2022

MINA fagrapport 77

Estimates of wolf density, abundance, and population dynamics in Scandinavia, 2013–2022

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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 have been 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 eighth consecutive seasons from 2013/2014 to 2021/2022. We adjusted the OPSCR model, originally used in previous abundance estimations, to increase the size of the area for which estimates are provided, as well as the degree of model realism.

Results We generated annual density maps and both total and jurisdiction-specific population sizes for wolf from the winter 2013/2014 to 2021/2022. Based on the OPSCR model, the Scandinavian wolf population was likely (95% credible interval) between 472 and 509 individuals in 2021/2022, with 381 to 417 individuals attributed to Sweden and 83 to 101 to Norway. In addition to annual density and jurisdiction-specific abundance estimates, we report annual estimates of cause-specific mortalities, recruitment, and detection probabilities.
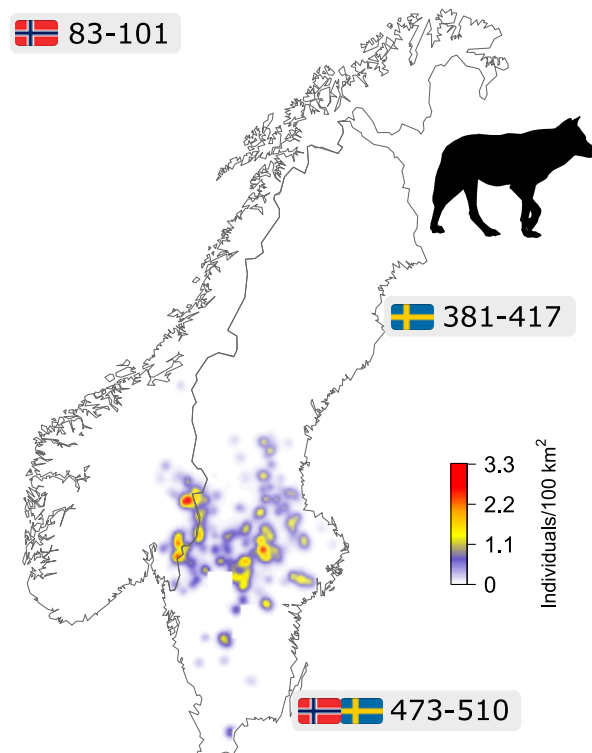
Density map and ranges of abundance
estimated for wolves in 2021/2022

Sammendrag

Bakgrunn Den skandinaviske bestanden av ulv (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 (www.rovbase.se ; www.rovbase.no).

Tilnærming Ved bruk av en Bayesiansk åpen romlig fangst-gjenfangst populasjons modell (OPSCR), utviklet av RovQuant, estimerte vi årlige tettheter og demografiske rater hos den skandinaviske ulvebestanden i åtte sesonger fra 2013/2014 til 2021/2022. Vi justerte OPSCR modellen som har vært brukt tidligere år slik at den nå omfatter et større geografisk område og har en større grad av realisme.

Resultater Vi laget årlige kart med tetthet av ulv fra 2013/2014 til 2021/2022, hvor bestandsstørrelsen både totalt og innenfor ulike administrative enheter kunne avledes. Basert på OPSCR modellen var den skandinaviske ulvebestanden mellom 472 og 509 individer i 2021/2022 (95% kredibelt intervall), med 381 til 417 individer i Sverige og 83 til 101 individer i Norge. I tillegg til årlige tettheter og områdespesifikke bestandsestimater, gir rapporten estimater på dødlighetsfaktorer, rekrutering og oppdagbarhet.
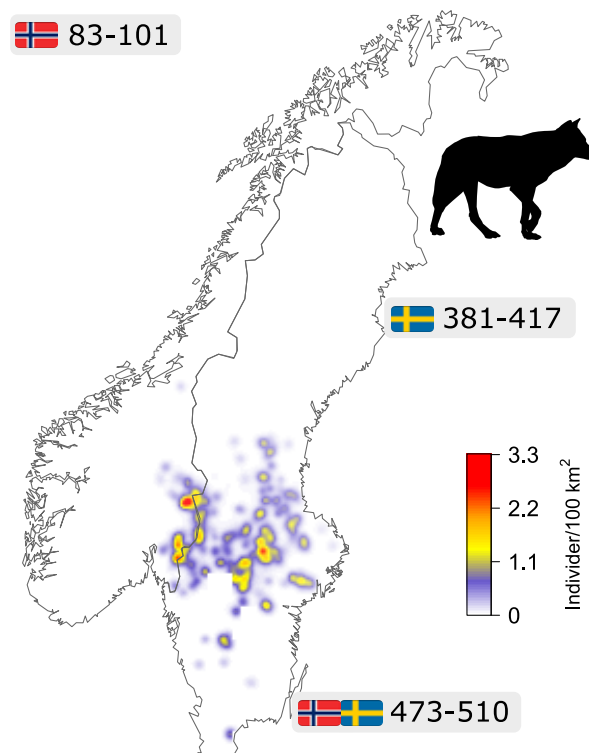
Kart som viser tetthet av jerv i 2021/2022 sammen med intervaller for estimert antall ulv

Contents

1 Introduction

Non-invasive genetic sampling (NGS) and dead recoveries, are a 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 individual animals 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 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., 2022). The conversion factor approach assumes that the relationship between total population size and the number of observed reproduction 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, including 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 March 2019 (Bischof et al., 2019a), jointly for wolves, bears and wolverines in December 2019 (Bischof et al., 2019b, 2020), for wolves in 2020 (Milleret et al., 2021b), and for wolverines in 2020 (Flagstad et al., 2021) and 2021 (Milleret et al., 2022b). During these and other analyses, RovQuant has continuously improved the performance of the OPSCR models. In the present report we summarize the analysis of a 9-year time series (2013/2014–2021/2022) 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 (with credible intervals) for Sweden, Norway, and both countries combined, as well as estimates by county in Sweden and large carnivore management regions in Norway.

- 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: Definitions and acronyms

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: 2022-05-13). 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 2013/2014 to 2021/2022.

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 (Wabakken et al., 2022). 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 then 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 (Fylkesmannen or SNO in Norway and Länsstyrelserna or the police authorities in Sweden). All other 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.

GPS search tracks Government employees involved in systematic searches for wolf DNA along roads and following wolf tracks (via snowmobiles, skis, snowshoes, etc.) 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 that were collected during wolf monitoring seasons since 2012 , skandobs.se;last extraction: 2022-06-09). Skandobs is a web application that allows anyone to anonymously register observations (visual, tracks, faeces, etc.) of bears, lynx, wolves, and wolverines in Scandinavia. This data consists of more than 20 000 records or possible large carnivore observations. Although most observations are not verified, they offer the best available proxy for spatio-temporal variation in

opportunistic 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; Wabakken et al., 2016, 2018). 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; Wabakken et al., 2016, 2018, 2020, 2022) 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). However, the Swedish Environmental Protection Agency requested that the study area be expanded to include the entire south of Sweden, following a corresponding expansion in the wolf range. This led to a $68\,400 km^2$ increase in the size of the study area (total= $(322400\ km^2)$, compared to the previous abundance estimations by RovQuant (Bischof et al., 2019b, 2020; Milleret et al., 2021b).

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).

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 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 was assigned as an "other" individual; 3) "alive adult scent-marking" if it is alive and was 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 occasion; or 5) "dead": if it has died but was not recovered dead. We then modelled the transition probabilities from one state to another between the monitoring season t and $t+1$ 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, 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 known locations of known packs at time $t-1$ (see Bischof et al. (2019b) and Bischof et al. (2020) for more details). For the following years ($t > 1$), the location of individual activity centers was a function of the distance from previous (at time $t-1$) activity centers, as well as a function of the locations of known packs. Contrary to previous OPSCR models, 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, wolf DNA materials are collected by two main processes. First, authorities collect DNA material and record the corresponding search effort during official searches ("structured monitoring" 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, for which search effort is not directly available ("unstructured" monitoring" thereafter). Currently, it is not possible to unambiguously distinguish between samples collected during the structured or unstructured monitoring in Rovbase. We therefore assigned each sample to the 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" monitoring if it was collected by the authorities (marked as collected by "Statsforvalteren" and "SNO" in Rovbase) and if it was located within 500m from a search track recorded the same day. All remaining samples were assigned to the unstructured monitoring.

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 respective 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 was assumed to be driven by different processes.

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

- Spatial-variation in effort using the length of GPS search tracks.

- 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 monitoring*** using:

- 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 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 influence the probability of being detected at subsequent occasions.

- Spatio-temporal variation in unstructured search effort Figure A.1. In order to obtain a proxy for the probability that a sample was collected by a member of the public, we checked whether any carnivore sample from Rovbase (excluding the ones used by the OPSCR model) or any observation from skandobs was recorded in each detector grid cell during each monitoring season (Oct 1 – Mar 31). This produced annual maps representing whether at least one carnivore presence index was collected for each detector, with the aim to identify areas with a non-null probability that an opportunistic wolf DNA sample would be collected if present.

