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Estimates of wolverine density, abundance, and population dynamics in Scandinavia, 2015/16–2024/25

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COVER PICTURE

Wolverine, Ridgeline plot of wolverine density in Norway and Sweden

NØKKELORD

Gulo gulo, jerv, tetthet, populasjonsdynamikk, deteksjonssannsynlighet, ikke-invaderende innsamling av genetisk materiale, åpen populasjon romlig fangst-gjenfangst, rovdyrforvaltning

KEY WORDS

Gulo gulo, wolverine, population density, population dynamics, detection probability, non-invasive genetic sampling, open-population spatial capture-recapture, carnivore management

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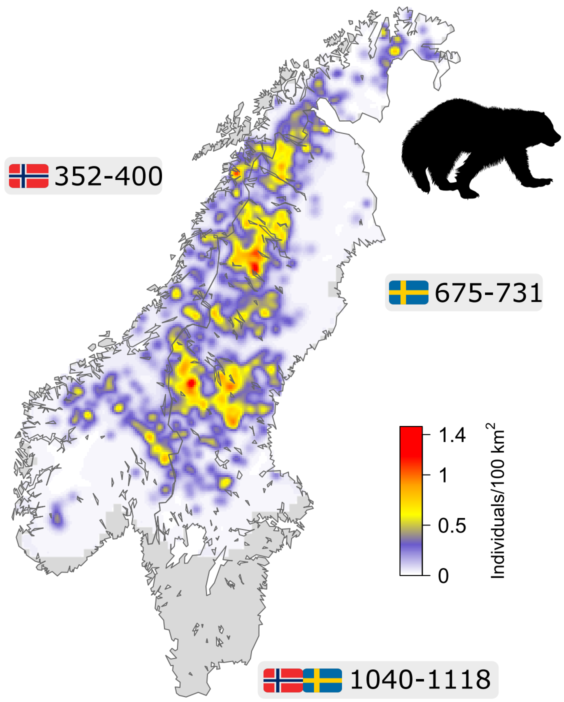
Summary

Background The Scandinavian wolverine (*Gulo gulo*) population is being monitored annually using non-invasive genetic sampling (NGS) and recovery of dead individuals. DNA extracted from feces, urine, hair, secretion, 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. (www.rovbase.se, www.rovbase.no).

Approach Using the Bayesian spatial capture-recapture (SCR) models developed by RovQuant, we estimated annual density, total and jurisdiction-specific population sizes and vital rates of the Scandinavian wolverine population for ten consecutive seasons from 2015/16 to 2024/25. We used single-season SCR models to estimate population size and map density in 2024/25, as they make less assumptions compared to open population SCR (OPSCR) models and their abundance estimates are relatively robust to model misspecifications. Contrary to OPSCR model, population size time series from single-season SCR models are not updated retrospectively with the addition of new monitoring seasons. OPSCR models remain useful, as they allow estimation of vital rates and yield abundance estimates when there are gaps in monitoring.

Results We generated annual density maps and estimated total and jurisdiction-specific population sizes for the wolverine between 2015/16 and 2024/25. Based on the single-season SCR model, the size of the Scandinavian wolverine population was likely (95% Bayesian credible interval) between 1040 and 1118 individuals in 2024/25, with 675 to 731 individuals attributed to Sweden and 352 to 400 to Norway. In addition to annual density and abundance estimates, we report, for each sex, annual estimates of cause-specific mortality, recruitment, and detection probability.

Discussion The overlap in the uncertainty around wolverine population size estimates between 2023/24 (1 012-1 072) and 2024/25 (1 040-1 118), precludes any conclusion regarding population trend. The demographic analyses also revealed that the significant drop in male survival estimated last year (Milleret et al., 2024a) was still visible and continued between 2023/24 and 2024/25.



Density map and ranges of abundance estimated for wolverines in 2024/2025

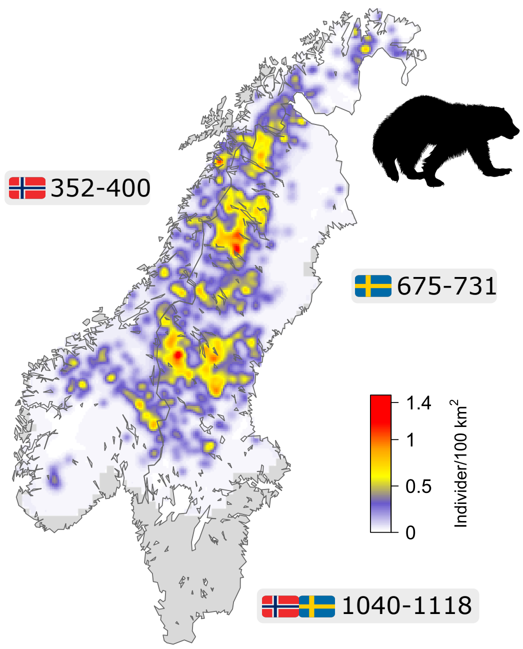
Sammendrag

Bakgrunn Den skandinaviske bestanden av jerv (*Gulo gulo*) blir overvåket årlig ved bruk av ikke-invasiv genetisk prøveinnsamling (NGS) og gjenfunn av døde individer. DNA fra skit, urin, hår, sekret 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 Bayesianske romlig fangst-gjenfangst-modeller (SCR-modeller) utviklet av RovQuant estimerte vi årlig tetthet, bestandsstørrelse og vitale rater for den skandinaviske jervebestanden i ti påfølgende sesonger fra 2015/16 til 2024/25. Vi benyttet enkeltsesongs-SCR-modeller for å estimere bestandsstørrelse og romlig tetthet i 2024/25 fordi disse modellene gjør færre antakelser sammenlignet med en åpen scr-populasjonsmodell (OPSCR). Bestandsestimater basert på SCR-modeller er relativt robuste når det gjelder feilspesifikasjoner i modellen. I motsetning til OPSCR-modeller blir tidsserier bestandsestimanter basert på enkeltsesongs-SCR-modeller ikke oppdatert i ettertid ved tillegg av nye overvåkningssesonger. Åpen populasjon-SCR-modeller (OPSCR) forblir nyttige, da de tillater estimering av vitale rater og produserer der det mangler data i overvåkningen.

Resultater Vi produserte årlige tetthetskart og estimerte total bestandsstørrelse og bestandsstørrelser i ulike administrative enheter mellom 2015/16 og 2024/25. Basert på enkeltsesongs-SCR-modellen var den skandinaviske jervebestanden på mellom 1040 og 1118 individer i 2024/25 (95% kredibelt intervall), med 675 til 731 individer i Sverige og 352 til 400 i Norge. I tillegg til årlige tetthets- og bestandsestimater, rapporterer vi for hvert kjønn årlige estimater av årsaksspesifikk dødelighet, rekruttering og oppdagbarhet.

Diskusjon Overlappet i usikkerhet rundt estimatene i bestandsstørrelse av jerv mellom 2023/24 (1 012-1 072) og 2024/25 (1 040-1 118) gjør en konklusjon om populasjonens utvikling vanskelig. Den demografiske analysen viste at den signifikante nedgangen i overlevelse hos hanner som ble påvist i fjor (Milleret et al., 2024a) fortsatt var til stede og fortsatte mellom 2023/24 og 2024/25.



