCR model produced annual estimates of legal hunting mortality, mortality associated with all other causes, and per capita recruitment rates (Figure 3; Table A.7). There was temporal variation in mortality rates, with the risk of mortality from causes other than culling generally higher than the risk of mortality from culling. Overall, scent-marking adult individuals had a higher survival compared to other individuals, with no pronounced systematic difference between sexes (Figure A.4).
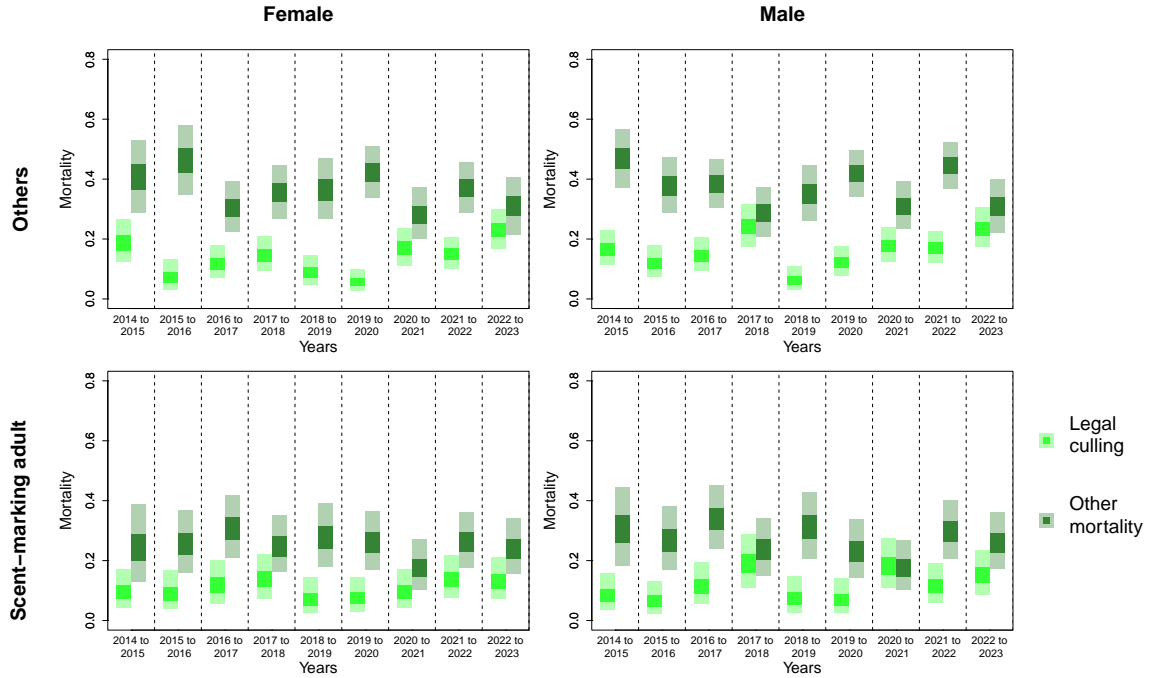
Figure 3: Mortality probabilities due to legal culling (light green) and all other causes (dark green) for female and male wolves. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Shown are overall estimates throughout the study area. Estimates refer to deaths occurring between the start of one sampling season and the start of the next.
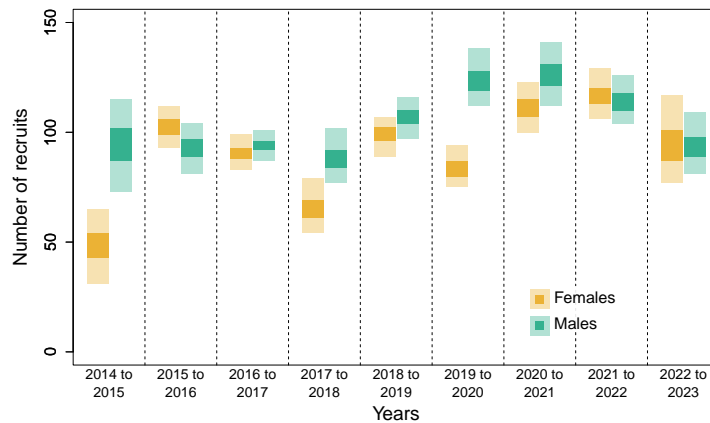
Figure 4: Estimated annual number of recruits for female and male wolves. Recruitment represents the number of new individuals present in the population on Oct 1 (i.e., individuals that were born between the two consecutive monitoring seasons and survived to Oct 1 or that immigrated in the study area). Darker and lighter bars show the 50% and 95% credible intervals, respectively.

3.4   Detection probability

The overall proportion of detected individuals in the study area was likely between 77% and 88% in 2023/2024 (Table A.11). The baseline detection probability for the structured and unstructured sampling varied both in time and space (Figure A.5 and Figure A.6). More specifically, the length of recorded search tracks positively affected detection probability of the structured sampling (2023/2024; males: $\beta_{2_{Structured}}$ =0.17, CrI: 0.12 - 0.22; females: $\beta_{2_{Structured}}$ = 0.28, CrI: 0.19 - 0.38; Table A.9). However, the previous detection of individuals and the average proportion of snow cover had no strong effect on detection probability for the structured sampling (Table A.9). Unstructured search effort derived using the observation data in Skandobs and Rovbase had a strong positive effect on detection probability during unstructured sampling (2023/2024; males: $\beta_{4_{Unstructured}}$ = 1.35, CrI: 0.78 - 2.06; females: $\beta_{4_{Unstructured}}$ = 1.67, CrI: 1.08 - 2.34; Table A.10). The effect of previous detection also tended to have a positive effect on detection probability during unstructured sampling, but the pattern was not consistent across years (Table A.10).

4 Suggestions for future improvements

RovQuant continues to work on improving the functionality and efficiency of OPSCR models. We recommend the following developments for future analyses of the Scandinavian wolf monitoring data:

1. Review and adjust spatial covariates on density. This may involve the addition of land cover and topographic variables.

2. Account for individual heterogeneity in detectability/space use, for example by using a finite-mixture approach (Cubaynes et al., 2010).

3. Consider alternative detection models that do not assume a half-normal shape and/or circular home ranges (Sutherland et al., 2015).

4. Account for spatial variation in vital rates (i.e., survival, recruitment; Milleret et al. 2022a).

5 Acknowledgements

6 Data availability

Data, R code to reproduce the analysis, as well as figures, tables, and raster maps (Figure A.3) are available at https://github.com/richbi/RovQuantPublic.