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 (Turek et al., 2021; de Valpine et al., 2017; NIMBLE Development Team, 2019) and nimbleSCR (Bischof et al., 2021) in R version 3.3.3 (R Core Team, 2018). We ran 4 chains each with 32000 iterations, including a 10000-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). Following this procedure, an individual detected near a border can have its model-predicted AC placed on different sides of that border in different model iterations. From this, the probability of designating the individual 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", REF) - individuals can be partially designated to both countries (REF).
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.2) 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.2). Yearly population growth rates (λ; Table A.5) were calculated as $\lambda_t = N_{t+1}/N_t$.

Focus on uncertainty Although we reported median (or mean for abundance; see below) estimates for all parameters in the tables, we intentionally focused the main results of our 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 16 940 (7 391 female; 9 549 male) genotyped wolf genetic samples were included in the analysis, of which 75% originated from Sweden. These samples were associated with 1 576 (717 female; 859 male) individuals. We did not include individuals with unknown sex in this analysis. Among all genotyped samples, 4 995 (2050 female; 2945 male) were assigned to the structured monitoring and 11 945 (5341 female; 6604 male) to unstructured monitoring. We also used 617 (264 female; 353 male) dead recoveries of wolves in the OPSCR model, of which 508 (213 female; 295 male) were due to legal culling and 109 (51 female; 58 male) due to other causes of mortality. The majority of dead recoveries (64%) 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.1, NGS individuals: Table A.2, dead recoveries: Table A.3)

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 472 and 509 individuals in 2021/2022 (Table 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 46% and 50% in 2021/2022. Based on the model-predicted location of ACs, we estimated that in 2021/2022, between 381 to 417 individuals could be attributed to Sweden and 83 to 101 to Norway (Table 1). See Table 1 for total and sex-specific estimates for each country and management area. See Table A.4 for annual estimates for all of Scandinavia and by region between 2012/2013 and 2021/2022. Note that estimates for different years (Figure A.3) shown here differ slightly from those provided in Bischof et al. (2020) and Milleret et al. (2021a). 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.4). Overall, average wolf density throughout the study area was likely between 0.15 and 0.16 wolves per 100 km^2 in 2021/2022 (Figure 1).

Table 1: Wolf population size estimates by sex and jurisdiction (Norway: carnivore management regions, Sweden: counties) in 2021/2022. 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	235.9 (225-249)	253.6 (241-268)	489.5 (472-509)
NORWAY	51.2 (44-59)	40.2 (36-45)	91.3 (83-101)
Region 2	0.2 (0-1)	0.2 (0-1)	0.3 (0-2)
Region 3	0.9 (0-3)	0.7 (0-2)	1.6 (0-4)
Region 4	12.8 (10-16)	14.7 (12-18)	27.5 (23-32)
Region 5	35.8 (30-42)	23.4 (20-28)	59.2 (52-67)
Region 6	1.5 (0-5)	1.3 (1-3)	2.8 (1-6)
SWEDEN	184.7 (175-196)	213.4 (201-228)	398.1 (381-417)
Örebro	23 (19-28)	36.1 (31-42)	59.1 (52-66)
Östergötland	4.2 (3-6)	5.8 (5-8)	10.1 (8-13)
Blekinge	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)
Dalarna	37.1 (32-43)	37.7 (32-45)	74.8 (67-83)
Gävleborg	25.9 (22-30)	25.5 (22-30)	51.4 (46-57)
Halland	0.2 (0-1)	0.4 (0-2)	0.6 (0-2)
Jämtland	5 (2-9)	4.2 (1-8)	9.1 (5-15)
Jönköping	4.3 (2-7)	4.1 (2-6)	8.4 (5-12)
Kalmar	0.2 (0-1)	0.3 (0-2)	0.6 (0-2)
Kronoberg	0.3 (0-2)	1.4 (1-3)	1.7 (1-4)
Södermanland	9.2 (7-11)	8.9 (7-12)	18.2 (15-22)
Skåne	1.3 (1-3)	2.4 (2-4)	3.7 (3-6)
Stockholm	2.9 (1-5)	2.3 (1-4)	5.2 (3-8)
Uppsala	5.4 (4-7)	6.6 (6-9)	12 (10-15)
Värmland	47.4 (41-54)	54.1 (48-60)	101.6 (93-111)
Västerbotten	0 (0-0)	0 (0-0)	0 (0-1)
Västernorrland	0.6 (0-2)	1.3 (0-4)	1.9 (0-5)
Västmanland	10.2 (7-14)	13 (9-17)	23.1 (18-29)
VästraGötaland	7.4 (4-11)	9.1 (6-13)	16.5 (12-22)
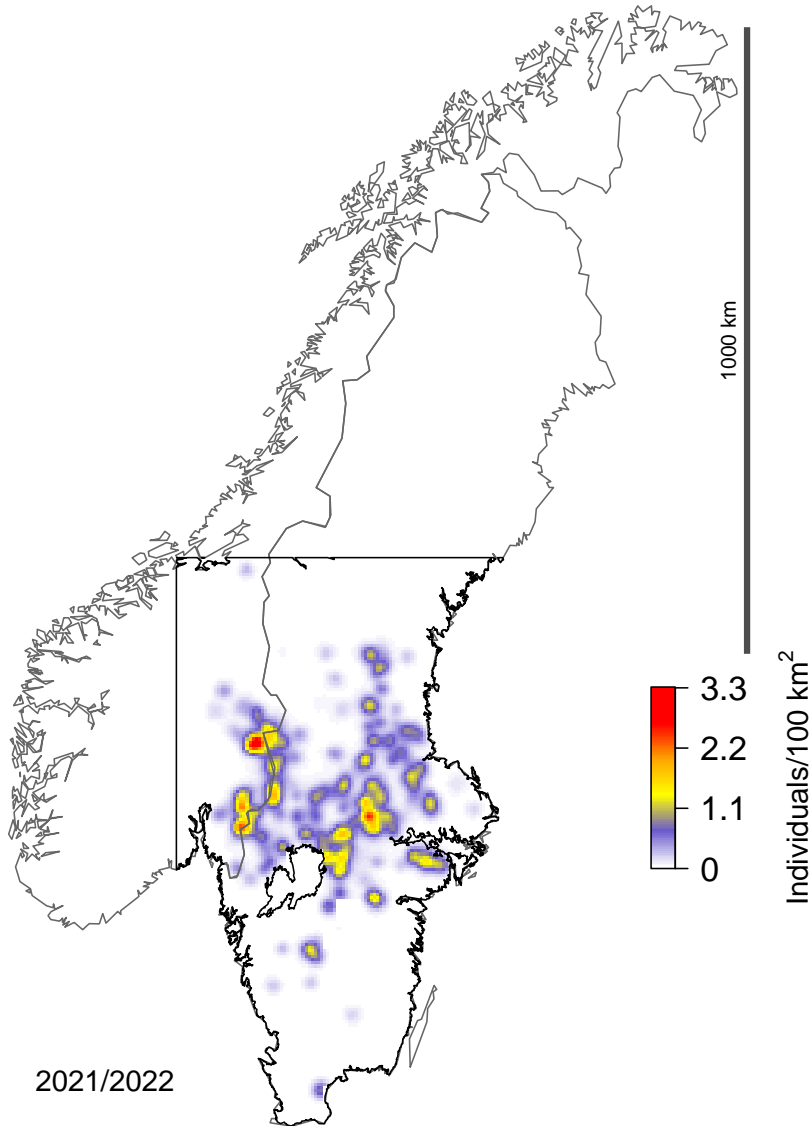
Figure 1: Wolf density based on individual utilization distributions throughout the study area (black polygon) in Scandinavia in 2021/2022. This map is freely available as a geo-referenced raster file at https://github.com/richbi/RovQuantPublic