Kart som viser tetthet av jerv i 2024/2025 sammen med intervaller for estimert antall jerv

Contents

1 Introduction

Sweden and Norway monitor large carnivores using non-invasive genetic sampling (NGS) and dead recoveries. Both countries have collected an extensive individual-based data set for the wolverine (*Gulo gulo*), which is stored in the Scandinavian large carnivore database Rovbase (www.rovbase.se, www.rovbase.no). 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 stored in Rovbase (Bischof et al., 2019b, 2020b). The analytical framework developed by RovQuant is based on Bayesian single-season spatial capture-recapture (SCR) and 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 (i.e., density) and vital rates (e.g., recruitment and survival). Importantly, the approach accounts for imperfect detection during sampling (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). Those methods bring 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 obtain tractable measures of uncertainty (Bischof et al., 2019a, 2020b).

Single-season SCR models use NGS detections from a given winter and thus provide spatially-explicit abundance estimates for that winter only. On the other hand, OPSCR models, can use the temporal information contained in the repeated genetic detections of individuals over multiple seasons, as well as dead recoveries, and can therefore estimate demographic parameters (i.e. recruitment, survival), in addition to spatially-explicit abundance. While OPSCR models are relatively recent and their robustness to violations of assumptions is still relatively unknown, single-season SCR models have been more thoroughly tested. Several studies suggest that estimates of abundance from single-season SCR models are relatively robust to model misspecifications (Bischof et al., 2020b; Moqanaki et al., 2021; Dupont et al., 2019; Dey et al., 2022; Theng et al., 2022). Single-season SCR models have the advantage of making fewer assumptions about the underlying processes to estimate abundance since vital rates and inter-annual movement are not estimated. Single-season SCR models are therefore a more conservative approach for obtaining estimates of abundance. However, a key limitation of single-season SCR models is that they ignore information available from preceding and subsequent seasons, and are thus unable to fill temporal and spatial gaps in sampling. OPSCR models, on the other hand, can fill those gaps (Milleret et al., 2020) and have for example been previously used to fill the gaps in wolverine NGS that occurred over several consecutive years in Norrbotten county (Milleret et al., 2023b).

With open-population spatial capture–recapture (OPSCR) models, abundance estimates for the entire time series are updated whenever a year of data is added or omitted, or when the model formulation is improved. This behavior is expected, as information from repeated detections of individuals is propagated across all years included in the analysis (Milleret et al., 2020). However, this can lead to challenges in the communication of results to different stakeholders, because abundance estimates and associated uncertainty published in previous years will be updated as new data become available. In agreement with the Swedish and Norwegian management authorities, it was therefore decided to use single-season SCR models to estimate annual abundance of wolverines going forward. This approach prevents retrospective changes to abundance estimates when additional years of data are incorporated. However, as population dynamic parameters cannot be estimated with SCR models, we continue to use OPSCR models to estimate annual survival and recruitment.

RovQuant reported abundance estimates for wolverines and wolves (*Canis lupus*) on an annual basis since 2019 (Bischof et al., 2019a,b, 2020b; Milleret et al., 2022b,c; Flagstad et al., 2021; Milleret et al., 2023b,c) and for brown bears (*Ursus arctos*) in Norway since 2022 (Dupont et al., 2022, 2023). During these and other analyses (Milleret et al., 2018, 2019; Bischof et al., 2020a; Dupont et al., 2021; Turek et al., 2021; Dey et al., 2022), RovQuant has continuously improved the performance of the SCR and OPSCR models. In the present report, we summarize the analysis of a 10-year time series (2014/15–2024/25) using the latest available wolverine monitoring data (Kleven et al., 2026) and the most recent versions of the SCR (to generate abundance estimates for 2024/2025) and OPSCR models (to generate survival and recruitment estimates for the entire time series). The newest data set includes information from the second comprehensive NGS in Norrbotten county in Sweden since 2019 (Milleret et al., 2024b). The 2023/24 and 2024/25 data are therefore more complete than the data available for previous analyses (Milleret et al., 2022a,b, 2023b).

We provide the following new information in this report:

- Sex-specific estimates of the number of wolverines for Sweden, Norway, and both countries combined, as well as estimates by county in Sweden and by carnivore management region in both countries based on single-season SCR models for the 2024/25 monitoring season.
- A map of wolverine density throughout the species' range in Scandinavia based on single-season SCR model for the 2024/25 season.
- Estimated proportions of individuals detected through non-invasive genetic sampling based on single-season SCR model for the 2024/25 season.
- Annual and sex-specific estimates of survival, cause-specific mortality, recruitment, and population growth rate between 2015/16 and 2024/25 based on OPSCR models.

All estimates are accompanied by their 95% Bayesian credible intervals.

Box 1: Terms and acronyms used

AC: Activity center. Model-based equivalent of 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 in this report to areas searched (e.g., habitat grid cells where searches for genetic samples were conducted). The searched area was defined as a 90 km buffer around all NGS data collected during the period considered.
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 potentially suitable habitat but was not searched (60km in this report).
Legal culling: Lethal removal of individuals by legal means, including licensed recreational hunting, management removals, and 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
p_0: 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).
RovQuant: Research group at the Norwegian University of Life Sciences (Ås, Norway) that develops and applies OPSCR models.

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: 2025-11-21). This database is used jointly by Norway and Sweden to record detailed information associated with large carnivore monitoring, including, but not limited to, 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 ten consecutive monitoring seasons from 2015/16 to 2024/25.

Non-invasive genetic sampling In Norway, the collection of wolverine scat, urine, glandular secretion, and hair is managed at the level of counties by SNO. Sample collection is conducted by SNO field officers, wardens at Statskog Fjelltjenesten (statskog.no), wardens at Fjellstyrene (fjellstyrene.no), local predator contacts, hunters and other members of the public. Rovdata (rovdata.no), a unit within the Norwegian Institute for Nature Research, has responsibility for the Norwegian large carnivore monitoring program. In Sweden, the collection of scat and hair is managed by Länsstyrelserna at the regional level and carried out by field officers from Länsstyrelserna. NGS collection was conducted primarily between December 1 and June 30 each year. Note that actual sampling periods occasionally deviate from the primary collection period. In 2023/24, NGS in Norrbotten county (Sweden) was performed between October 1 and May 15. In 2024/25 NGS throughout Sweden was performed between October 1 and June 2. Nonetheless, in all seasons, including 2023/24 and 2024/25, the vast majority of samples were obtained after December 1 (Milleret et al., 2024b). For consistency with previous estimations, we only included samples collected throughout Scandinavia between December 1 and June 30 in this analysis. NGS data collected late in the monitoring season and suspected to be from cubs were also excluded. This means that we only retained samples from individuals that were one year or older. DNA was isolated with an extraction robot (Maxwell 16, KingFisher or QIAsymphony instrument) and the samples were genotyped using 96 SNPs (Single Nucleotide Polymorphism) on a microfluidic-based platform (Biomark X9 instrument) for sex determination and individual identification. For further details on the DNA analysis procedure see Flagstad et al. (2004), Ekblom et al. (2018), Flagstad et al. (2021), Lansink et al. (2022), and Kleven et al. (2026).