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Appendices
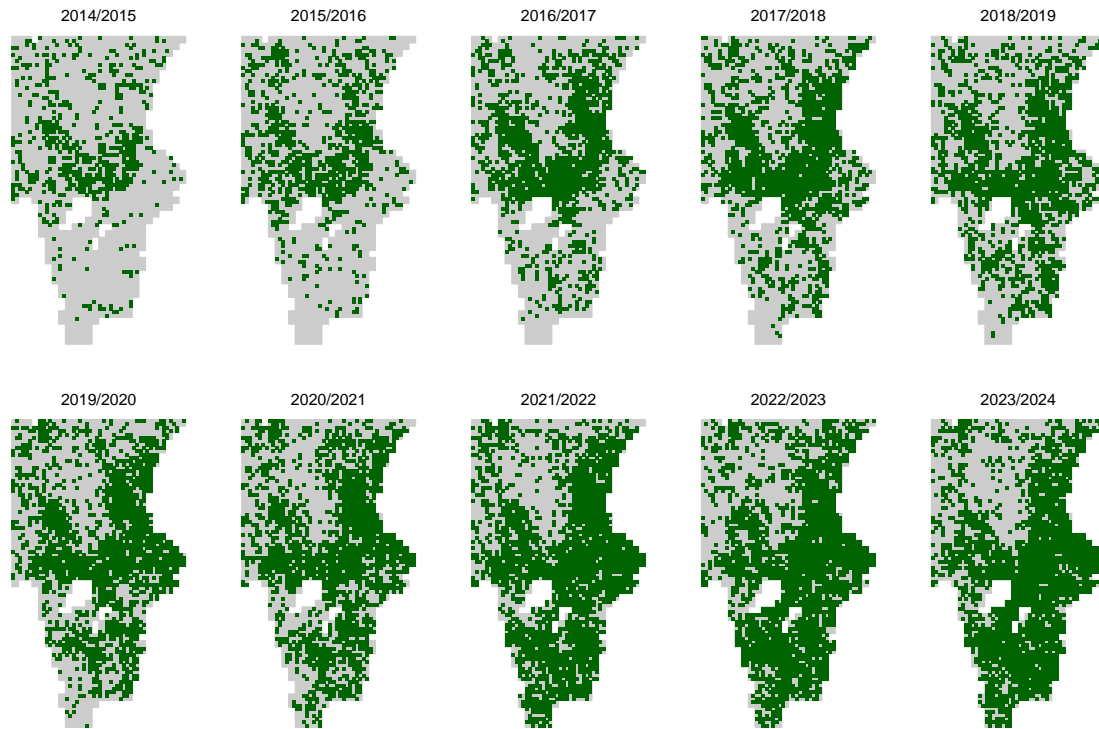
Figure A.1: Covariate used to account for spatio-temporal variation in unstructured sampling in the study area. Green cells (10 x 10 km) represent areas with at least one carnivore record in Rovbase (rovbase.no, rovbase.se, excluding the ones used in the OPSCR model) or an observation record from Skandobs (skandobs.se, skandobs.no) during a given monitoring season (Oct 1 – Mar 31).
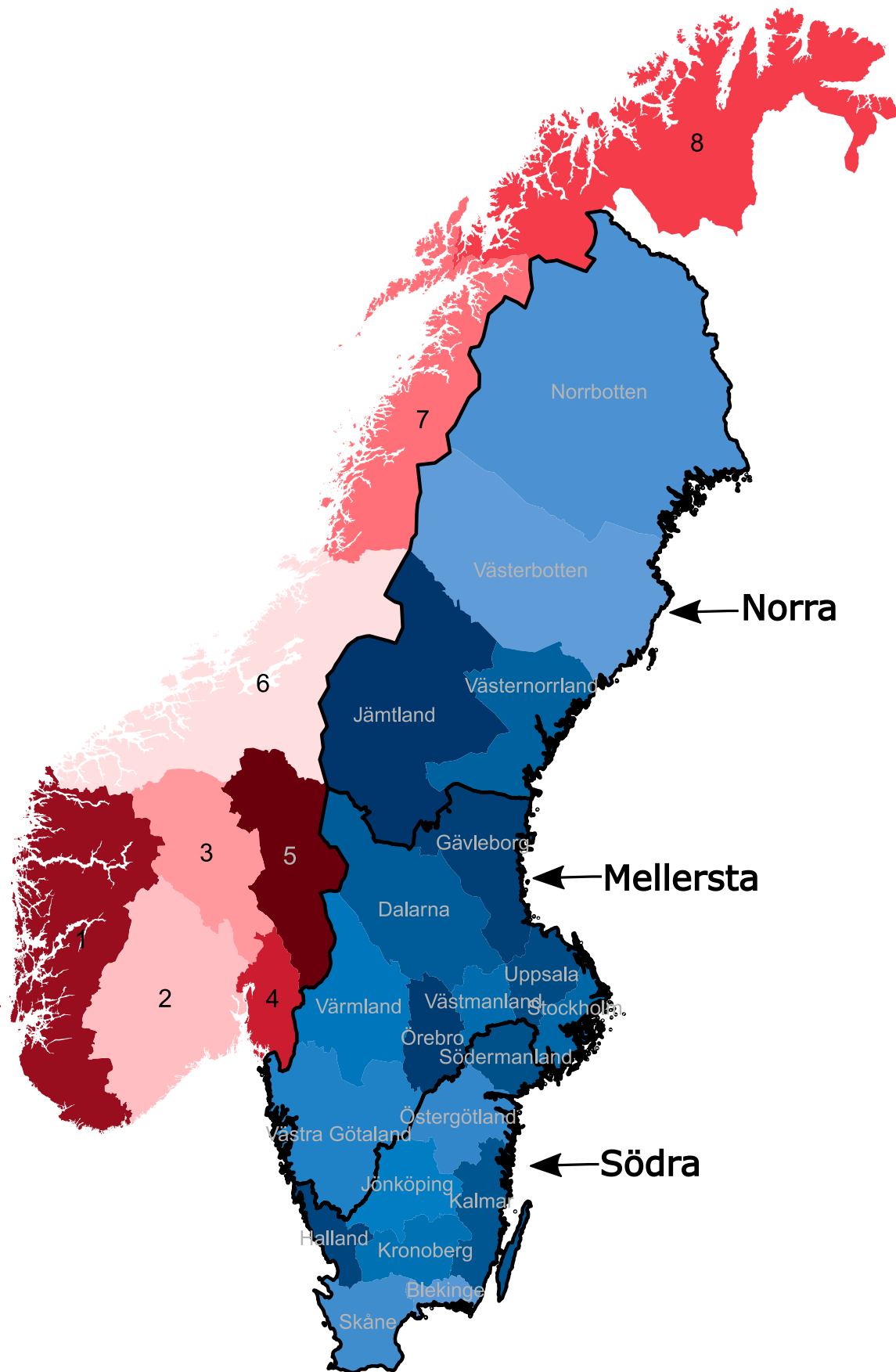
Figure A.2: Management jurisdictions in Norway and Sweden. Shaded polygons show carnivore management regions in Norway and counties in Sweden. Thick outlines delineate Swedish carnivore management regions ("Rovdjursförvaltningsområden") encompassing multiple counties.
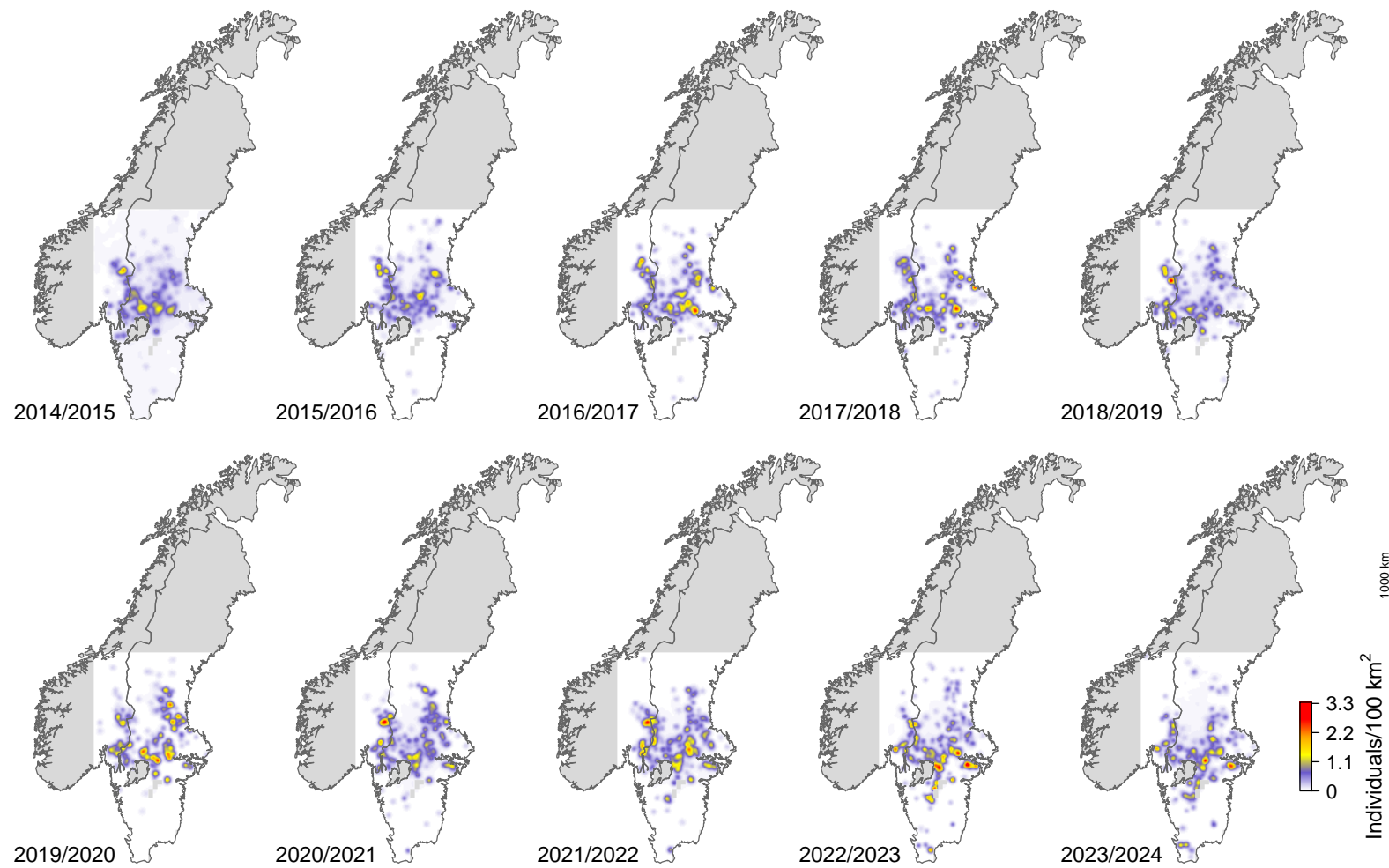
Figure A.3: Wolf density based on individual utilization distributions throughout the study area (white background) in Scandinavia between 2014/2015 and 2023/2024. These maps are freely available as geo-referenced raster files at https://github.com/richbi/RovQuantPublic.