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 2; Table A.6). There was temporal variation in mortality rates, with a risk of mortality from other causes than culling generally higher than the risk of mortality from culling. Overall, scent-marking individuals had a higher survival compared to other individuals, with no pronounced systematic differences between sexes (Figure A.5).
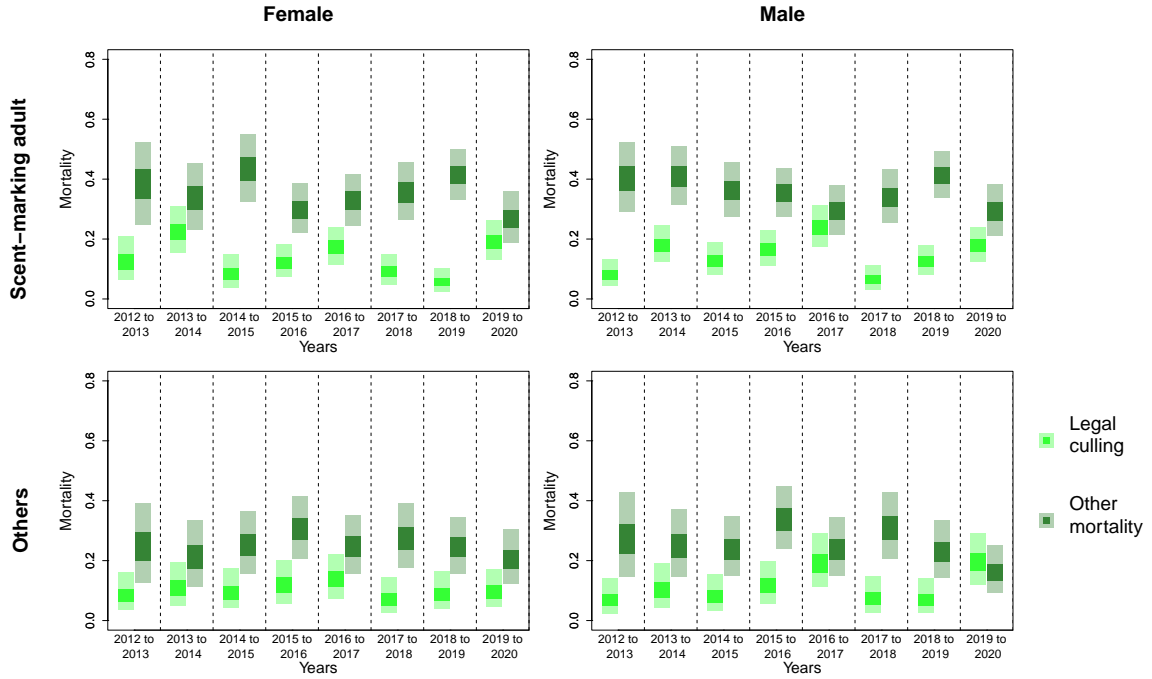
Figure 2: Mortality probabilities due to legal culling (light green) and all other causes (dark green) for female and male wolves. Shown are overall estimates throughout the study area. Estimates refer to deaths occurring between the start of one sampling season and the start of the next.
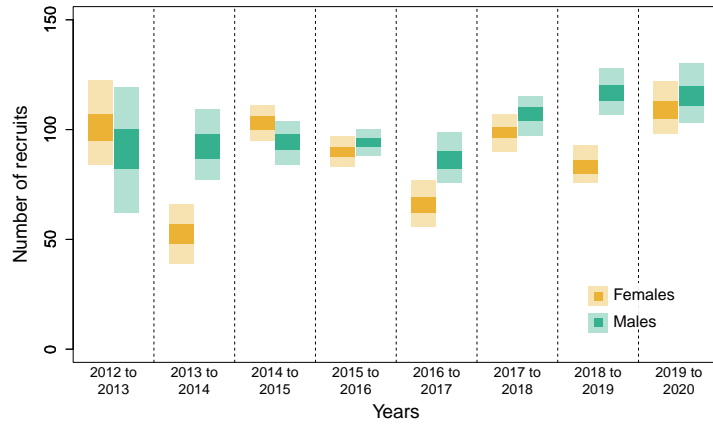
Figure 3: Estimated annual number of recruits for female and male wolves. Recruitment represents the number of new individuals present in the population on Oct 1 (individuals recently born and that immigrate in the study area). Bars represent the 95% credible interval. Estimates refer to number of individuals recruited between the start of one sampling season and the start of the next.

3.4 Detection probability

The overall proportion of detected individuals in the population was likely between 86% and 93% in 2021/22 (Table A.10). The baseline detection probability for the structured and unstructured sampling varied both in time and space (Figure A.6 and Figure A.7). More specifically, the length of recorded search tracks positively affected detection probability of the structured sampling (2021/2022; males: $\beta = 0.22$, CrI: 0.16 - 0.29; females: $\beta = 0.20$, CrI: 0.12 - 0.27; Table A.8). 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.8).

For the unstructured sampling, the effect of spatio-temporal variation in opportunistic search effort derived using the observation data in Skandobs and Rovbase had a strong positive effect (2021/2022; males: $\beta = 1.27$, CrI: 0.84 - 1.71; females: $\beta = 1.46$, CrI: 1.00 - 1.95; Table A.9). The effect of previous detection also tended to have a positive effect on detection probability for the unstructured sampling, but the pattern was not consistent across years (Table A.9).

4   Summary of improvements made

The analysis described in this report includes the following adjustments compared with previous analyses of wolf density in Scandinavia by RovQuant (Bischof et al., 2020; Flagstad et al., 2021; Milleret et al., 2021b):

1. Addition of data from the 2021/2022 monitoring season and exclusion of the 2012/2013 winter monitoring season.

2. Expansion of the study area for which estimates are generated by inclusion of the south of Sweden.

3. Only dead recoveries and live detection were used to reconstruct the state of individuals, age has been ignored to limit the risk of bias.

4. Replaced the half-normal movement model with the exponential for modelling inter-annual movement.

5. Separated estimation of the inter-annual movement parameter by social states (scent-marking adult vs. other).

6. Separated estimation of the scale parameter of the detection function (related to home range size) by social states (scent-marking adult vs. other).

7. Used separate detection submodels for structured and unstructured sampling to account for fundamental differences in how samples accumulate and how variation in search effort is accounted for.

8. Allowed for annual variation in all covariates on the detection submodel (i.e. covariates are time-dependent).

9. Used carnivore observation reports in Skandobs and ancillary carnivore samples recorded in Rovbase to generate a new covariate that serves as a proxy for sampling effort (spatially and temporally varying) during unstructured sampling.

5   Suggestions for future improvements

RovQuant continues to work on improving the functionality and efficiency of OPSCR models. We plan to test and potentially implement the following developments in 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. Distinguish between dispersing and non-dispersing individuals, for example by using a finite-mixture approach (REF).

3. Consider alternative detection models that do not assume a half-normal shape and/or circular home ranges (REF).

4. Account for spatial variation in survival (Milleret et al., 2022a)

6   Acknowledgements

7   Data availability

Data, R code to reproduce the analysis, as well as figures, tables, and raster maps (Figure A.4) are available on GitHub https://github.com/richbi/RovQuantPublic