Dead recoveries In Scandinavia, all 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 Statsforvalteren in Norway and Länsstyrelserna or the police in Sweden). All wolverines 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, following the same procedure as for non-invasive genetic samples.

GPS search tracks Government employees involved in systematic searches for wolverine DNA following wolverine tracks (via snowmobiles, skis, snowshoes, etc.) document their effort with GPS track logs, which are registered in Rovbase 3.0. GPS search tracks were included in the OPSCR and single-season SCR models to account for spatial and temporal variation in search effort during NGS.

Observation reports in Skandobs We used all observation records in the Skandobs database that were recorded during the wolverine monitoring seasons since 2015 (skandobs.se, skandobs.no; last extraction: 2025-09-15). Skandobs is a web application that allows anyone to anonymously register observations (visual, tracks, feces, etc.) of bears, lynx (*Lynx lynx*), wolves, and wolverines in Scandinavia. This data currently consists of more than 120 000 records of possible large carnivore observations. Although most observations are not verified, they offer the best available proxy for spatio-temporal variation in opportunistic effort at this time.

2.2 Spatial capture-recapture model

We used 1) a Bayesian single-season spatial capture-recapture (SCR) model to obtain abundance estimates and map density in 2024/25 and 2) an open-population spatial capture-recapture (OPSCR) model to obtain estimates of population dynamics parameters over the period 2015/16 - 2024/25 (Bischof et al., 2019b).

These models address three challenges associated with population-level wildlife inventories:

1. Detection is imperfect and sampling effort is 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 the geographic area the population occupies, 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 modeling movement of individuals between years, the OPSCR model has been shown previously to reduce bias in demographic parameters (Ergon and Gardner, 2014; Schaub and Royle, 2014; Gardner et al., 2018).

We first describe the OPSCR model and then the single-season SCR model, which is a simplified version of the OPSCR model.

2.2.1 Open spatial capture-recapture model

The OPSCR model is composed of three sub-models:

1. A model for population dynamics and population size.
2. A model for density and individual movement.
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's life history is represented by a succession of up to 3 discrete states: (1) "unborn" if the individual has not yet been recruited into the population (state "unborn" is required for the data augmentation procedure, see below); (2) "alive" if it is alive; (3) "dead" if it is dead. We then modeled the transition from one state to another between consecutive monitoring seasons (t to $t+1$) to estimate vital rates (recruitment and mortality). More details are available in Bischof et al. (2019b) and Bischof et al. (2020b). This formulation of the population dynamic model means that, contrary to previous analyses (Bischof et al., 2019b, 2020b; Flagstad et al., 2021; Milleret et al., 2022b), we did not use dead recoveries or model cause-specific mortality directly in the OPSCR model. Cause-specific mortality was instead derived after model fitting (see section "Other derived parameters"). 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 ACs (Zhang et al., 2023). In the first year, individuals were located according to an intensity surface, which was a function of the average locations of all known dens recorded between 2009 and 2025 (see Bischof et al., 2019b and Bischof et al., 2020b for more details). For all subsequent years ($t > 1$), the location of individual ACs was a function of the distance from previous AC locations (at time $t-1$) and the locations of known wolverine dens (at time $t-1$). Similar to the wolf abundance estimation by Milleret et al. (2023c), 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 AC 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 AC and the detector (Royle et al., 2014).

In Scandinavia, DNA material from live wolverines is 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, which means that 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 "Länsstyrelsen" or "SNO" in Rovbase) and located within 500 m from a GPS search track recorded the same day. All remaining samples were assigned to the unstructured sampling. In total, 145 DNA samples were obtained using hair traps, these samples were considered as being part of the unstructured sampling.

We assumed that both structured and unstructured sampling could in theory occur within the entire study area and therefore used the same 10×10 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., 2020b). However, spatial and temporal variation in the probability to detect a sample during structured or unstructured sampling were assumed to be driven by different processes.

We accounted for spatial, temporal and individual heterogeneity in detectability during ***structured sampling*** using:

- Spatio-temporal variation in search effort represented by the length of GPS search tracks in each detector grid cell.
- Spatio-temporal variation in snow cover during the monitoring period calculated as the average percentage of snow cover in each detector grid cell (MODIS at 0.1 degrees resolution, https://cmr.earthdata.nasa.gov, accessed 2025-09-10).
- Spatio-temporal variation in monitoring regimes between jurisdictions (groups of counties in Sweden, carnivore management regions in Norway, Figure A.4).
- Individual variation linked with a detection during the previous occasion (monitoring season) that could be expected to influence the probability of being detected at the next occasion.

We accounted for spatial, temporal, and individual heterogeneity in detectability during ***unstructured sampling*** using:

- Spatio-temporal distribution of ancillary samples and samples not successfully genotyped (Figure A.1). For each detector grid cell and during each monitoring season (Dec 1 -

Jun 30), we identified whether a) any carnivore sample had been registered in Rovbase (excluding successfully genotyped wolverine samples already used in the OPSCR analysis), b) any observation of carnivores had been registered in Skandobs or c) if a hair trap sample had been collected. Hair traps were also used in Norrbotten in 2024 to collect a few DNA samples (see above). Roughly, this binary variable distinguishes areas with very low detection probability from those with a higher 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 during the monitoring period calculated as the average percentage of snow cover in each detector grid cell (MODIS at 0.1 degrees resolution, https://cmr.earthdata.nasa.gov, accessed 2025-09-10).
- Spatial variation in accessibility measured as the average distance to the nearest road.
- Spatio-temporal variation between countries (Figure A.5).
- Individual and temporal variation linked with a previous detection that could influence the probability of being detected at subsequent occasions.

For winters and areas without comprehensive sampling effort (i.e., Norrbotten county in Sweden in all winters except 2016/17, 2017/18, 2018/19, 2023/24, and 2024/25), we removed all samples collected within the county and fixed detection probability to 0 for both structured and unstructured sampling. 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. (2020b).

Model fitting We fitted sex-specific Bayesian OPSCR models using MCMC simulation with NIMBLE version 0.12.2 (de Valpine et al., 2017; Turek et al., 2021; de Valpine et al., 2022) and RovQuant's R package nimbleSCR version 0.2.0 (Bischof et al., 2021) in R version 4.1.0 (R Core Team, 2021). We ran 4 chains each with 37 500 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 before deriving abundance estimates. We considered models as converged when the Gelman-Rubin diagnostics (Rhat, Gelman and Rubin, 1992) was $\leq$1.1 for all parameters and when mixing between chains was satisfactory based on visual inspection of trace plots.

2.2.2 Single-season spatial capture-recapture model

The single season SCR model uses data from the winter 2024/25 only. It is therefore a simplified version of the OPSCR model presented above.
The SCR model is composed of three sub-models:

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

Population size sub-model As in the OPSCR model, we used data augmentation to estimate population size (Royle et al., 2014). However, in this case the individual state z_i can only take two values (1 if the individual is considered as part of the population and 0 otherwise), and there is no state transition. Thus, z_i follows a Bernoulli distribution with probability ψ.

Density sub-model We used a Bernoulli point process to model the distribution of individual ACs (Zhang et al., 2023). Individual ACs were located according to an intensity surface, which was a function of the locations of all known dens recorded between 2009 and 2025 (see Bischof et al., 2019b and Bischof et al., 2020b).