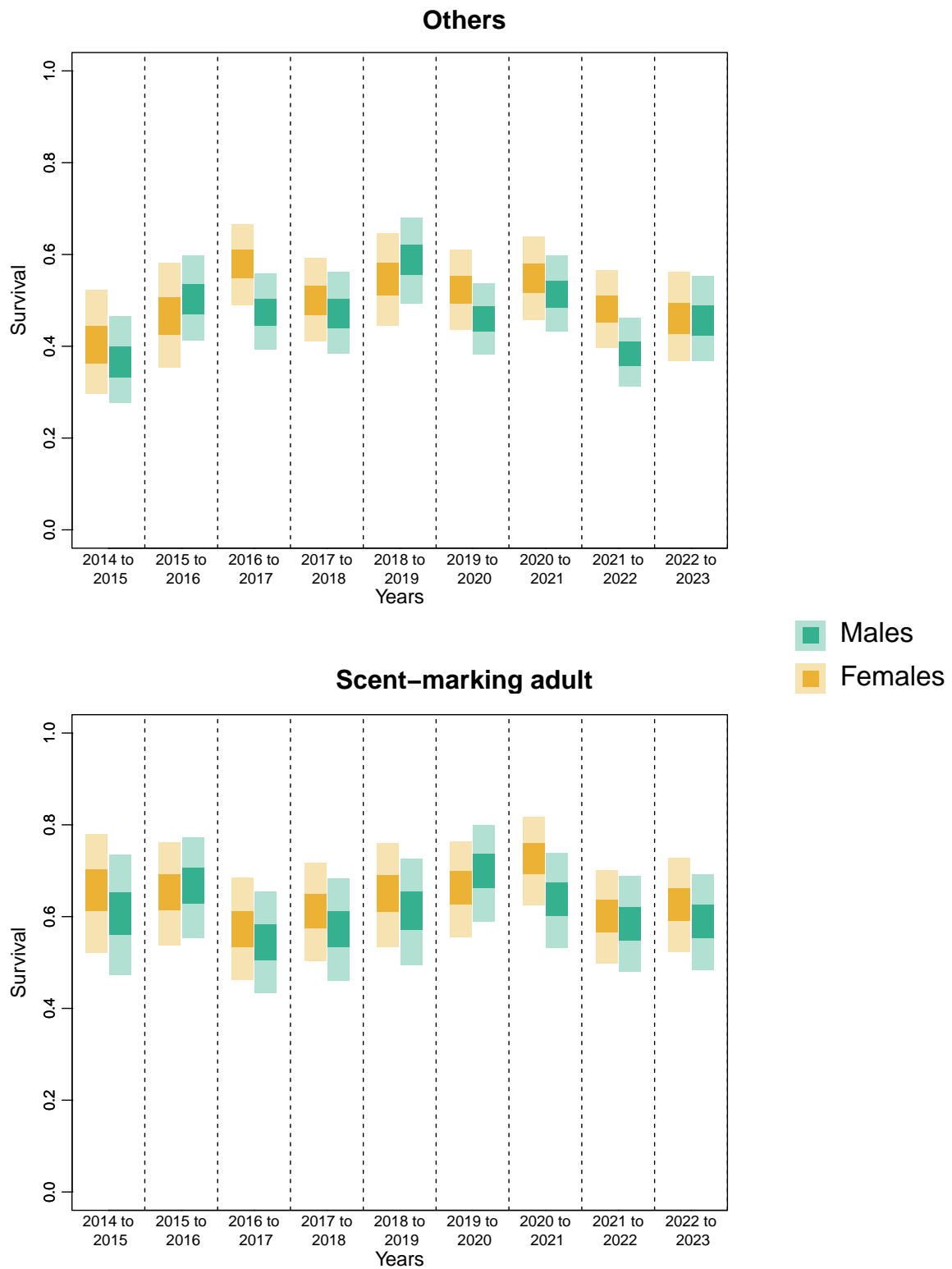
Figure A.4: Annual survival probabilities for scent-marking adults and other individuals and for female and male wolves. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Combined mortality probabilities (and therefore overall survival) are obtained by adding the mortality probabilities due to legal culling and all other causes (Figure 3). Shown are overall estimates for the entire study area between 2014/2015 and 2023/2024.
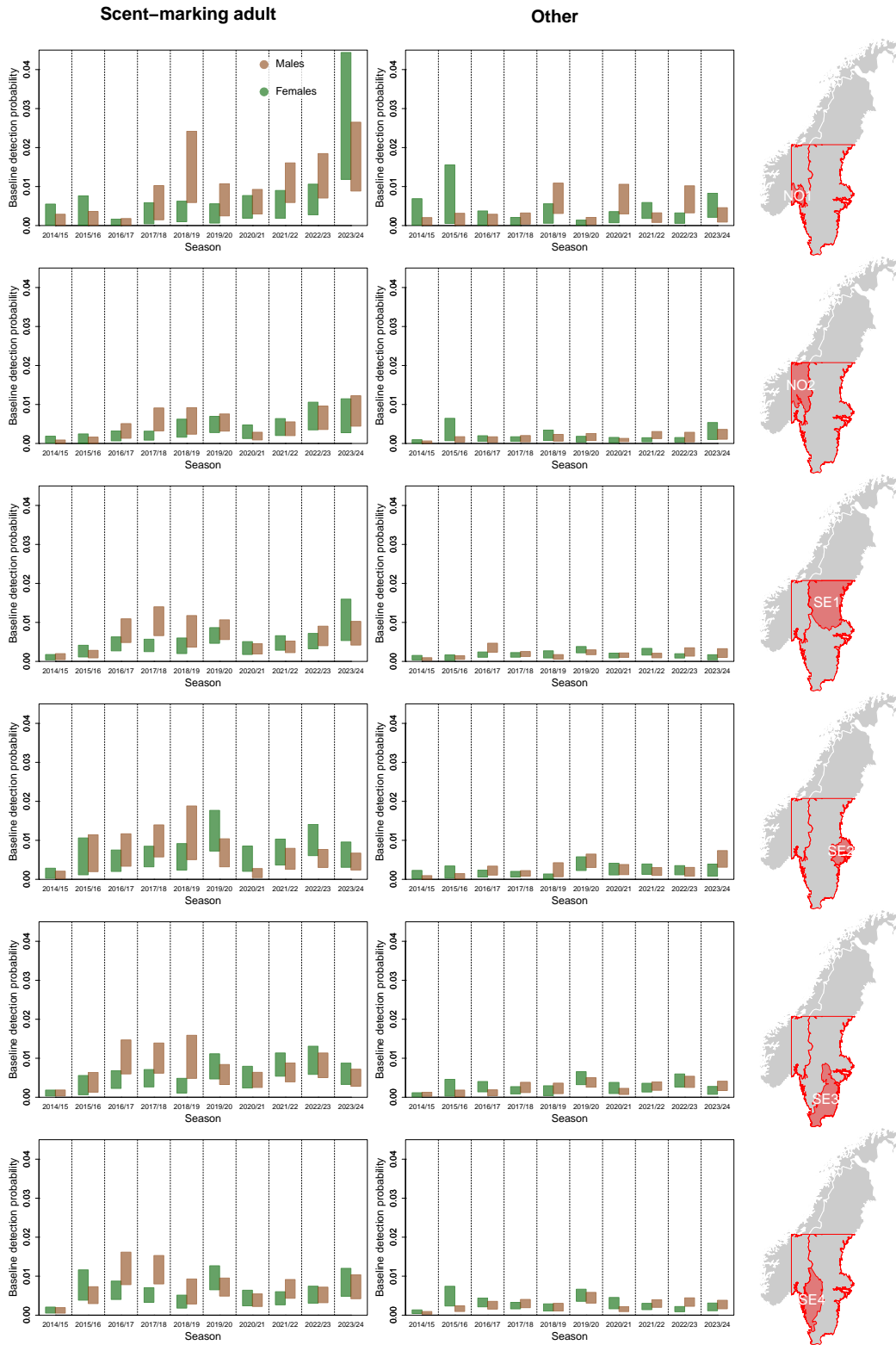
Figure A.5: Sex-specific baseline detection probabilities ($p_{0_{structured}}$) of scent-marking adults and other individuals for the different Scandinavian jurisdictions during structured sampling as estimated by the open-population spatial capture-recapture model. Bars represent 95% credible intervals. Results are separated into panels based on regions. Estimates are