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Appendices
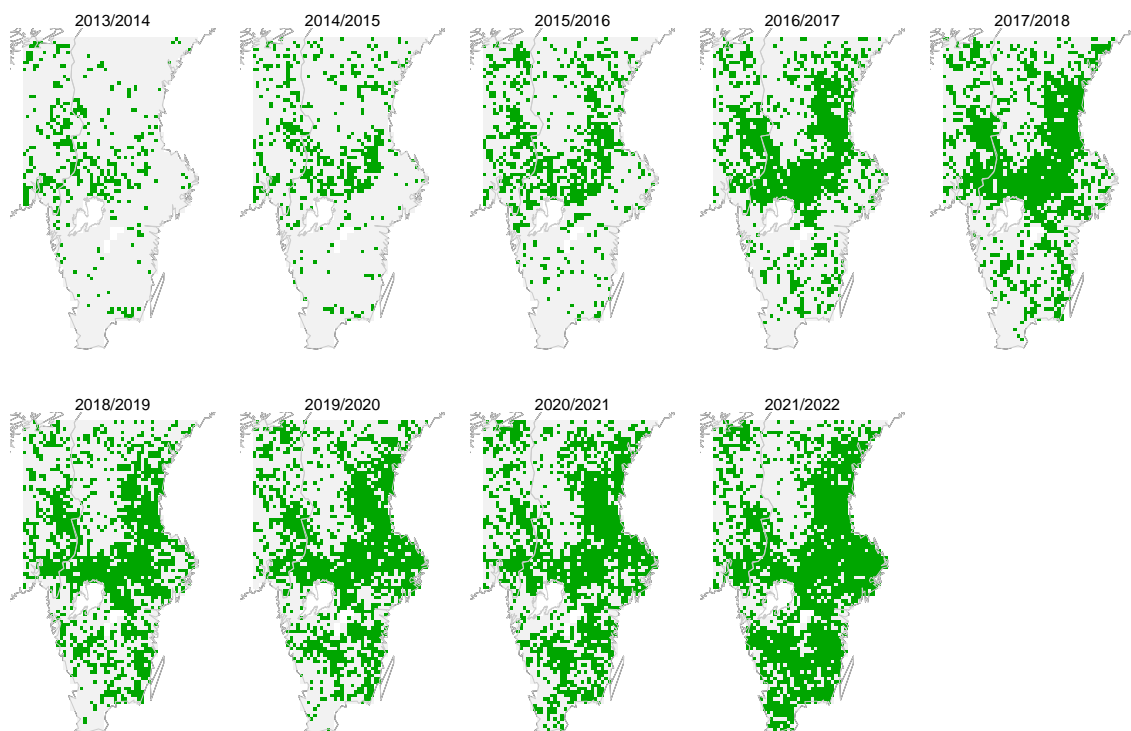
Figure A.1: Covariate used to account for spatio-temporal variation in unstructured search effort in the study area. Green cells (10 x 10 km) represent areas with at least one carnivore record from Rovbase (rovbase.no, excluding the ones used by the OPSCR model) or an observation record from Skandobs (skandobs.no) during each monitoring season (Oct 1 – Mar 31).
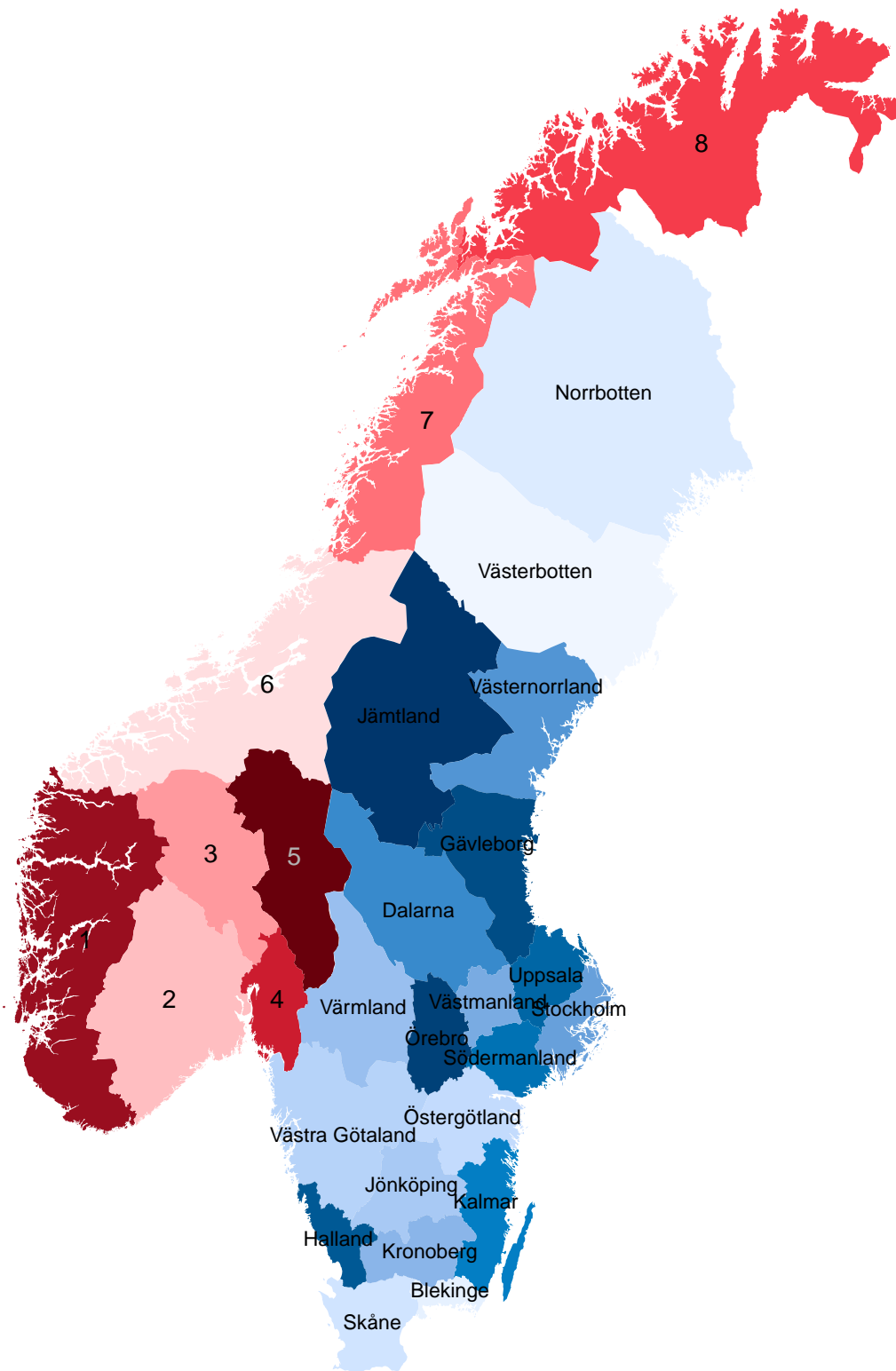
Figure A.2: Management units in Norway (carnivore management regions) and Sweden (counties).
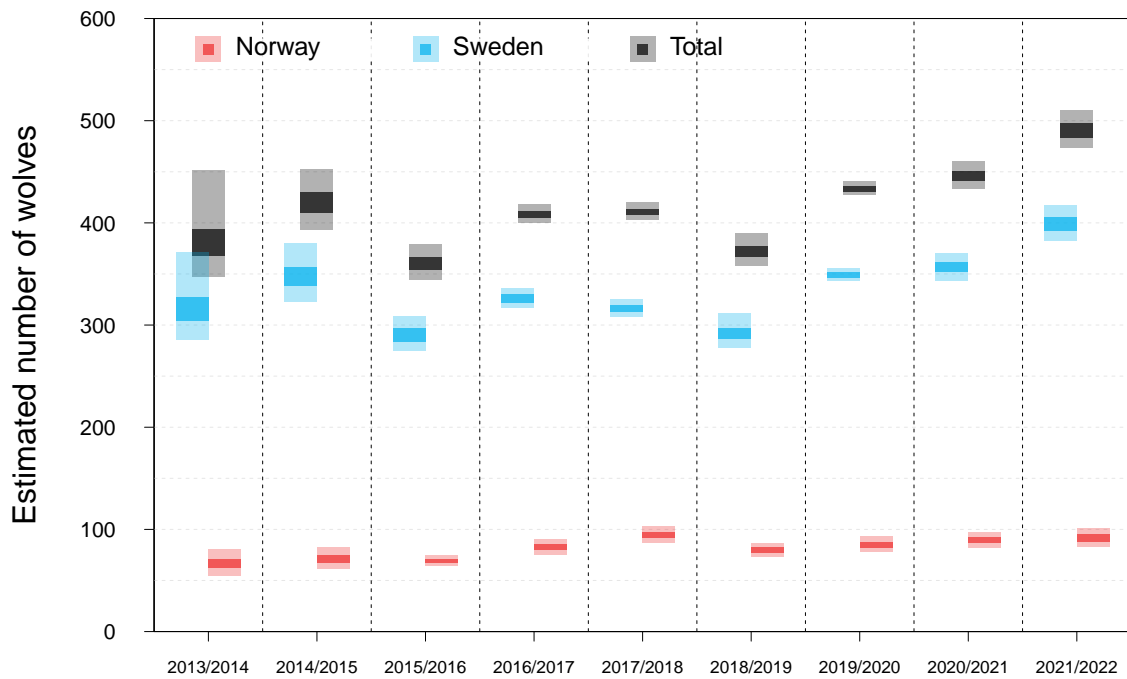
Figure A.3: Total (black) and country-specific (blue: Sweden, red: Norway) annual wolf population size estimates in Scandinavia between 2013/2014 and 2021/2022. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Credible intervals indicate uncertainty in estimates given the model and data used to generate the estimates. Changes in the model and the data can result in different estimates and associated uncertainty. Note the higher precision (lower uncertainty) in the three monitoring seasons (2016/17, 2017/18, 2019/20) with higher sampling intensity.
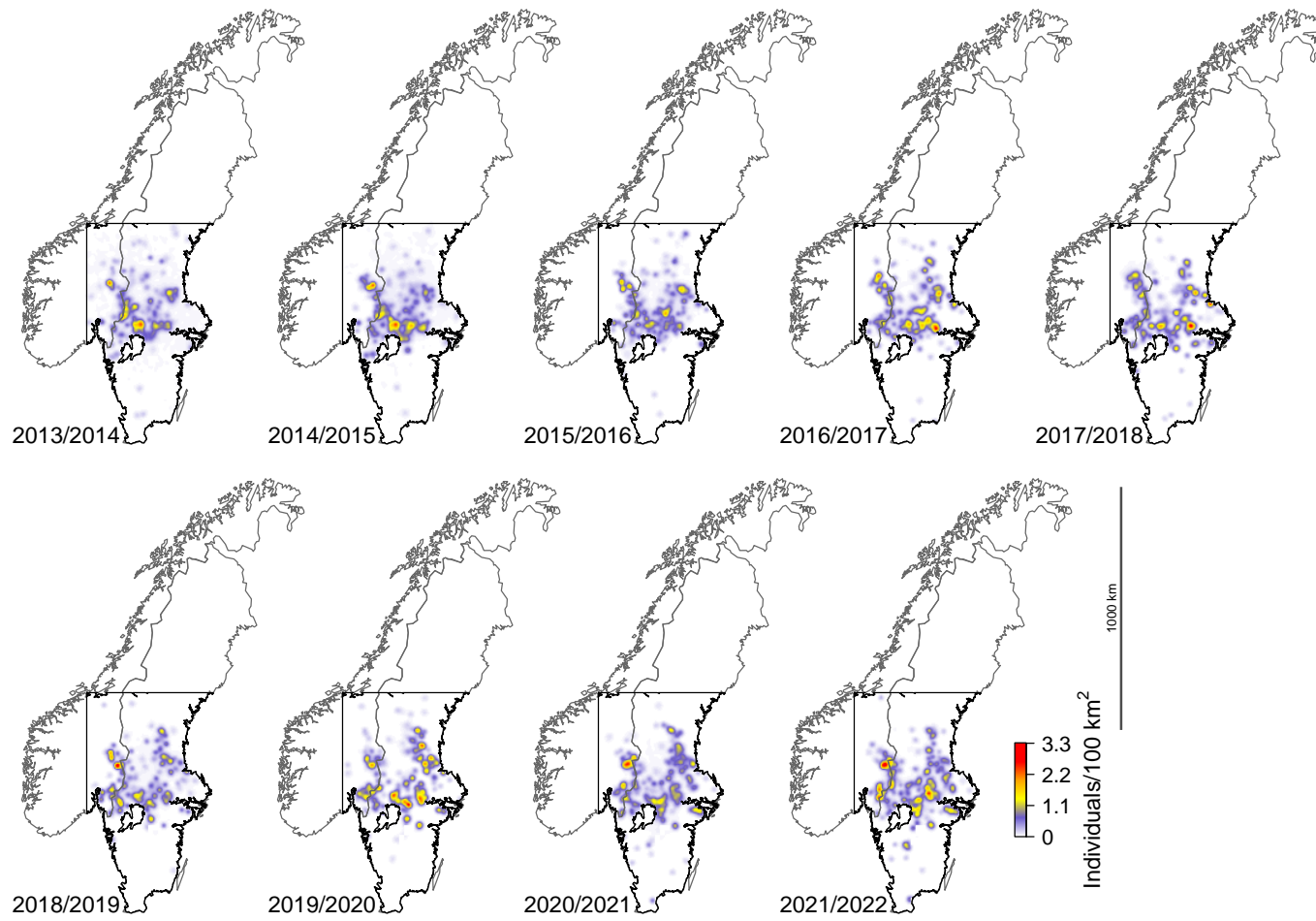
Figure A.4: Wolf density based on individual utilization distributions throughout the study area (black polygon) in Scandinavia between 2013/2014 and 2021/2022. These maps are freely available as geo-referenced raster files at https://github.com/richbi/RovQuantPublic.