Detection sub-model We used the same detection sub-model as in the OPSCR model (see above).

Model fitting We fitted sex-specific Bayesian SCR models using the same procedure as for the the OPSCR models. We ran 4 chains each with 50 000 iterations, including a 20 000 iterations burn-in period.

2.2.3 Abundance estimates

To obtain an estimate of abundance for any given area, we summed the number of predicted AC locations (individuals detected during sampling or predicted to be alive by the model) that fell within that area for each iteration of the MCMC. This produced a posterior distribution of abundance for that area. From such posteriors, abundance estimates and the associated uncertainty can be extracted for any spatial unit, including countries, counties or management regions (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 wolverines detected along the Swedish and Norwegian border as individual wolverines can be partially designated to both countries (Bischof, 2015; 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 and male) parameter estimates were obtained by merging posterior samples from the sex-specific models before calculating the mean and 95% credible interval of the combined posteriors.

We followed this approach to estimate abundance in 2024/25 based on the AC locations predicted by the single-season SCR model. All prior abundance estimates presented in this report are based on previously published OPSCR analyses available in Milleret et al. (2024a) .

2.2.4 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 activity center of an individual, but also take into account the area over which that individual's activity is spread, i.e., its space use (Bischof et al., 2020b). 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., 2020b). Note that this approach assumes circular home ranges of average size for all individuals of a given sex and does not take into account individual variation in home-range size and shape.

We followed this approach to create the wolverine population density map in 2024/25, based on the AC locations and scale parameters (σ) estimated by the single-season SCR models. Density maps for previous winters are based on previously published OPSCR analyses (Milleret et al., 2024a).

2.2.5 Other derived parameters

The average proportion of individuals detected and the associated uncertainty were obtained by dividing the number of individuals detected through NGS each year (Table A.2) by the corresponding mean abundance estimates and associated credible interval limits, respectively.

We derived the proportion of females in the population and the associated uncertainty by dividing the estimated number of females by the total abundance for each iteration (Table 1), thus generating a posterior distribution of the proportion of females from which the median and credible interval could be derived. Annual population growth rates (λ; Table A.6) were calculated similarly as $\lambda_t = N_{t+1}/N_t$ for each iteration of the MCMC chains.

2.2.6 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 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 26 502 (11 734 female; 14 768 male) genotyped wolverine genetic samples were included in the analysis, of which 48% originated from Sweden. These samples were associated with 3 195 (1690 female; 1505 male) individuals. We did not include individuals with unknown sex in this analysis. During the last sampling period (winter 2024/25), a total of 3 304 DNA samples (1 373 female; 1 931 male) were successfully genotyped. Among all genotyped samples, 19 347 (8559 female; 10788 male) were assigned to structured sampling and 7 155 (3175 female; 3980 male) to unstructured sampling. Annual total and country-specific tallies of detections and associated individuals, as well as dead recoveries are provided in the appendices (NGS samples: Table A.1, number of individuals detected: Table A.2, number of dead recoveries: Table A.3)

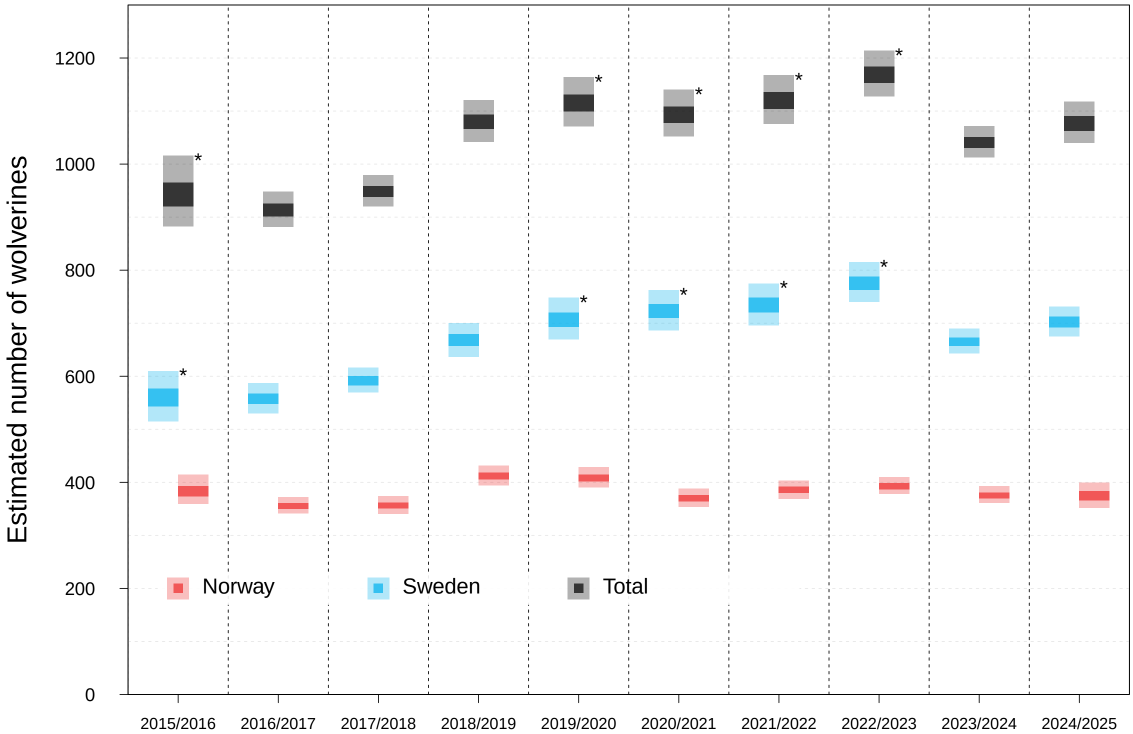


Figure 1: Total (black) and country-specific (blue: Sweden, red: Norway) annual wolverine population size estimates in Scandinavia between 2015/16 and 2024/25. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Credible intervals indicate uncertainty in estimates given the model and data used to generate the estimates. Total estimates in Sweden and for the entire study area that include estimates from Norrbotten county without comprehensive NGS in that county are marked with *. Note that, estimates for the most recent monitoring season (2024/25) were obtained using the single-season SCR model described in this report. Estimates for earlier seasons (2015/16-2023/24) are based on the OPSCR model and were previously reported in Milleret et al. (2024a). See Box 2 for additional details.

3.2 Density and abundance

Wolverine abundance for the entire study area (632 350 km^2, excluding the buffer area) was likely (95% credible interval) between 1 040 and 1 118 individuals in 2024/25 (Table 1, Figure 1, Figure 2). Estimates refer to the status of the population at the start of the annual sampling period (December 1). The proportion of females in the Scandinavian wolverine population was likely between 58% and 61% in 2024/25. Based on the model-predicted location of ACs, we estimated that in 2024/25, between 675 and 731 individuals could be attributed to Sweden and 352 to 400 to Norway. The estimated number of wolverines in 2024/2025 (1 040-1 118) is comparable to the estimated number of wolverines in 2023/24 (1 012-1 072). See Table 1 for total and sex-specific estimates for each country and carnivore management region and Table A.4 for annual estimates for all of Scandinavia and by region between 2015/16 and 2024/25.