shown for the mean values of the detection covariates. Note that baseline detection probability (p_0) is a theoretical value of detection probability when a detector coincides with the location of an individual's activity center. It is not to be confused with detectability, i.e, the overall probability of detecting an individual.
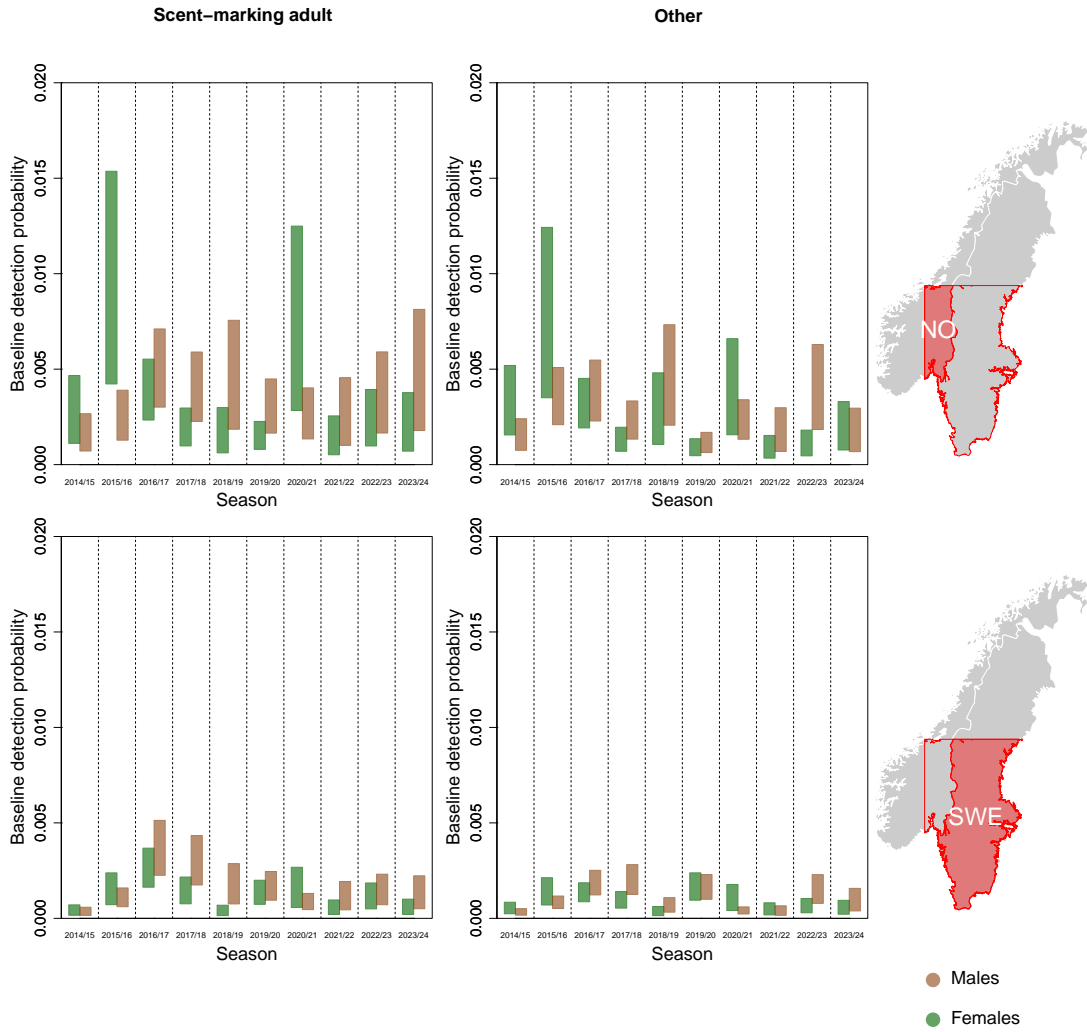
Figure A.6: Sex- and country-specific baseline detection probabilities ($p_{0\,unstructured}$) of scent-marking adults and others individuals during unstructured sampling as estimated by the open-population spatial capture-recapture model. Bars represent 95% credible intervals. Estimates are shown for the mean values of the detection covariates. Note that baseline detection probability (p_0) is a theoretical value of detection probability when a detector coincides with the location of an individual's activity center. It is not to be confused with detectability, i.e, the overall probability of detecting an individual.