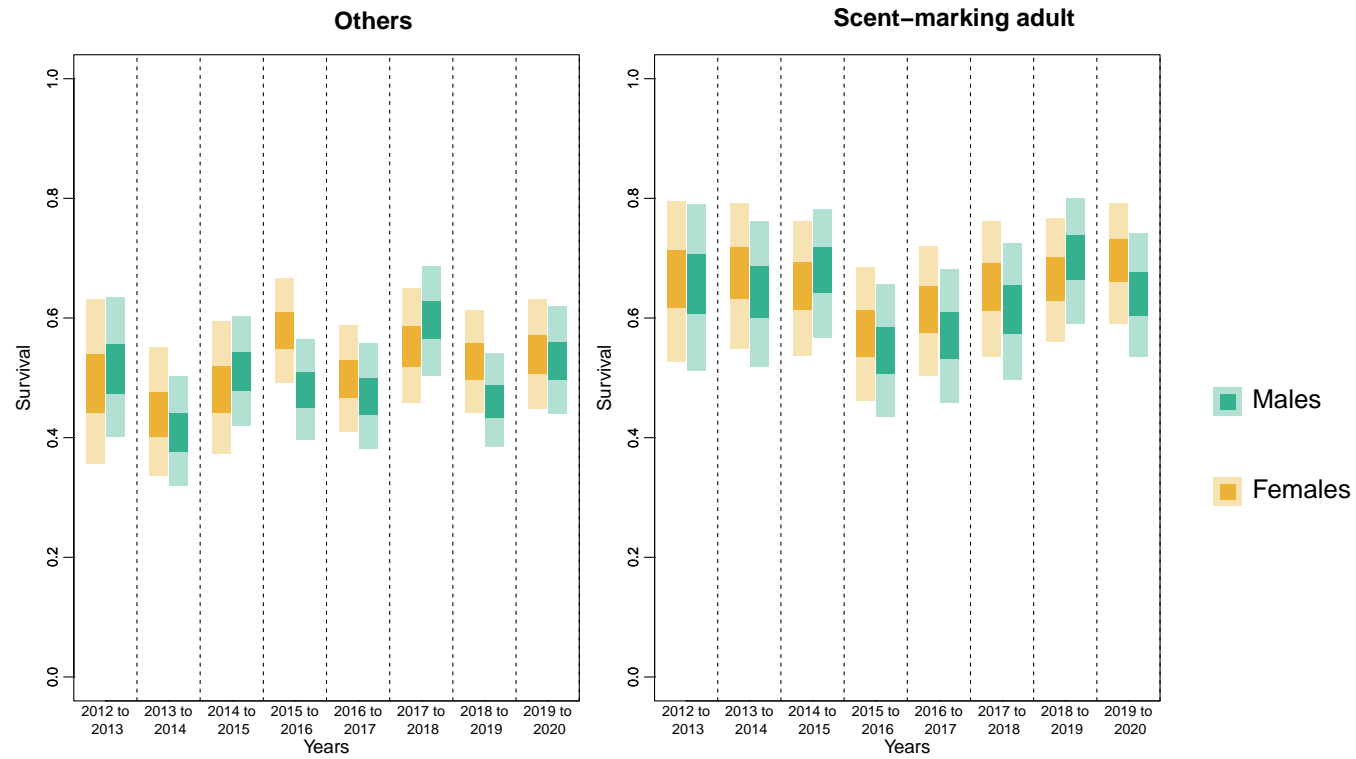
Figure A.5: Annual survival probabilities for scent-marking and other individuals and for female and male wolves. Overall mortality probabilities (and therefore overall survival) are obtained by adding the mortality probabilities due to legal culling and all other causes (Figure 2). Shown are overall estimates throughout the study area between 2013/2014 and 2021/202.
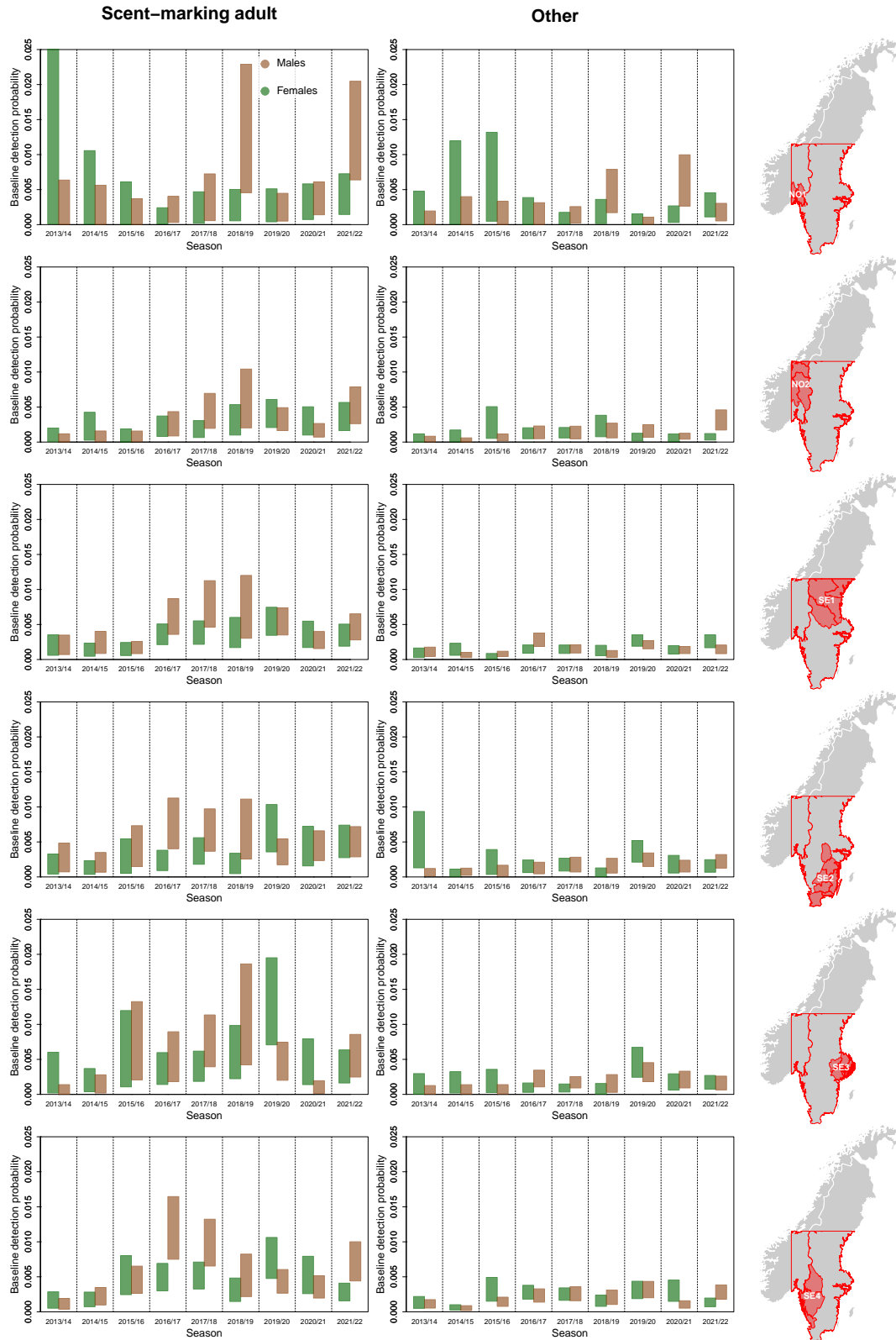
Figure A.6: Sex-specific baseline detection probabilities ($p_{0S}structured$) of scent-marking adults and others individuals for the different Scandinavian jurisdictions during structured sampling as estimated by the open-population spatial capture-recapture model. Bars represent 95% credible intervals for males and females. 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.
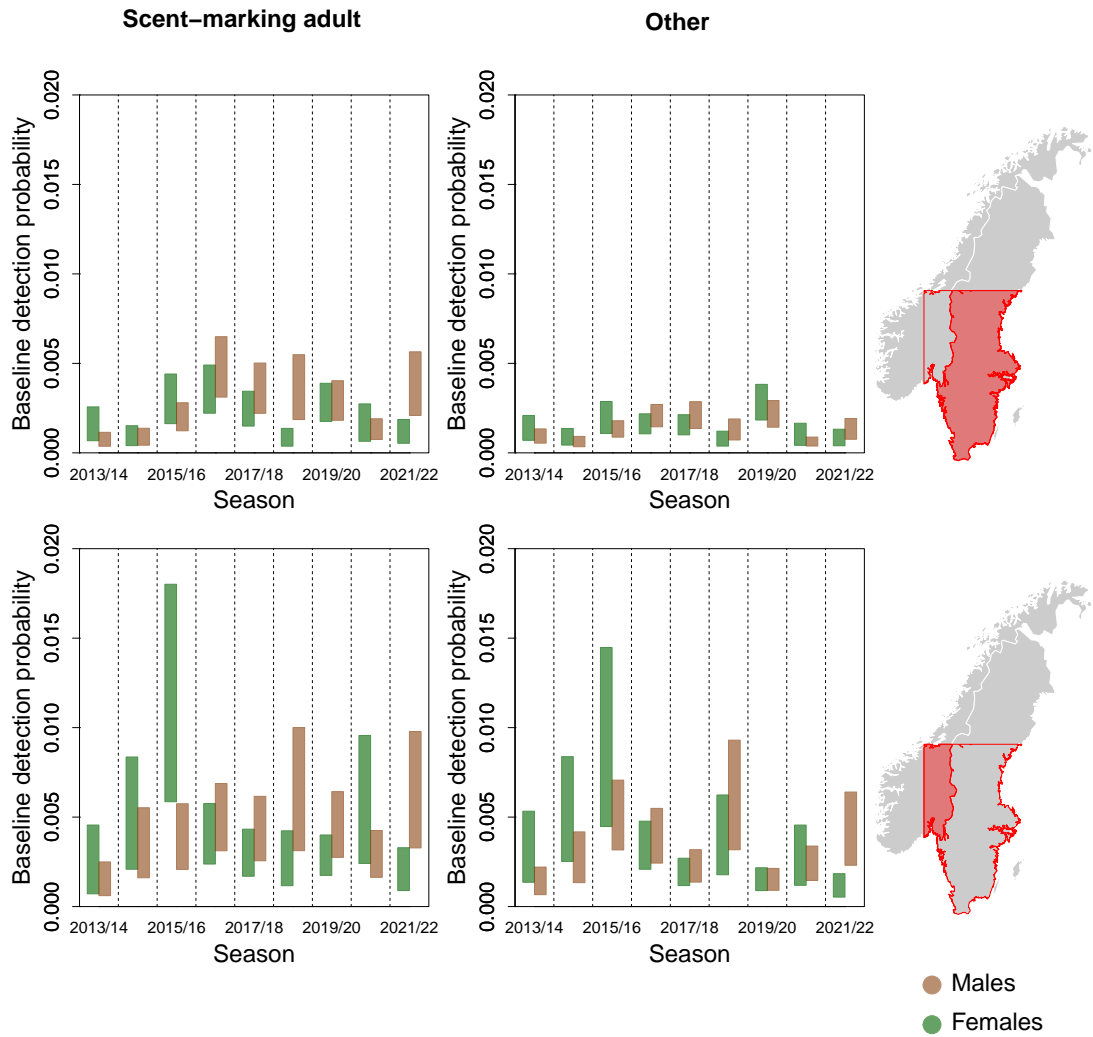
Figure A.7: Sex- and country-specific baseline detection probabilities ($p_{0\,Unstructured}$) of scent-marking adults and others individuals during the unstructured sampling as estimated by the open-population spatial capture-recapture model. Estimates are shown for the mean values of the detection 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 - March 31) between 2013/2014 and 2021/2022.