The analysis yielded annual density maps, which illustrate changes in the distribution of wolverines over time (Figure A.3).

Table 1: Wolverine population size estimates obtained from the single-season spatial capture-recapture model in 2024/2025 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 by counties ("Län" in Sweden); see Figure A.2 for a labeled map. Only counties and management units that are within or that intersect the study area are included in the table. The percentage of the total area of each unit included in the analysis is provided in the column "% Area". 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 AC locations of wolverines. 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. Estimates for Norwegian counties are provided in (Table A.5).

	Females	Males	Total	% Area
TOTAL	648.1 (613-685)	428.8 (413-446)	1076.9 (1040-1118)	85
NORWAY	227.7 (209-249)	147 (136-160)	374.7 (352-400)	96
Region 1	7.9 (3-14)	8 (5-12)	16 (10-23)	88
Region 2	6.4 (3-11)	7.7 (5-11)	14 (9-20)	87
Region 3	18.5 (15-24)	8.4 (6-11)	26.9 (22-33)	100
Region 4	1.3 (0-4)	1.6 (0-4)	2.8 (1-6)	83
Region 5	32.5 (26-39)	33.5 (30-38)	66 (59-74)	100
Region 6	52.4 (43-62)	32.3 (27-39)	84.7 (74-98)	100
Region 7	51.8 (46-58)	28.8 (25-33)	80.6 (74-88)	100
Region 8	56.9 (51-65)	26.8 (23-31)	83.7 (76-93)	100
SWEDEN	420.4 (395-448)	281.8 (271-293)	702.2 (675-731)	77
Norra	359.9 (338-385)	228.4 (219-239)	588.4 (564-615)	100
Jämtland	131.6 (120-146)	77.7 (72-84)	209.3 (195-226)	100
Norrbotten	125.5 (114-139)	69.1 (63-76)	194.6 (181-210)	100
Västerbotten	85.1 (74-97)	52.9 (49-58)	138 (126-151)	100
Västernorrland	17.7 (13-24)	28.8 (25-33)	46.5 (40-54)	100
Mellersta	60.2 (52-70)	53.3 (48-59)	113.5 (103-124)	75
Dalarna	29.1 (24-35)	23.4 (21-27)	52.5 (47-59)	100
Gävleborg	18.3 (15-23)	20.9 (18-24)	39.1 (34-44)	100
Örebro	2.5 (1-5)	1.2 (0-3)	3.8 (1-7)	100
Stockholm	0.1 (0-1)	0 (0-1)	0.1 (0-1)	4
Uppsala	1.4 (0-4)	1.3 (0-3)	2.7 (0-6)	86
Värmland	7.3 (4-12)	5.8 (3-9)	13.1 (8-18)	100
Västmanland	0.9 (0-3)	0.4 (0-2)	1.2 (0-4)	81
VästraGötaland	0.6 (0-3)	0.3 (0-2)	0.9 (0-3)	12
Södra	0.2 (0-1)	0.1 (0-1)	0.3 (0-2)	1
Östergötland	0.1 (0-1)	0 (0-1)	0.2 (0-1)	4
Södermanland	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	7

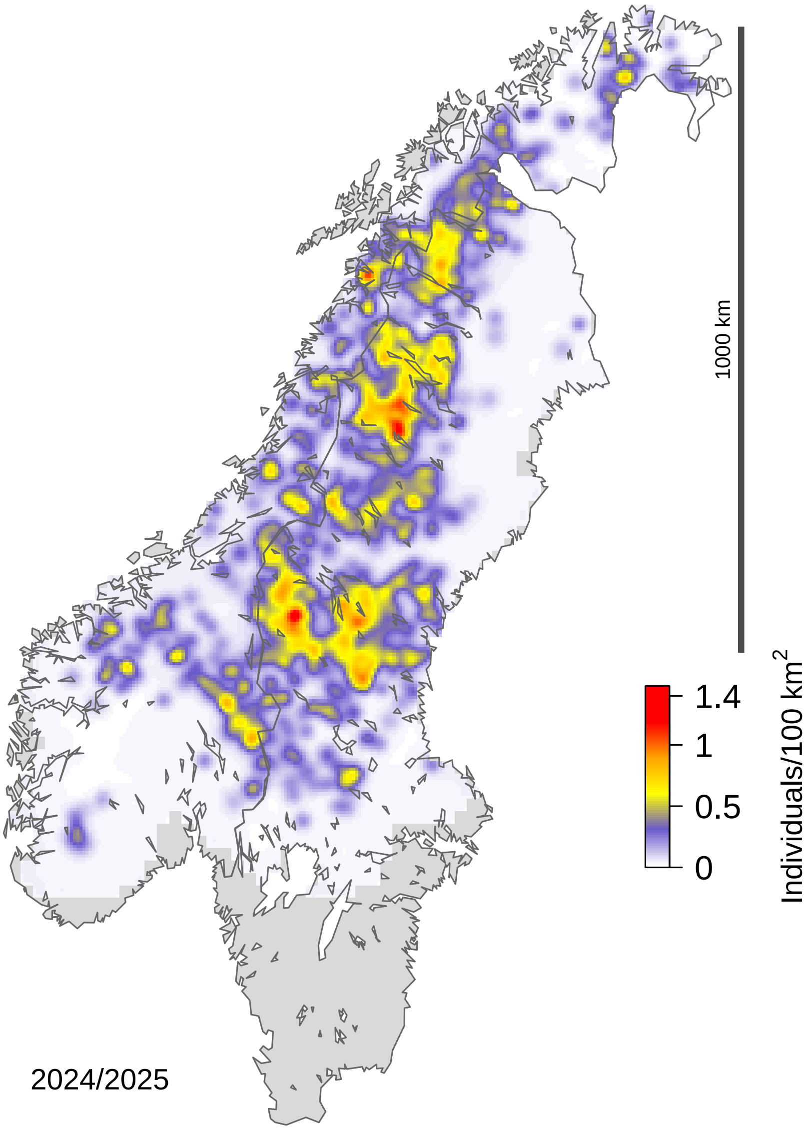


Figure 2: Wolverine density based on individual utilization distributions in Scandinavia in 2024/25 obtained from the single-season SCR model. The grey background represents areas that were considered not searched and therefore not included in the analysis. This map is available as a geo-referenced raster file at https://github.com/richbi/RovQuantPublic

3.3 Vital rates

The OPSCR model produced annual estimates of survival and per capita recruitment rates (Table A.7). Overall, females had a higher survival probability than males (Figure 3). Since 2022-2023, male wolverines experienced a significant apparent drop in survival (0.66-0.77 between 2022-2023, 0.58-0.68 between 2023-2024, and 0.52-0.62 between 2024-2025, Figure 3, Table A.7).