Table A.1: Annual number of wolf non-invasive genetic samples included in the analysis. Numbers are reported by country, for females (F) and males (M), and for each type of sampling (structured and unstructured). We included only samples collected within the study area during the primary monitoring period (Oct 1 - Mar 31) between 2014/2015 and 2023/2024.

		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	Structured	3	5	6	11	22	11	36	43	53	93	47	80	51	133	73	162	57	117	95	152
	Unstructured	91	105	141	174	248	198	238	240	178	252	196	252	272	330	136	230	103	97	90	132
Sweden	Structured	99	120	137	200	373	582	474	665	221	293	597	717	281	457	416	500	374	447	245	355
	Unstructured	83	107	103	177	467	548	606	836	129	166	842	832	257	342	286	386	453	480	249	316
Total	Structured	102	125	143	211	395	593	510	708	274	386	644	797	332	590	489	662	431	564	340	507
	Unstructured	174	212	244	351	715	746	844	1076	307	418	1038	1084	529	672	422	616	556	577	339	448

Table A.2: Annual number of wolf non-invasive genetic samples included in the analysis. Numbers are reported by country, for females (F) and males (M). We included only samples collected within the study area during the primary monitoring period (Oct 1 - March 31) between 2014/2015 and 2023/2024.

	2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	94	110	147	185	270	209	274	283	231	345	243	332	323	463	209	392	160	214	185	284
Sweden	182	227	240	377	840	1130	1080	1501	350	459	1439	1549	538	799	702	886	827	927	494	671
Total	276	337	387	562	1110	1339	1354	1784	581	804	1682	1881	861	1262	911	1278	987	1141	679	955

Table A.3: Annual number of individual wolves detected via non-invasive genetic sampling and included in the analysis. Numbers are reported by country, for females (F) and males (M), and for each type of sampling (structured and unstructured). We included only individuals associated with samples collected within the study area during the primary monitoring period (Oct 1 - Mar 31) between 2014/2015 and 2023/2024. Some individuals were detected in both countries during the same year, hence the sum of the national counts can exceed the total number of unique individuals detected in Scandinavia.

		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	Structured	2	4	5	6	11	7	18	17	16	21	17	22	22	25	31	34	20	24	22	24
	Unstructured	27	31	29	44	46	37	47	44	31	44	36	45	37	53	41	48	27	20	22	31
Sweden	Structured	59	71	68	82	111	130	115	126	81	91	136	153	107	115	129	148	127	138	99	106
	Unstructured	47	59	55	86	104	124	120	144	69	71	146	158	98	115	126	128	140	138	101	110
Total	Structured	61	75	73	88	121	136	130	140	93	108	150	171	124	135	152	174	143	157	117	123
	Unstructured	73	87	80	124	142	156	161	178	96	110	178	194	134	163	159	166	164	156	123	138

Table A.4: Number of cause-specific dead recoveries of wolves in Scandinavia between 2014 and 2024 that were included in the OPSCR analysis. Numbers are reported by country, for females (F) and males (M). Note that dead recovery data from the final season (2023/2024) were not used in this analysis because survival is modeled as part of the transition from one season to the next.

	Country	2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	0	0	1	3	0	0	1	3	1	1	1	1	0	2	1	2	0	1	1	1
	Sweden	9	10	8	6	4	5	8	2	4	5	5	7	8	5	1	6	1	2	3	1
Legal culling	Norway	3	5	5	1	6	6	18	16	10	8	6	12	11	16	13	23	10	9	10	7
	Sweden	32	32	7	20	17	23	12	31	4	4	6	12	18	30	22	18	39	40	18	21
Total	Total	44	47	21	30	27	34	39	52	19	18	18	32	37	53	37	49	50	52	32	30

Table A.5: Annual abundance estimates for wolf at several spatial scales: the entire study area, by country, by management unit (carnivore management regions in Norway and "Rovdjursförvaltningsområden" in Sweden), and counties ("Län" in Sweden); see also Figure A.2. Only counties and management units that are within or that intersect the study area are included in the table. Estimates are based on model-estimated activity center locations. Credible intervals (95%) are shown in parentheses. Small deviations between the total estimate and the sum of abundance estimates from the constituent subregions may arise due to rounding. Note that the numbers reported here are predictions from a statistical model which always represents an oversimplification of reality and is based on available data (NGS and dead recoveries). As a consequence, especially at the local scale, the model-estimated number of wolves based on DNA sampling can deviate from the number of wolves inferred from ancillary observations (e.g., camera traps).