		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	Structured	0	1	3	2	6	8	15	13	26	31	33	66	36	42	27	86	54	113
	Unstructured	53	83	92	108	142	176	252	195	247	251	199	279	207	291	299	377	172	239
Sweden	Structured	65	88	80	101	100	156	285	437	348	486	158	202	377	463	180	304	257	346
	Unstructured	118	147	101	126	139	222	558	694	733	1016	191	257	1062	1085	355	495	421	563
Total	Structured	65	89	83	103	106	164	300	450	374	517	191	268	413	505	207	390	311	459
	Unstructured	171	230	193	234	281	398	810	889	980	1267	390	536	1269	1376	654	872	593	802

Table A.2: 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 - March 31) between 2013/2014 and 2021/2022. 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.

		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	Structured	0	1	2	2	5	6	9	9	17	16	13	19	16	16	15	21	24	29
	Unstructured	18	27	27	32	29	43	45	36	47	44	34	47	37	45	38	55	49	48
Sweden	Structured	43	53	53	60	55	73	103	118	101	114	70	78	117	133	88	97	102	131
	Unstructured	64	84	55	67	70	102	115	138	130	147	91	93	155	174	120	138	156	167
Total	Structured	43	54	55	62	60	79	111	127	116	128	80	95	130	146	101	116	124	152
	Unstructured	77	106	79	95	96	139	151	168	170	180	120	133	187	207	157	184	191	199

Table A.3: Number of cause-specific dead recoveries of wolves in Scandinavia between 2013 and 2021 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 (2021/2022) were not used in this analysis because survival is modeled as part of the transition from one season to the next.

	Country	2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	1	3	0	0	1	2	0	0	1	4	1	1	1	1	1	1	1	1
	Sweden	4	5	8	11	7	6	4	2	5	2	4	5	4	7	7	4	1	3
Legal culling	Norway	5	7	4	8	6	6	7	7	18	15	10	11	6	14	13	16	12	18
	Sweden	12	13	33	32	8	20	19	27	15	31	4	5	7	13	19	35	15	17
Total	Total	22	28	45	51	22	34	30	36	39	52	19	22	18	35	40	56	29	39

Table A.4: Annual abundance estimates for wolf at three spatial scales: the entire study area, by country, and by management unit. The latter refers to counties ("Län") in Sweden and large carnivore management regions in Norway (Figure A.2). 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.

	2013/2014	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022
TOTAL	384.4 (348-447)	420.1 (393-452)	360 (345-379)	408 (399-418)	410.3 (403-419)	372.3 (357-389)	433.5 (427-441)	445.6 (433-461)	489.5 (472-509)
NORWAY	67.2 (55-82)	72.1 (62-84)	69.5 (65-75)	82.1 (75-90)	94.4 (87-103)	79.6 (74-86)	85.2 (78-93)	89.2 (82-97)	91.3 (83-101)
Region 2	2.1 (1-5)	0.4 (0-2)	0.2 (0-1)	0.6 (0-2)	0.7 (0-3)	0.8 (0-2)	0.9 (0-3)	0.3 (0-2)	0.3 (0-2)
Region 3	4.8 (2-9)	2.8 (0-6)	0.5 (0-2)	1.1 (0-3)	1.6 (0-5)	0.6 (0-3)	2.7 (1-5)	1.2 (0-4)	1.6 (0-4)
Region 4	9.9 (6-15)	7.2 (4-11)	11.7 (9-15)	16.2 (13-20)	22.1 (18-26)	24.8 (21-29)	28.1 (24-33)	25.2 (21-30)	27.5 (23-32)
Region 5	46 (37-56)	58.7 (51-67)	56.6 (53-61)	63.2 (57-70)	68.5 (63-75)	51.6 (47-57)	51.3 (46-57)	61.5 (55-68)	59.2 (52-67)
Region 6	4.4 (1-9)	3 (0-7)	0.5 (0-2)	1 (0-3)	1.4 (0-4)	1.7 (1-4)	2.3 (1-5)	1 (0-3)	2.8 (1-6)
SWEDEN	317.2 (285-370)	347.9 (323-379)	290.5 (275-309)	325.9 (316-336)	315.9 (308-325)	292.6 (277-309)	348.3 (342-355)	356.4 (343-371)	398.1 (381-417)
Örebro	32.5 (27-39)	50.6 (41-61)	29.9 (23-38)	39.6 (35-45)	35.5 (31-40)	39.6 (33-47)	50 (45-55)	47.5 (41-55)	59.1 (52-66)
Östergötland	3.2 (0-7)	2.2 (0-5)	1.2 (0-4)	2.1 (1-4)	3.3 (3-5)	3.6 (2-6)	9.8 (9-11)	7.5 (6-10)	10.1 (8-13)
Blekinge	0.6 (0-2)	0.5 (0-2)	0.3 (0-2)	1.1 (1-2)	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.2 (0-1)
Dalarna	66.7 (56-80)	72.4 (62-84)	75.4 (67-85)	80.9 (74-88)	63.6 (58-70)	57.4 (49-67)	68.5 (64-74)	66.6 (59-75)	74.8 (67-83)
Gävleborg	23.9 (17-32)	28.8 (22-37)	39.3 (33-46)	50.4 (45-56)	54.7 (50-59)	45.8 (39-53)	69.6 (65-74)	62.3 (57-68)	51.4 (46-57)
Halland	1.3 (0-4)	1 (0-3)	0.4 (0-2)	0.3 (0-2)	0.1 (0-1)	0.3 (0-2)	0.1 (0-1)	1.3 (1-3)	0.6 (0-2)
Jämtland	19 (12-28)	17.7 (11-25)	15.2 (10-21)	14.7 (10-20)	7.2 (4-12)	13.2 (9-19)	15.6 (12-20)	15 (11-20)	9.1 (5-15)
Jönköping	3.5 (1-7)	3.1 (1-6)	1.9 (1-4)	0.6 (0-3)	0.3 (0-2)	0.9 (0-3)	1.3 (0-3)	2.2 (1-5)	8.4 (5-12)
Kalmar	2.2 (0-6)	1.4 (0-4)	0.7 (0-3)	0.3 (0-2)	1 (0-2)	1.5 (1-3)	0.4 (0-2)	1.4 (1-3)	0.6 (0-2)
Kronoberg	2.6 (0-6)	2.4 (0-5)	1.3 (0-4)	1.3 (1-3)	0.4 (0-2)	0.6 (0-2)	0.6 (0-2)	1.5 (1-3)	1.7 (1-4)
Södermanland	3.9 (1-8)	2 (0-5)	1.7 (0-5)	3 (2-5)	12.2 (11-14)	4.3 (2-7)	7.9 (6-10)	14.4 (11-18)	18.2 (15-22)
Skåne	3.3 (1-7)	1.9 (0-5)	1.1 (0-3)	1.3 (1-3)	2 (1-3)	0.5 (0-2)	0.2 (0-2)	2.6 (2-4)	3.7 (3-6)
Stockholm	3.4 (0-7)	3.5 (1-6)	4.1 (2-6)	2.5 (2-4)	4.3 (2-6)	2.1 (0-5)	3.4 (1-5)	7.2 (4-11)	5.2 (3-8)
Uppsala	4.2 (1-9)	4.2 (1-8)	4.1 (1-7)	5.4 (3-9)	8.4 (6-12)	6.5 (4-10)	4.8 (3-7)	7.4 (5-10)	12 (10-15)
Värmland	109 (97-124)	115.5 (103-129)	88.3 (80-97)	89 (81-97)	87.9 (82-94)	85.7 (77-95)	82.4 (77-88)	80.8 (72-90)	101.6 (93-111)
Västerbotten	0.1 (0-1)	0.1 (0-1)	0 (0-1)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Västernorrland	7.3 (4-12)	5.3 (2-10)	4.2 (1-8)	2.5 (1-5)	0.7 (0-3)	2.6 (0-6)	0.9 (0-3)	1.7 (0-5)	1.9 (0-5)
Västmanland	16.9 (12-23)	19.7 (15-25)	14.3 (10-19)	25.9 (23-30)	26.6 (23-30)	17.1 (12-23)	27.1 (23-32)	19.9 (15-25)	23.1 (18-29)
VästraGötaland	13.6 (8-20)	15.5 (11-21)	7.3 (4-11)	4.7 (2-9)	7.7 (4-11)	10.9 (7-15)	5.3 (3-8)	16.8 (12-22)	16.5 (12-22)