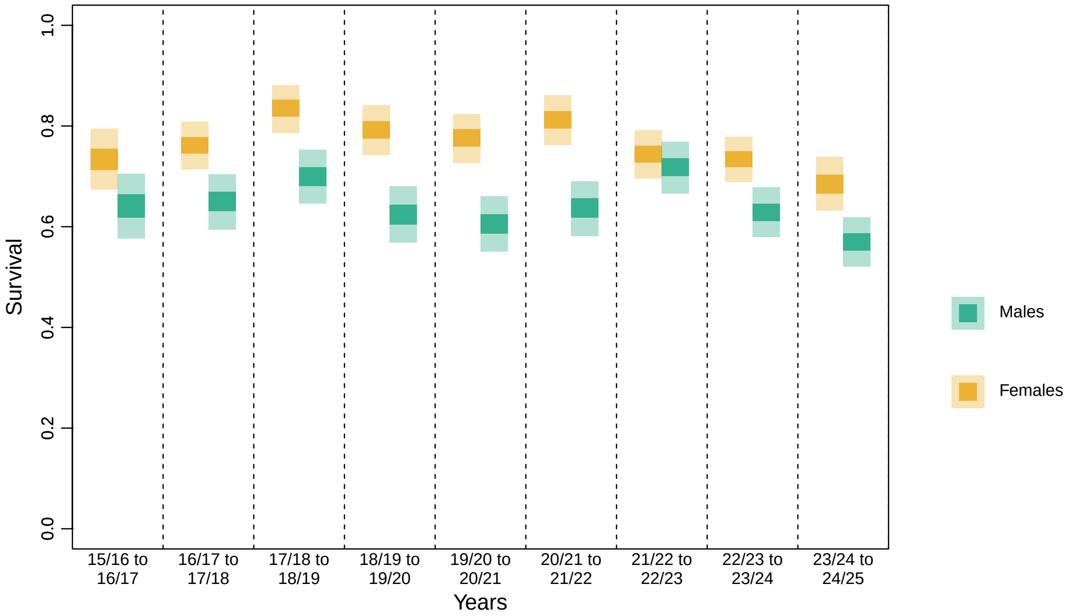


Figure 3: Annual survival probabilities for male and female wolverines. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Shown are overall estimates for the entire study area between 2016/17 and 2024/25.

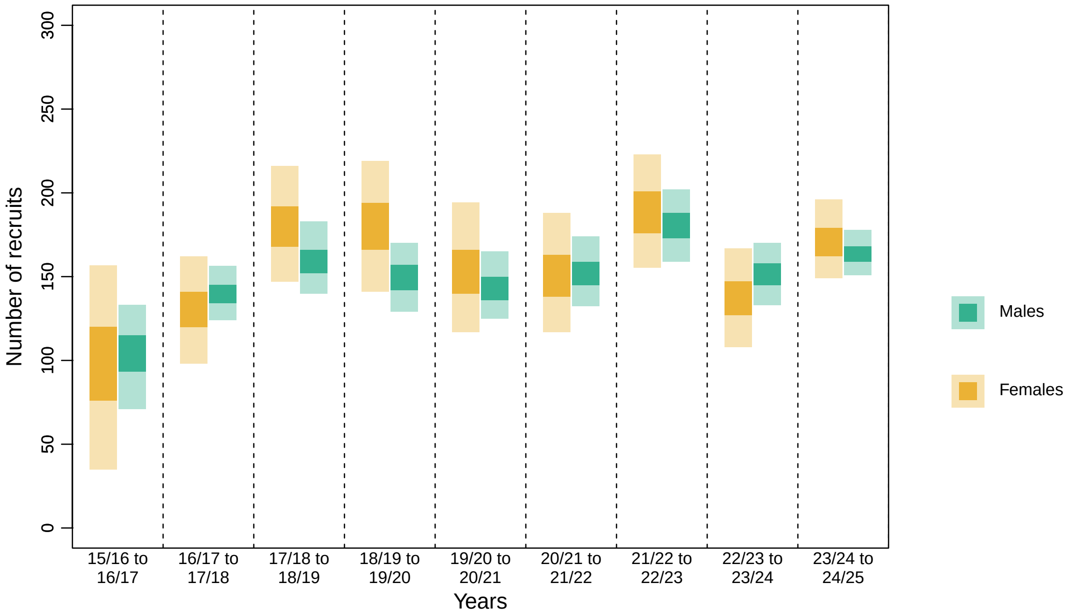


Figure 4: Estimated annual number of male and female recruits in the Scandinavian wolverine population between the start of one sampling season and the start of the next. Recruitment represents the number of new individuals present in the population on Dec 1 (i.e., individuals that were born between the two consecutive monitoring seasons and survived to Dec 1 or that immigrated into the study area). Darker and lighter bars show the 50% and 95% credible intervals, respectively.

3.4 Detection probability

Based on the single-season SCR model, the overall proportion of detected individuals in the population was likely between 82% and 87% in 2024/25, and overall, larger in Norway than in Sweden (Table A.8). The baseline detection probability for the structured and unstructured sampling varied across space (Figure A.4 and Figure A.5). More specifically, the length of recorded search tracks positively affected detection probability during structured sampling (2024/25; males: $\beta = 0.40$, CrI: 0.35 - 0.45; females: $\beta = 0.39$, CrI: 0.33 - 0.45; Table A.10). Detection of an individual during the previous year and the average proportion of snow cover had no significant effect on detection probability during structured sampling for females, but did have a significant and positive effect for males (2024/25 previous detection: $\beta = 0.40$, CrI: 0.25 - 0.54; 2024/25 snow cover: $\beta = 0.13$, CrI: 0.02 - 0.24; Table A.10). The proxy for search effort during unstructured searches, derived using the observation data in Skandobs, ancillary samples in Rovbase, and hair trap samples, had a strong positive effect on detection probability during unstructured sampling (2024/25; males: $\beta = 0.66$, CrI: 0.44 - 0.88; females: $\beta = 0.48$, CrI: 0.23 - 0.74; Table A.11). Detection of an individual during the previous year also had a strong positive effect on detection probability during unstructured sampling (2024/25; males: $\beta = 0.66$, CrI: 0.44 - 0.89; females: $\beta = 0.46$, CrI: 0.19 - 0.74; Table A.11). Finally, the average proportion of snow cover had a positive effect on detection probability during unstructured sampling, but the effects was stronger for males than for females (2024/25; males: $\beta = 0.57$, CrI: 0.42 - 0.72; females: $\beta = 0.27$, CrI: 0.09 - 0.44; Table A.11)

4 Discussion

The overlap in the uncertainty around wolverine population size estimates between 2023/24 (1 012-1 172) and 2024/25 (1 040-1 118) precludes any conclusion regarding population trend. The drop in survival of female wolverines observed last year (2023-2024, Milleret et al. 2024a) is slightly less obvious in this year's analysis (Figure 3). However, the model also estimates a drop in the survival of males since 2022-2023. At this stage, and as already discussed in previous reports (Milleret et al., 2023b, 2024a), we cannot be certain that this pattern is a consequence of real processes in population dynamics or due to an analytical artifact. Such issues can arise with a mismatch between the observation and ecological process of the OPSCR model. For example, it is possible that an unaccounted drop in detectability of individuals in 2023/24 and 2024/25 is manifested as an apparent (and false) decrease in survival.