	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022	2022/2023	2023/2024
TOTAL	471 (432-515)	372.6 (354-394)	411.8 (402-423)	413.9 (405-424)	378.3 (361-399)	436.7 (429-446)	455 (440-472)	509.5 (494-527)	482.6 (469-499)	439.5 (414-470)
NORWAY	82.7 (71-97)	72.3 (67-79)	82.5 (75-91)	95.4 (87-104)	80 (74-87)	86.4 (79-94)	89 (82-97)	90.8 (82-100)	64.2 (57-73)	63.6 (56-73)
Region 2	1.3 (0-4)	0.3 (0-2)	0.8 (0-3)	0.8 (0-3)	0.9 (0-2)	1.3 (0-4)	0.3 (0-2)	0.6 (0-2)	0.8 (0-3)	0.6 (0-3)
Region 3	4.9 (1-9)	0.7 (0-3)	1.3 (0-4)	2 (0-5)	1 (0-3)	3.1 (1-6)	1.3 (0-4)	2.2 (0-5)	2.3 (0-6)	1.5 (0-5)
Region 4	9.9 (6-15)	12.4 (10-16)	16.4 (13-20)	22 (18-26)	24.1 (20-28)	27.4 (23-32)	23.7 (19-28)	26 (21-31)	23.9 (20-28)	20.7 (17-24)
Region 5	60 (52-69)	57.8 (54-63)	62.4 (57-69)	68.9 (63-75)	51.9 (47-57)	52 (47-58)	62.5 (56-69)	59.6 (53-67)	35.7 (30-42)	38.1 (33-45)
Region 6	6.6 (2-13)	1 (0-3)	1.5 (0-4)	1.8 (0-5)	2 (1-5)	2.6 (1-6)	1.2 (0-4)	2.5 (1-5)	1.5 (0-5)	2.7 (1-6)
SWEDEN	388.3 (355-426)	300.3 (282-322)	329.3 (318-341)	318.5 (309-329)	298.4 (281-319)	350.4 (344-358)	366 (351-383)	418.7 (403-436)	418.4 (406-432)	375.8 (353-403)
Norra	34.2 (23-47)	23.3 (16-31)	18.2 (13-24)	8.6 (4-14)	18.8 (12-26)	17.4 (13-22)	18.6 (14-25)	12.8 (7-19)	22.9 (17-29)	22.4 (14-32)
Jämtland	25.5 (17-36)	18.2 (12-25)	15.3 (10-21)	7.7 (4-13)	15 (9-21)	16.2 (12-21)	15.9 (11-21)	10.3 (6-16)	15.2 (11-21)	15.5 (9-23)
Västerbotten	0.2 (0-1)	0.1 (0-1)	0 (0-1)	0 (0-0)	0 (0-1)	0 (0-0)	0 (0-1)	0 (0-1)	0 (0-1)	0 (0-1)
Västernorrland	8.6 (3-15)	5.1 (1-10)	2.9 (1-6)	0.9 (0-3)	3.8 (1-8)	1.2 (0-4)	2.6 (0-6)	2.5 (0-6)	7.7 (5-11)	6.9 (3-12)
Mellersta	319.6 (296-347)	262.8 (249-278)	298.6 (289-309)	289 (281-298)	265.3 (251-282)	311.4 (305-319)	313.6 (300-328)	356.4 (343-371)	321.7 (311-334)	281.7 (264-302)
Dalarna	77.5 (66-90)	78.2 (70-88)	81.3 (75-88)	63.1 (57-69)	58.3 (49-68)	69.7 (65-75)	71.1 (63-80)	78.9 (71-88)	60.1 (53-68)	56.2 (47-67)
Gävleborg	33 (25-42)	42.6 (36-50)	49.8 (44-56)	54.2 (49-59)	45.5 (39-53)	69.4 (65-74)	60.8 (56-66)	50.4 (45-56)	33.7 (29-38)	21.4 (16-28)
Örebro	46.2 (38-55)	25.7 (20-32)	38.1 (33-43)	35 (31-39)	38.3 (31-46)	49.9 (44-55)	49.2 (42-57)	58.1 (51-65)	53.6 (48-60)	55.7 (50-62)
Stockholm	6.5 (3-11)	4.9 (2-8)	2.8 (2-5)	4.7 (3-7)	2.6 (0-5)	3.4 (2-5)	8.3 (5-12)	7 (4-10)	7.7 (4-11)	4.5 (3-7)
Uppsala	7.7 (3-13)	5.5 (2-10)	6.6 (4-10)	9.3 (6-13)	7.2 (4-11)	4.9 (3-7)	8.3 (6-12)	13 (10-16)	7.6 (5-11)	9.4 (7-12)
Värmland	103.8 (92-117)	83 (75-91)	88.3 (81-96)	87.9 (82-94)	84.6 (76-94)	82.1 (77-88)	79.3 (70-89)	106.2 (96-116)	100 (92-108)	67.3 (60-76)
Västmanland	22 (16-28)	14.3 (10-19)	26.1 (23-30)	26.3 (23-30)	15.9 (12-21)	26.6 (22-31)	18.4 (14-24)	23.4 (18-29)	27.3 (23-32)	23 (20-27)
VästraGötaland	22.9 (16-31)	8.6 (5-13)	5.5 (2-10)	8.6 (5-13)	13 (8-18)	5.3 (3-8)	18.3 (13-24)	19.3 (14-25)	31.7 (27-37)	44.2 (39-49)
Södra	34.4 (23-48)	14.2 (7-23)	12.5 (8-18)	20.9 (18-25)	14.2 (9-21)	21.6 (18-26)	33.8 (27-41)	49.6 (43-57)	73.8 (68-80)	71.7 (66-79)
Blekinge	1.3 (0-4)	0.5 (0-2)	1.2 (1-2)	0.1 (0-1)	0.2 (0-1)	0.2 (0-1)	0.2 (0-1)	0.3 (0-2)	0.1 (0-1)	0.3 (0-2)
Halland	2.6 (0-6)	0.6 (0-3)	0.4 (0-2)	0.2 (0-1)	0.5 (0-2)	0.3 (0-2)	1.6 (1-3)	0.8 (0-3)	1.2 (0-3)	2.2 (1-4)
Jönköping	6.1 (2-11)	2.9 (1-6)	1 (0-3)	0.6 (0-2)	1.4 (0-4)	1.4 (0-3)	2.9 (1-6)	9 (6-13)	13.8 (11-17)	8.9 (6-13)
Kalmar	3.9 (1-8)	1.3 (0-4)	0.5 (0-2)	1.1 (0-3)	1.7 (1-4)	0.5 (0-2)	1.8 (1-4)	1.2 (0-4)	0.8 (0-3)	1.2 (0-4)
Kronoberg	5 (1-10)	2.1 (0-5)	1.6 (1-3)	0.6 (0-2)	0.8 (0-3)	0.7 (0-2)	2 (1-4)	2 (1-4)	3.2 (2-5)	4.9 (3-8)
Östergötland	5.9 (2-11)	2.4 (0-6)	2.6 (1-6)	3.7 (3-6)	4.2 (2-8)	10 (9-12)	8.4 (6-12)	12.1 (9-16)	10.4 (9-13)	10.4 (8-14)
Skåne	4.8 (1-10)	1.7 (0-5)	1.5 (1-3)	2.1 (1-4)	0.7 (0-3)	0.4 (0-2)	2.8 (2-5)	5 (4-7)	12.3 (12-14)	17.8 (17-20)
Södermanland	4.8 (1-9)	2.8 (0-6)	3.6 (2-6)	12.4 (11-15)	4.8 (2-8)	8.1 (6-11)	14 (10-18)	19.3 (16-24)	32 (29-36)	26 (24-29)

Table A.6: Annual population growth rate estimates for the wolf population in Scandinavia ("Total") and separately for Norway and Sweden. Estimates were derived using the posterior distributions of annual abundance estimates (Table 1). Credible intervals (95%) are shown in parentheses.

	2014-2015	2015-2016	2016-2017	2017-2018	2018-2019	2019-2020	2020-2021	2021-2022	2022-2023
Norway	0.88 (0.73-1.04)	1.14 (1.00-1.29)	1.16 (1.02-1.32)	0.84 (0.75-0.94)	1.08 (0.96-1.22)	1.03 (0.91-1.16)	1.02 (0.90-1.16)	0.71 (0.60-0.83)	0.99 (0.83-1.19)
Sweden	0.78 (0.69-0.87)	1.10 (1.02-1.18)	0.97 (0.92-1.01)	0.94 (0.88-1.01)	1.18 (1.10-1.25)	1.04 (1.00-1.10)	1.14 (1.08-1.21)	1.00 (0.95-1.05)	0.90 (0.84-0.97)
Total	0.79 (0.71-0.88)	1.11 (1.04-1.17)	1.01 (0.97-1.04)	0.91 (0.87-0.97)	1.16 (1.09-1.21)	1.04 (1.00-1.09)	1.12 (1.07-1.17)	0.95 (0.91-0.99)	0.91 (0.85-0.98)

Table A.7: Estimates of the demographic parameters obtained from the sex-specific wolf OPSCR models. Parameters represent transition rates from Oct 1 to Sep 30 in the following year. State 2 and 3 represent other and scent-marking individuals, respectively. Median estimates and 95% credible intervals (in parentheses) for per capita recruitment rate (ρ), survival (ϕ), transition probability from other to scent-marking adult state (ψ), mortality due to legal culling (h) and mortality due to other causes (w) are presented for males (M) and females (F).

	State	2014-2015		2015-2016		2016-2017		2017-2018		2018-2019	
		M	F	M	F	M	F	M	F	M	F
ρ	-	0.54 (0.37-0.72)	0.35 (0.19-0.52)	0.66 (0.52-0.79)	1.16 (0.94-1.37)	0.65 (0.58-0.72)	0.72 (0.63-0.81)	0.64 (0.55-0.76)	0.48 (0.39-0.60)	0.80 (0.66-0.93)	0.85 (0.69-0.98)
ϕ	2	0.37 (0.28-0.47)	0.40 (0.29-0.52)	0.50 (0.41-0.60)	0.46 (0.35-0.58)	0.47 (0.39-0.56)	0.58 (0.49-0.67)	0.47 (0.38-0.56)	0.50 (0.41-0.59)	0.59 (0.49-0.68)	0.55 (0.44-0.65)
	3	0.61 (0.47-0.74)	0.66 (0.52-0.78)	0.67 (0.55-0.77)	0.65 (0.54-0.76)	0.54 (0.43-0.65)	0.57 (0.46-0.69)	0.57 (0.46-0.68)	0.61 (0.50-0.72)	0.61 (0.49-0.73)	0.65 (0.53-0.76)
ψ	-	0.36 (0.23-0.52)	0.34 (0.21-0.51)	0.33 (0.22-0.45)	0.53 (0.37-0.68)	0.41 (0.30-0.53)	0.44 (0.33-0.56)	0.34 (0.23-0.46)	0.27 (0.17-0.38)	0.35 (0.25-0.47)	0.48 (0.35-0.61)
h	2	0.16 (0.11-0.23)	0.19 (0.12-0.27)	0.12 (0.07-0.18)	0.07 (0.03-0.13)	0.14 (0.09-0.20)	0.12 (0.07-0.18)	0.24 (0.17-0.32)	0.15 (0.09-0.21)	0.06 (0.03-0.11)	0.09 (0.05-0.15)
	3	0.08 (0.04-0.16)	0.09 (0.04-0.17)	0.06 (0.02-0.13)	0.09 (0.04-0.17)	0.11 (0.06-0.20)	0.12 (0.06-0.20)	0.19 (0.11-0.29)	0.14 (0.07-0.22)	0.07 (0.03-0.15)	0.07 (0.02-0.14)
w	2	0.47 (0.37-0.56)	0.41 (0.28-0.53)	0.38 (0.29-0.47)	0.46 (0.35-0.58)	0.38 (0.30-0.47)	0.30 (0.22-0.39)	0.29 (0.20-0.37)	0.35 (0.27-0.45)	0.35 (0.26-0.44)	0.36 (0.27-0.47)
	3	0.30 (0.18-0.44)	0.24 (0.13-0.39)	0.27 (0.17-0.38)	0.25 (0.16-0.37)	0.34 (0.24-0.45)	0.31 (0.21-0.42)	0.24 (0.15-0.34)	0.25 (0.16-0.35)	0.31 (0.21-0.43)	0.28 (0.18-0.39)