Table A.5: 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.

	2013-2014	2014-2015	2015-2016	2016-2017	2017-2018	2018-2019	2019-2020	2020-2021
Norway	1.08 (0.86-1.38)	0.97 (0.84-1.16)	1.18 (1.03-1.33)	1.15 (1.02-1.29)	0.85 (0.76-0.94)	1.07 (0.95-1.20)	1.05 (0.92-1.18)	1.03 (0.91-1.16)
Sweden	1.10 (0.96-1.25)	0.83 (0.76-0.92)	1.12 (1.05-1.20)	0.97 (0.93-1.00)	0.93 (0.87-0.99)	1.19 (1.12-1.26)	1.02 (0.98-1.07)	1.12 (1.06-1.18)
Total	1.10 (0.96-1.23)	0.86 (0.79-0.93)	1.13 (1.08-1.19)	1.01 (0.98-1.03)	0.91 (0.87-0.96)	1.16 (1.11-1.22)	1.03 (1.00-1.07)	1.10 (1.05-1.16)

Table A.6: 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. Median estimates and 95% credible intervals (in parentheses) for per capita recruitment rate (ρ), survival (ϕ), transition probability from other to scent-marking state (ψ), mortality due to legal culling (h) and mortality due to other causes (w) are presented for males (M) and females (F).

	State	2013/2014 M	2013/2014 F	2014/2015 M	2014/2015 F	2015/2016 M	2015/2016 F	2016/2017 M	2016/2017 F
ρ	-	0.57 (0.32-0.84)	1.27 (0.90-1.67)	0.57 (0.43-0.72)	0.41 (0.27-0.57)	0.71 (0.58-0.82)	1.19 (0.98-1.37)	0.66 (0.60-0.72)	0.73 (0.65-0.80)
ϕ	2	0.51 (0.40-0.63)	0.49 (0.35-0.63)	0.41 (0.32-0.50)	0.44 (0.33-0.55)	0.51 (0.42-0.60)	0.48 (0.37-0.59)	0.48 (0.40-0.57)	0.58 (0.49-0.67)
	3	0.66 (0.51-0.79)	0.67 (0.52-0.80)	0.64 (0.52-0.76)	0.68 (0.55-0.79)	0.68 (0.56-0.78)	0.65 (0.53-0.76)	0.55 (0.43-0.66)	0.58 (0.46-0.69)
ψ	-	0.20 (0.11-0.32)	0.41 (0.23-0.60)	0.41 (0.28-0.55)	0.39 (0.25-0.55)	0.35 (0.24-0.47)	0.55 (0.40-0.70)	0.42 (0.30-0.54)	0.45 (0.34-0.56)
h	2	0.08 (0.04-0.13)	0.12 (0.06-0.21)	0.18 (0.12-0.25)	0.22 (0.15-0.31)	0.13 (0.08-0.19)	0.08 (0.04-0.15)	0.17 (0.11-0.23)	0.12 (0.07-0.18)
	3	0.06 (0.02-0.14)	0.08 (0.03-0.16)	0.10 (0.04-0.19)	0.11 (0.05-0.20)	0.08 (0.03-0.15)	0.09 (0.04-0.17)	0.11 (0.06-0.20)	0.12 (0.06-0.20)
w	2	0.40 (0.29-0.52)	0.38 (0.25-0.52)	0.41 (0.31-0.51)	0.34 (0.23-0.45)	0.36 (0.27-0.46)	0.43 (0.32-0.55)	0.35 (0.27-0.44)	0.30 (0.22-0.39)
	3	0.27 (0.14-0.43)	0.25 (0.12-0.39)	0.25 (0.14-0.37)	0.21 (0.11-0.34)	0.24 (0.15-0.35)	0.25 (0.15-0.36)	0.34 (0.24-0.45)	0.30 (0.20-0.41)

	State	2017/2018 M	2017/2018 F	2018/2019 M	2018/2019 F	2019/2020 M	2019/2020 F	2020/2021 M	2020/2021 F
2021/2022									
ρ	-	0.63 (0.55-0.74)	0.50 (0.42-0.59)	0.82 (0.69-0.94)	0.86 (0.72-0.99)	0.73 (0.66-0.81)	0.63 (0.56-0.71)	0.71 (0.60-0.82)	0.85 (0.73-0.98)
ϕ	2	0.47 (0.38-0.56)	0.50 (0.41-0.59)	0.60 (0.50-0.69)	0.55 (0.46-0.65)	0.46 (0.38-0.54)	0.53 (0.44-0.61)	0.53 (0.44-0.62)	0.54 (0.45-0.63)
	3	0.57 (0.45-0.68)	0.61 (0.50-0.72)	0.61 (0.49-0.72)	0.65 (0.53-0.76)	0.70 (0.59-0.80)	0.67 (0.56-0.77)	0.64 (0.53-0.74)	0.70 (0.59-0.79)
ψ	-	0.34 (0.23-0.46)	0.28 (0.18-0.40)	0.36 (0.25-0.47)	0.48 (0.35-0.61)	0.39 (0.29-0.51)	0.38 (0.27-0.50)	0.36 (0.26-0.47)	0.36 (0.26-0.48)
h	2	0.24 (0.17-0.31)	0.17 (0.11-0.24)	0.06 (0.03-0.11)	0.09 (0.05-0.15)	0.13 (0.08-0.18)	0.06 (0.03-0.10)	0.18 (0.12-0.24)	0.19 (0.13-0.26)
	3	0.19 (0.11-0.29)	0.14 (0.07-0.22)	0.07 (0.03-0.15)	0.07 (0.02-0.14)	0.07 (0.02-0.14)	0.09 (0.04-0.16)	0.19 (0.12-0.29)	0.10 (0.04-0.17)
w	2	0.29 (0.21-0.38)	0.33 (0.24-0.42)	0.34 (0.25-0.43)	0.36 (0.26-0.45)	0.41 (0.33-0.49)	0.41 (0.33-0.50)	0.29 (0.21-0.38)	0.27 (0.19-0.36)
	3	0.24 (0.15-0.34)	0.24 (0.16-0.35)	0.31 (0.21-0.43)	0.27 (0.17-0.39)	0.23 (0.14-0.33)	0.24 (0.16-0.35)	0.16 (0.09-0.25)	0.20 (0.12-0.31)

Table A.7: 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 dens on AC locations (Bischof et al., 2020). The scale parameter σ of the detection function is expressed in kilometers estimated separately for other (σ_1) and scent-marking (σ_2) individuals. λ represents the mean of the exponential movement parameter, describing individual movement distances between years, estimated separately for other (λ_1) and scent-marking (λ_2) individuals. Credible intervals (95%) are shown in parentheses. * represents parameters that were not estimated every year.