Compared to previous reports, in which population size estimates were obtained using OPSCR models (Milleret et al., 2022b, 2023b, 2024a), we used a single-season SCR model to estimate population size in 2024/25. OPSCR models have the advantage of using the temporal information contained in the repeated genetic detections of individuals and dead recoveries to obtain spatially-explicit abundance estimates, but also population dynamics parameters. However, every year, when we analyze the data collected over the last 10 years, we omit one year of data at the beginning and add one year of data at the end, as the time series is shifted forward by one year. As a consequence, nine previously reported annual estimated are re-estimated. With such a complete re-analysis and update of the time series, deviations with previously published estimates can be expected because of 1) additional information about individual detections and dead recoveries are used (e.g., individuals not detected in 2023/24 can be detected in 2024/25), 2) adjustment in monitoring strategy that were not accounted correctly in the model, 3) improvements in the model formulation. When deviations in the estimates occur between different models, or between models using different data, it is challenging to determine which models produce the most reliable estimates as the truth is unknown. Even though OPSCR models have been developed to overcome challenges that could not be addressed by SCR models, they are comparatively new and their robustness to violations of assumptions is still relatively unknown. In contrast, single-season SCR models have been more thoroughly tested and several studies suggest that estimates of abundance from single-season SCR models are robust to model misspecifications (Bischof et al., 2020b; Theng et al., 2022; Moqanaki et al., 2021; Dey et al., 2022; Dupont et al., 2019). For these reasons, and to avoid constant retrospective changes to earlier abundance estimate, a single-season SCR model was chosen for this year analysis.

Box 2: SCR *vs.* OPSCR models

For transparency, we provide below a summary of the differences in wolverine population size estimates obtained using three different analyses (Figure 5):

- OPSCR24 shows the results presented in Milleret et al. (2024a) from an OPSCR model using data from 2014/15 to 2023/24.
- OPSCR25 shows the OPSCR model presented in this report that used data from 2015/16 to 2024/25.
- SCR25 shows the results from multiple single-season SCR models (2015/16 to 2024/25) using data from only one winter at a time.

Estimates show substantial overlap among the three models in 2016/17, and from 2019/20 to 2022/23. In contrast, estimates from the single-season models (SCR25) are lower than those obtained from both OPSCR models in 2017/18 and 2018/19. For the seasons 2015/16 and 2023/24, OPSCR24 yielded higher estimates than the other two models. In 2024/25, estimates from OPSCR25 and SCR25 models are comparable. The underlying causes for the observed discrepancies are not yet fully understood. RovQuant is working on identifying the mechanisms behind these patterns.

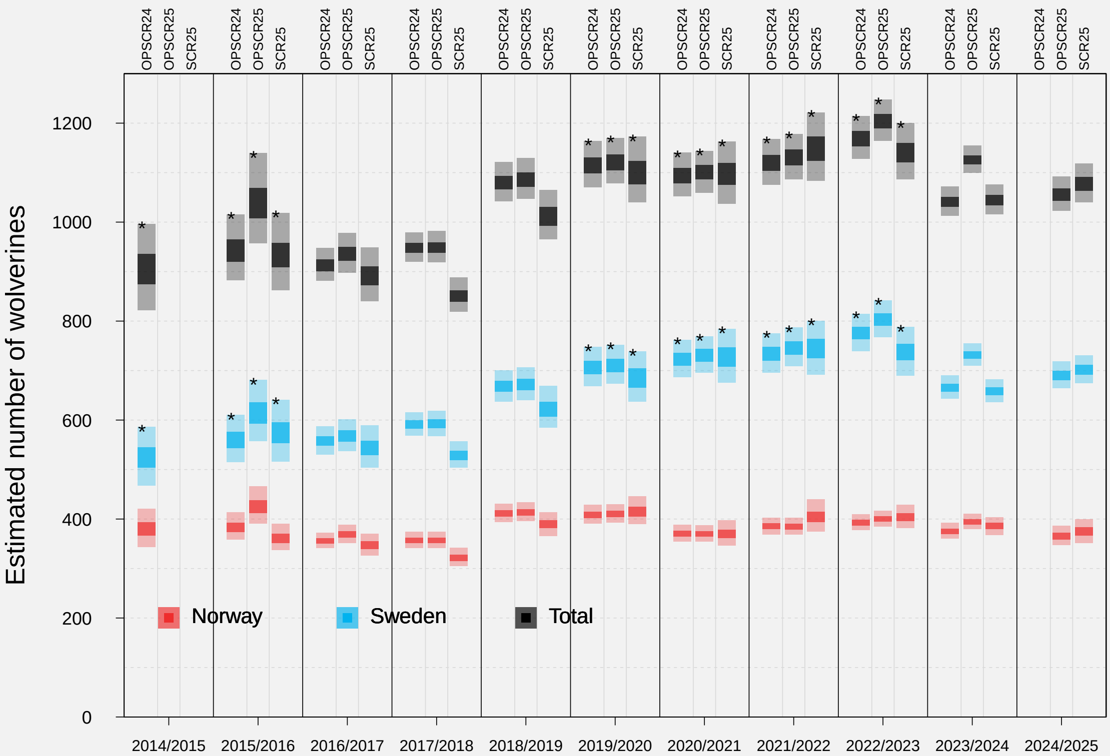


Figure 5: Summary of the wolverine population size estimates obtained in Sweden (blue), in Norway (red) and in both countries (Total, black) using three different models and different years of data. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Each of the three models are presented in a column for each season, 1) OPSCR analysis of the 2014/15-2023/24 time series (OPSCR24, Milleret et al. (2024a)), 2) OPSCR analysis of the 2015/16-2024/25 time series presented in this report (OPSCR25), and 3) single-season SCR models applied to all seasons from 2015/16 to 2024/25 (SCR25).

5 Summary and suggestions of improvements

5.1 Summary of improvements made

The analysis described in this report includes the following adjustments compared with previous analyses of wolverine density in Scandinavia by RovQuant (Milleret et al., 2023b):

1. Addition of data from the 2024/25 monitoring season.
2. Correction of an error in the creation of the covariate used to account for spatio-temporal variation in unstructured sampling (Figure A.1).

5.2 Suggestions for future improvements

RovQuant continues to work on improving the functionality and efficiency of SCR and OPSCR models. We plan to test and potentially implement the following developments in future analyses of the Scandinavian wolverine monitoring data:

1. Using empirical data and simulations, investigate potential causes for observed deviations between estimate generated by different analysis (SCR vs. OPSCR, shifted time series).
2. Review and adjust spatial covariates on density (Moqanaki et al., 2023). This is especially relevant as Sweden has stopped recording den locations.
3. Account for individual heterogeneity in detection for example by using a finite-mixture approach (Cubaynes et al., 2010).
4. Consider alternative detection models that do not assume a half-normal shape and/or circular home ranges (Sutherland et al., 2015; Dey et al., 2022).
5. Account for spatial variation in vital rates (Milleret et al., 2023a).
6. Consider integrating NGS through hair traps as a separate observation process in the SCR/OPSCR model. This will better exploit available effort information and help prepare for potential expansion of fixed DNA collection stations in future NGS bouts.

5.3 Other recommendations

In addition, we suggest the following:

1. Report information about how samples are selected for DNA analysis so that this can be accounted for during analysis.
2. Unambiguously and consistently indicate the species targeted during searches when recording GPS search tracks.
3. Clearly identify and delineate areas excluded from structured and unstructured sampling and indicate the reason for exclusion (e.g., unable to search the area or low priority due to assumed absence of the target species).
4. Explore the feasibility of using station-based detectors (e.g., hair snares or similar) for better control over the observation process.
5. Investigate better proxy to quantify spatio-temporal variation in snow tracking conditions and detectability.