	State	2019-2020		2020-2021		2021-2022		2022-2023	
		M	F	M	F	M	F	M	F
ρ	-	0.76 (0.68-0.86)	0.62 (0.55-0.71)	0.74 (0.62-0.86)	0.86 (0.74-0.98)	0.61 (0.53-0.70)	0.73 (0.64-0.83)	0.61 (0.51-0.72)	0.58 (0.47-0.73)
ϕ	2	0.46 (0.38-0.54)	0.52 (0.43-0.61)	0.51 (0.43-0.60)	0.55 (0.46-0.64)	0.38 (0.31-0.46)	0.48 (0.40-0.57)	0.46 (0.37-0.55)	0.46 (0.37-0.56)
	3	0.70 (0.59-0.80)	0.66 (0.55-0.76)	0.64 (0.53-0.74)	0.73 (0.62-0.82)	0.58 (0.48-0.69)	0.60 (0.50-0.70)	0.59 (0.48-0.69)	0.63 (0.52-0.73)
ψ	-	0.39 (0.28-0.50)	0.38 (0.27-0.50)	0.35 (0.25-0.46)	0.35 (0.25-0.47)	0.46 (0.34-0.58)	0.46 (0.35-0.58)	0.31 (0.21-0.44)	0.42 (0.30-0.55)
h	2	0.12 (0.08-0.18)	0.05 (0.02-0.10)	0.18 (0.12-0.24)	0.17 (0.11-0.24)	0.17 (0.12-0.23)	0.15 (0.10-0.21)	0.23 (0.17-0.31)	0.23 (0.17-0.30)
	3	0.07 (0.02-0.14)	0.07 (0.03-0.14)	0.18 (0.11-0.27)	0.09 (0.04-0.17)	0.11 (0.06-0.19)	0.14 (0.07-0.22)	0.15 (0.08-0.24)	0.13 (0.07-0.21)
w	2	0.42 (0.34-0.50)	0.42 (0.33-0.51)	0.31 (0.23-0.39)	0.28 (0.20-0.37)	0.45 (0.37-0.52)	0.37 (0.29-0.46)	0.31 (0.22-0.40)	0.31 (0.21-0.41)
	3	0.23 (0.14-0.34)	0.26 (0.17-0.36)	0.18 (0.10-0.27)	0.17 (0.10-0.27)	0.30 (0.20-0.40)	0.26 (0.17-0.36)	0.26 (0.17-0.36)	0.24 (0.15-0.34)

Table A.8: Estimates of the spatial and movement process parameters obtained from the sex-specific wolf OPSCR models. β_{dens} represents the effect of the number of known wolf packs on AC locations (Bischof et al., 2020). The scale parameter σ of the detection function is expressed in kilometers and estimated separately for other (σ_1) and scent-marking (σ_2) individuals. τ represents the mean of the exponential movement parameter, describing individual movement distances between years, estimated separately for other (τ_1) and scent-marking (τ_2) individuals. Credible intervals (95%) are shown in parentheses. Parameters that were assumed to be constant across years are marked with *.

	2014/2015 M	2014/2015 F	2015/2016 M	2015/2016 F	2016/2017 M	2016/2017 F	2017/2018 M	2017/2018 F	2018/2019 M	2018/2019 F
β_{dens}^*	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)
σ_1	7.88 (7.03-8.89)	7.06 (6.25-8.04)	8.09 (7.47-8.78)	6.38 (5.76-7.13)	7.47 (7.04-7.93)	7.93 (7.48-8.41)	7.64 (7.29-8.04)	8.18 (7.77-8.61)	7.32 (6.78-7.92)	6.64 (6.07-7.29)
σ_2	8.60 (7.81-9.51)	8.37 (7.50-9.38)	8.36 (7.75-9.05)	7.33 (6.75-8.01)	7.93 (7.60-8.29)	7.91 (7.56-8.30)	7.89 (7.59-8.20)	7.36 (7.04-7.70)	8.45 (7.99-8.95)	8.23 (7.69-8.81)
τ_1^*	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)
τ_2^*	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)

	2019/2020 M	2019/2020 F	2020/2021 M	2020/2021 F	2021/2022 M	2021/2022 F	2022/2023 M	2022/2023 F	2023/2024 M	2023/2024 F
β_{dens}^*	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)	0.28 (0.26-0.30)	0.29 (0.27-0.31)
σ_1	7.92 (7.62-8.25)	7.59 (7.28-7.93)	7.85 (7.38-8.36)	7.36 (6.85-7.95)	7.06 (6.64-7.51)	7.81 (7.33-8.34)	6.33 (5.94-6.75)	7.35 (6.88-7.87)	7.08 (6.57-7.66)	6.94 (6.34-7.64)
σ_2	8.03 (7.70-8.38)	7.76 (7.45-8.10)	7.65 (7.29-8.03)	7.10 (6.73-7.50)	7.64 (7.31-7.99)	7.79 (7.38-8.24)	7.33 (7.00-7.69)	6.55 (6.24-6.90)	8.39 (7.97-8.84)	7.07 (6.67-7.51)
τ_1^*	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)	71.22 (68.64-74.03)	63.19 (60.75-65.83)
τ_2^*	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)	6.95 (6.44-7.51)	4.34 (3.97-4.76)

Table A.9: Estimates of the detection process parameters for the structured sampling $\beta_{1\,Structured}$ corresponds to the effect of previous detection of an individual on detection probability, $\beta_{2\,Structured}$ to the effect of search-effort (track length) on detection probability, and $\beta_{3\,Structured}$ to the effect of average snow cover during the monitoring period on detection probability ($p_{0\,Structured}$). Coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	2014/2015 M	2014/2015 F	2015/2016 M	2015/2016 F	2016/2017 M	2016/2017 F	2017/2018 M	2017/2018 F	2018/2019 M	2018/2019 F
$\beta_{1\,Structured}$	0.27 (-0.21-0.75)	0.16 (-0.35-0.65)	-0.19 (-0.58-0.19)	-0.21 (-0.64-0.25)	0.08 (-0.21-0.40)	0.25 (-0.05-0.54)	-0.11 (-0.37-0.17)	0.34 (0.05-0.62)	-0.34 (-0.80-0.10)	-0.02 (-0.40-0.37)
$\beta_{2\,Structured}$	0.43 (0.32-0.53)	0.44 (0.33-0.55)	0.41 (0.31-0.51)	0.40 (0.27-0.54)	0.25 (0.18-0.32)	0.32 (0.25-0.39)	0.34 (0.28-0.40)	0.32 (0.25-0.38)	0.33 (0.24-0.41)	0.37 (0.28-0.46)
$\beta_{3\,Structured}$	0.27 (-0.11-0.66)	-0.07 (-0.48- 0.35)	0.01 (-0.41-0.42)	-0.63 (-1.20--0.08)	-0.22 (-0.47-0.04)	-0.08 (-0.40- 0.22)	0.02 (-0.30-0.35)	0.29 (-0.09- 0.70)	0.16 (-0.18-0.50)	0.00 (-0.42- 0.43)