	2013/2014		2014/2015		2015/2016		2016/2017		2017/2018	
	M	F	M	F	M	F	M	F	M	F
β^*_{dens}	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)
σ_1	7.56 (6.76-8.50)	6.29 (5.61-7.11)	8.49 (7.73-9.40)	8.38 (7.55-9.36)	8.31 (7.71-8.99)	7.27 (6.70-7.92)	7.91 (7.58-8.27)	7.90 (7.54-8.29)	7.91 (7.61-8.22)	7.31 (6.99-7.64)
σ_2	7.17 (6.47-8.05)	6.61 (5.79-7.61)	7.79 (6.95-8.85)	6.76 (6.01-7.65)	8.04 (7.41-8.76)	6.41 (5.76-7.18)	7.46 (7.03-7.92)	7.95 (7.51-8.44)	7.63 (7.28-8.04)	8.11 (7.72-8.54)
λ^*_1	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)
λ^*_2	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)

	2018/2019		2019/2020		2020/2021		2021/2022	
	M	F	M	F	M	F	M	F
β^*_{dens}	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)	0.46 (0.44-0.48)	0.47 (0.45-0.49)
σ_1	8.37 (7.93-8.85)	8.17 (7.64-8.74)	8.02 (7.69-8.38)	7.72 (7.41-8.05)	7.66 (7.31-8.03)	7.07 (6.71-7.49)	7.51 (7.19-7.85)	7.76 (7.35-8.22)
σ_2	7.26 (6.73-7.84)	6.60 (6.06-7.25)	7.93 (7.62-8.26)	7.54 (7.23-7.86)	7.88 (7.41-8.41)	7.42 (6.90-8.02)	6.78 (6.37-7.22)	7.90 (7.42-8.43)
λ^*_1	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)	7.00 (6.44-7.63)	4.83 (4.37-5.32)
λ^*_2	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)	75.14 (69.93-80.96)	48.05 (44.33-52.58)

Table A.8: 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, $\beta_{3\,Structured}$ 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.

	2013/2014		2014/2015		2015/2016		2016/2017		2017/2018	
	M	F	M	F	M	F	M	F	M	F
$\beta_{1\,Structured}$	0.44 (-0.14-1.05)	0.43 (-0.24-1.10)	-0.14 (-0.68-0.39)	-0.40 (-0.96-0.14)	-0.31 (-0.72-0.10)	-0.29 (-0.80-0.21)	-0.09 (-0.43-0.24)	0.24 (-0.08-0.57)	-0.08 (-0.41-0.22)	0.40 (0.07-0.71)
$\beta_{2\,Structured}$	0.20 (0.09-0.30)	0.18 (0.07-0.29)	0.33 (0.22-0.44)	0.46 (0.34-0.58)	0.35 (0.25-0.46)	0.35 (0.19-0.50)	0.23 (0.16-0.30)	0.32 (0.25-0.40)	0.30 (0.23-0.37)	0.28 (0.20-0.35)
$\beta_{3\,Structured}$	-0.27 (-0.71-0.17)	0.20 (-0.34-0.74)	0.08 (-0.35-0.51)	-0.39 (-0.84-0.07)	0.19 (-0.24-0.63)	-0.18 (-0.74-0.38)	-0.19 (-0.45-0.08)	-0.26 (-0.59-0.06)	-0.10 (-0.43-0.22)	-0.22 (-0.63-0.19)

	2018/2019		2019/2020		2020/2021		2021/2022	
	M	F	M	F	M	F	M	F
$\beta_{1\,Structured}$	-0.33 (-0.88-0.22)	-0.09 (-0.54-0.37)	0.17 (-0.11-0.45)	0.01 (-0.27-0.29)	0.66 (0.29-1.02)	0.08 (-0.39-0.51)	0.17 (-0.15-0.49)	0.16 (-0.17-0.49)
$\beta_{2\,Structured}$	0.31 (0.20-0.41)	0.34 (0.24-0.44)	0.29 (0.21-0.36)	0.25 (0.16-0.33)	0.20 (0.13-0.25)	0.18 (0.11-0.26)	0.22 (0.16-0.29)	0.20 (0.12-0.27)
$\beta_{3\,Structured}$	-0.18 (-0.57-0.20)	-0.08 (-0.56-0.41)	-0.14 (-0.40-0.11)	0.20 (-0.06-0.47)	0.30 (0.07-0.54)	0.22 (-0.07-0.51)	0.18 (-0.06-0.42)	0.01 (-0.29-0.30)

Table A.9: Estimates of the detection process parameters for the other sampling $\beta_{1Unstructured}$ corresponds to the effect of previous detection of an individual on 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, $\beta_{4Unstructured}$ to the effect of spatio-temporal heterogeneity in unstructured sampling. Coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	2013/2014		2014/2015		2015/2016		2016/2017		2017/2018	
	M	F	M	F	M	F	M	F	M	F
$\beta_{1Unstructured}$	1.06 (0.67-1.47)	0.49 (-0.06-1.00)	0.33 (-0.05-0.69)	0.33 (-0.10-0.75)	0.33 (0.04-0.61)	-0.20 (-0.52-0.13)	0.17 (-0.06-0.41)	0.30 (0.09-0.52)	0.19 (0.00-0.37)	0.62 (0.44-0.82)
$\beta_{2Unstructured}$	-0.43 (-0.96–0.03)	-0.48 (-1.40- 0.16)	-1.08 (-2.20–0.26)	-1.09 (-2.57–0.04)	-0.13 (-0.59- 0.27)	-0.47 (-1.24- 0.13)	-0.28 (-0.65- 0.03)	-0.48 (-1.00–0.04)	-1.52 (-2.39–0.79)	-0.79 (-1.35–0.30)
$\beta_{3Unstructured}$	0.31 (0.05-0.58)	0.14 (-0.18- 0.49)	-0.05 (-0.33-0.22)	-0.35 (-0.64–0.05)	0.14 (-0.12-0.41)	-0.05 (-0.37- 0.27)	-0.13 (-0.29-0.03)	-0.03 (-0.21- 0.14)	-0.15 (-0.30-0.01)	-0.17 (-0.36- 0.02)
$\beta_{4Unstructured}$	1.01 (0.70-1.33)	1.21 (0.83-1.57)	0.79 (0.48-1.10)	0.70 (0.36-1.06)	0.60 (0.35-0.87)	0.60 (0.29-0.93)	1.07 (0.81-1.36)	1.15 (0.84-1.48)	1.23 (0.93-1.52)	1.31 (0.98-1.65)

	2018/2019		2019/2020		2020/2021		2021/2022	
	M	F	M	F	M	F	M	F
$\beta_{1Unstructured}$	-0.01 (-0.33-0.32)	0.82 (0.48-1.19)	0.14 (-0.04-0.31)	0.47 (0.30-0.64)	0.78 (0.54-1.02)	0.54 (0.26-0.84)	0.03 (-0.20-0.27)	0.41 (0.15-0.67)
$\beta_{2Unstructured}$	-0.41 (-1.06- 0.08)	0.15 (-0.48- 0.75)	-0.66 (-1.30–0.13)	-0.73 (-1.57–0.05)	-0.63 (-1.44–0.03)	0.05 (-0.96- 2.50)	-0.03 (-0.52- 0.34)	-0.79 (-2.17- 0.26)
$\beta_{3Unstructured}$	-0.05 (-0.28-0.19)	-0.29 (-0.54-0.04)	0.03 (-0.08-0.13)	0.04 (-0.08- 0.17)	-0.05 (-0.20-0.09)	-0.14 (-0.31- 0.02)	-0.02 (-0.16-0.11)	-0.14 (-0.30- 0.01)
$\beta_{4Unstructured}$	0.77 (0.42-1.15)	1.27 (0.84-1.74)	1.53 (1.24-1.87)	1.37 (1.08-1.68)	1.36 (1.02-1.70)	1.52 (1.12-2.02)	1.27 (0.84-1.71)	1.46 (1.00-1.95)

Table A.10: 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.2) divided by the total and sex-specific abundance estimates obtained from the OPSCR models (Table A.4). Credible intervals (95%) are shown in parentheses.

	2013/2014	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022
M	0.56 (0.45-0.64)	0.56 (0.50-0.61)	0.81 (0.75-0.86)	0.90 (0.87-0.92)	0.93 (0.91-0.96)	0.79 (0.74-0.84)	0.95 (0.93-0.97)	0.86 (0.82-0.89)	0.89 (0.84-0.93)
F	0.62 (0.55-0.69)	0.57 (0.52-0.62)	0.74 (0.68-0.79)	0.89 (0.85-0.91)	0.91 (0.88-0.94)	0.76 (0.71-0.80)	0.94 (0.92-0.97)	0.86 (0.82-0.89)	0.90 (0.86-0.95)
Total	0.58 (0.50-0.65)	0.56 (0.52-0.60)	0.78 (0.74-0.81)	0.89 (0.87-0.91)	0.92 (0.90-0.94)	0.78 (0.74-0.81)	0.95 (0.93-0.96)	0.86 (0.83-0.88)	0.89 (0.86-0.93)