	2019/2020 M	2019/2020 F	2020/2021 M	2020/2021 F	2021/2022 M	2021/2022 F	2022/2023 M	2022/2023 F	2023/2024 M	2023/2024 F
$\beta_{1\,Structured}$	0.06 (-0.18-0.29)	0.03 (-0.20-0.26)	0.78 (0.44-1.11)	0.30 (-0.08-0.69)	0.39 (0.11-0.68)	0.00 (-0.28-0.27)	0.22 (-0.06-0.50)	0.06 (-0.23-0.35)	0.10 (-0.24-0.45)	-0.20 (-0.59-0.22)
$\beta_{2\,Structured}$	0.40 (0.33-0.46)	0.35 (0.28-0.42)	0.25 (0.19-0.31)	0.25 (0.18-0.33)	0.28 (0.22-0.35)	0.28 (0.22-0.35)	0.34 (0.26-0.42)	0.36 (0.29-0.43)	0.17 (0.12-0.22)	0.28 (0.19-0.38)
$\beta_{3\,Structured}$	0.04 (-0.14-0.24)	0.10 (-0.10- 0.31)	0.34 (0.14-0.54)	0.42 (0.18- 0.68)	0.40 (0.20-0.62)	0.17 (-0.07- 0.42)	0.05 (-0.13-0.22)	0.16 (-0.04- 0.36)	0.27 (0.07-0.47)	-0.10 (-0.32- 0.12)

Table A.10: Estimates of the detection process parameters for the unstructured sampling $\beta_{1Unstructured}$ corresponds to the effect of previous detection of an individual on baseline detection probability, $\beta_{2Unstructured}$ to the effect of distance to the nearest roads on detection probability, $\beta_{3Unstructured}$ to the effect of average snow cover during the monitoring period on detection probability, and $\beta_{4Unstructured}$ to the effect of spatio-temporal heterogeneity in unstructured sampling derived using the observation data in Skandobs and Rovbase. Coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	2014/2015		2015/2016		2016/2017		2017/2018		2018/2019	
	M	F	M	F	M	F	M	F	M	F
$\beta_{1Unstructured}$	0.74 (0.35-1.14)	0.57 (0.11-1.01)	0.45 (0.14-0.75)	-0.20 (-0.54-0.15)	0.09 (-0.14-0.33)	0.32 (0.10-0.55)	0.21 (0.02-0.41)	0.66 (0.45-0.87)	0.03 (-0.31-0.37)	0.92 (0.52-1.33)
$\beta_{2Unstructured}$	-1.34 (-2.57–0.43)	-1.51 (-3.06–0.40)	-0.11 (-0.58- 0.29)	-0.52 (-1.30- 0.08)	-0.40 (-0.84–0.04)	-0.54 (-1.08–0.09)	-1.27 (-2.06–0.60)	-0.79 (-1.37–0.28)	-0.25 (-0.86- 0.21)	0.30 (-0.34- 0.91)
$\beta_{3Unstructured}$	0.19 (-0.11- 0.49)	-0.18 (-0.50- 0.14)	0.32 (0.00- 0.67)	-0.07 (-0.51- 0.36)	-0.09 (-0.27- 0.10)	-0.03 (-0.23- 0.17)	-0.26 (-0.48–0.04)	-0.29 (-0.55–0.03)	-0.31 (-0.57–0.04)	-0.60 (-0.88–0.32)
$\beta_{4Unstructured}$	0.96 (0.61-1.32)	0.85 (0.47-1.24)	0.77 (0.48-1.07)	0.85 (0.49-1.25)	1.08 (0.76-1.40)	1.19 (0.86-1.53)	1.25 (0.90-1.62)	1.69 (1.25-2.14)	1.17 (0.70-1.70)	1.78 (1.19-2.44)

	2019/2020		2020/2021		2021/2022		2022/2023		2023/2024	
	M	F	M	F	M	F	M	F	M	F
$\beta_{1Unstructured}$	0.22 (0.03-0.41)	0.56 (0.38-0.75)	0.83 (0.54-1.10)	0.55 (0.24-0.86)	0.12 (-0.17-0.41)	0.44 (0.16-0.72)	0.51 (0.25-0.76)	0.47 (0.21-0.72)	0.13 (-0.20-0.46)	0.77 (0.40-1.13)
$\beta_{2Unstructured}$	-0.72 (-1.48–0.11)	-0.49 (-1.30- 0.14)	-0.95 (-1.82–0.26)	2.00 (-0.04- 3.54)	0.11 (-0.39- 0.56)	-1.42 (-3.35- 0.01)	0.36 (-0.41- 1.08)	-0.35 (-1.59- 0.66)	0.11 (-0.64- 0.79)	0.36 (-0.20- 1.03)
$\beta_{3Unstructured}$	0.03 (-0.08- 0.14)	0.11 (0.00- 0.23)	-0.23 (-0.39–0.07)	-0.28 (-0.46–0.09)	-0.11 (-0.26- 0.04)	-0.22 (-0.38–0.05)	-0.52 (-0.63–0.41)	-0.36 (-0.48–0.25)	-0.26 (-0.40–0.12)	-0.42 (-0.57–0.26)
$\beta_{4Unstructured}$	1.61 (1.25-2.02)	1.84 (1.42-2.26)	1.27 (0.90-1.65)	1.58 (1.09-2.18)	2.05 (1.39-2.80)	1.52 (0.94-2.22)	1.24 (0.74-1.80)	1.75 (1.20-2.31)	1.35 (0.78-2.06)	1.67 (1.07-2.34)

Table A.11: Average proportion of individuals detected via non-invasive genetic sampling (NGS) in Scandinavia. Values were calculated as the number of individuals detected with NGS (Table A.3) divided by the total and sex-specific abundance estimates obtained from the OPSCR models (Table A.5). Credible intervals (95%) are shown in parentheses.

	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022	2022/2023	2023/2024
M	0.50 (0.44-0.55)	0.78 (0.72-0.83)	0.89 (0.85-0.92)	0.93 (0.90-0.96)	0.78 (0.72-0.83)	0.95 (0.92-0.97)	0.82 (0.78-0.86)	0.86 (0.81-0.90)	0.89 (0.85-0.93)	0.87 (0.80-0.93)
F	0.51 (0.44-0.58)	0.72 (0.66-0.77)	0.88 (0.84-0.91)	0.90 (0.86-0.93)	0.75 (0.69-0.80)	0.94 (0.91-0.96)	0.86 (0.82-0.89)	0.87 (0.83-0.90)	0.86 (0.81-0.89)	0.79 (0.71-0.87)
Total	0.50 (0.46-0.55)	0.75 (0.71-0.79)	0.88 (0.86-0.91)	0.91 (0.89-0.93)	0.76 (0.72-0.80)	0.94 (0.92-0.96)	0.84 (0.81-0.87)	0.86 (0.83-0.89)	0.87 (0.84-0.90)	0.83 (0.77-0.88)