6 Acknowledgements

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7 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

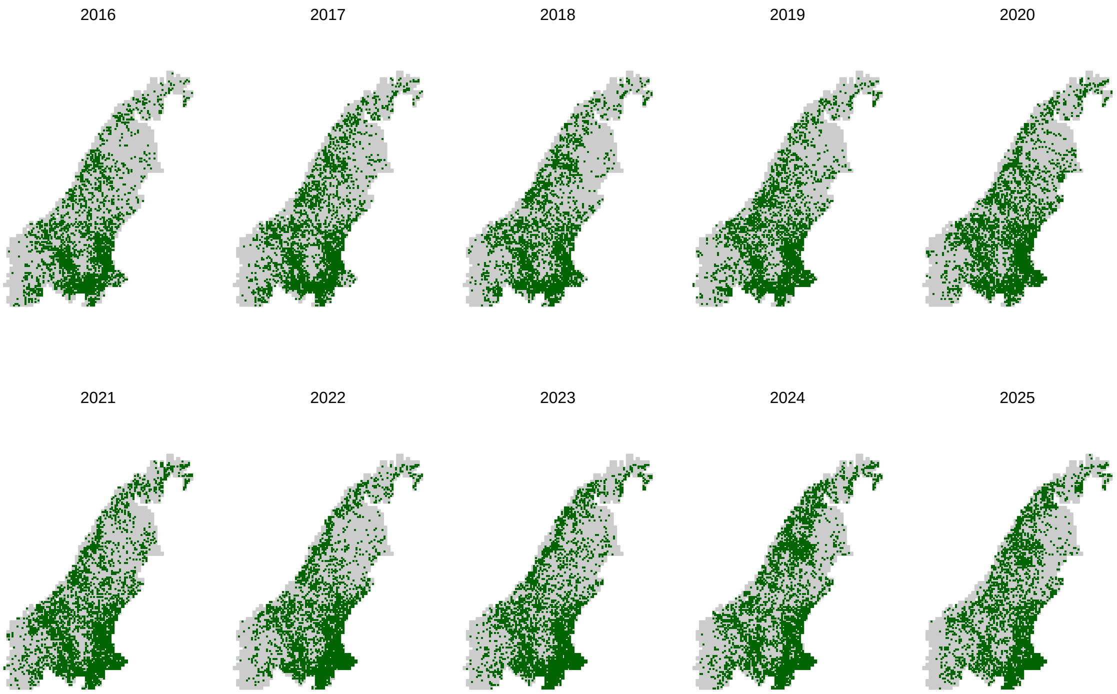

Figure A.1: Covariate used to account for spatio-temporal variation in unstructured sampling in the study area. Green cells (10×10 km) represent areas with at least one carnivore record from Rovbase (rovbase.no, rovbase.se, excluding the wolverine samples used in the OPSCR and single-season SCR models) or an observation record from Skandobs (skandobs.se, skandobs.no) during a given monitoring season (Dec 1 – Jun 30).

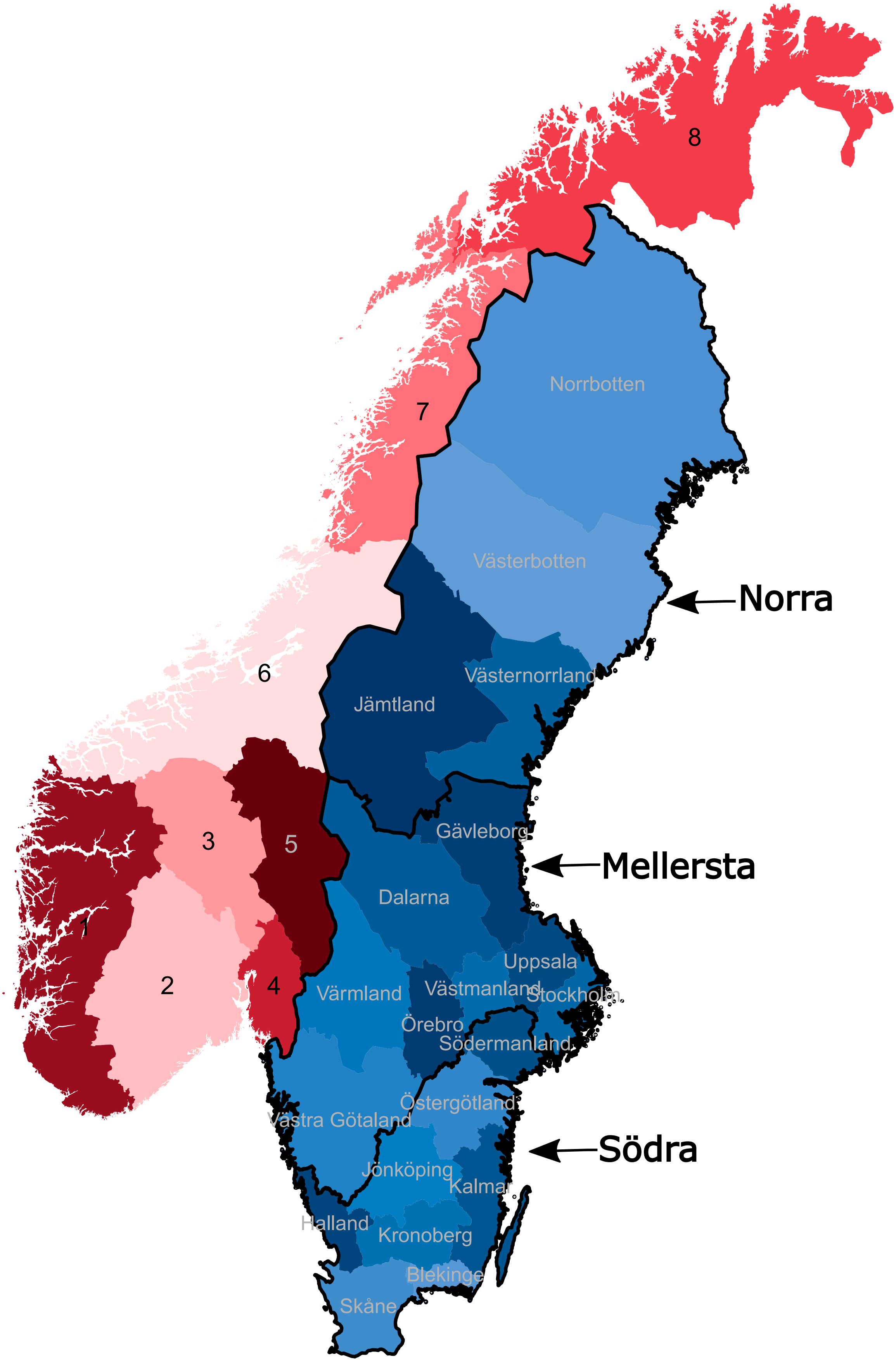

Figure A.2: Management jurisdictions in Norway and Sweden. Polygons with different shading represent carnivore management regions in Norway and counties in Sweden. Thick outlines delineate Swedish carnivore management regions ("Rovdjursförvaltningsområden") encompassing multiple counties.

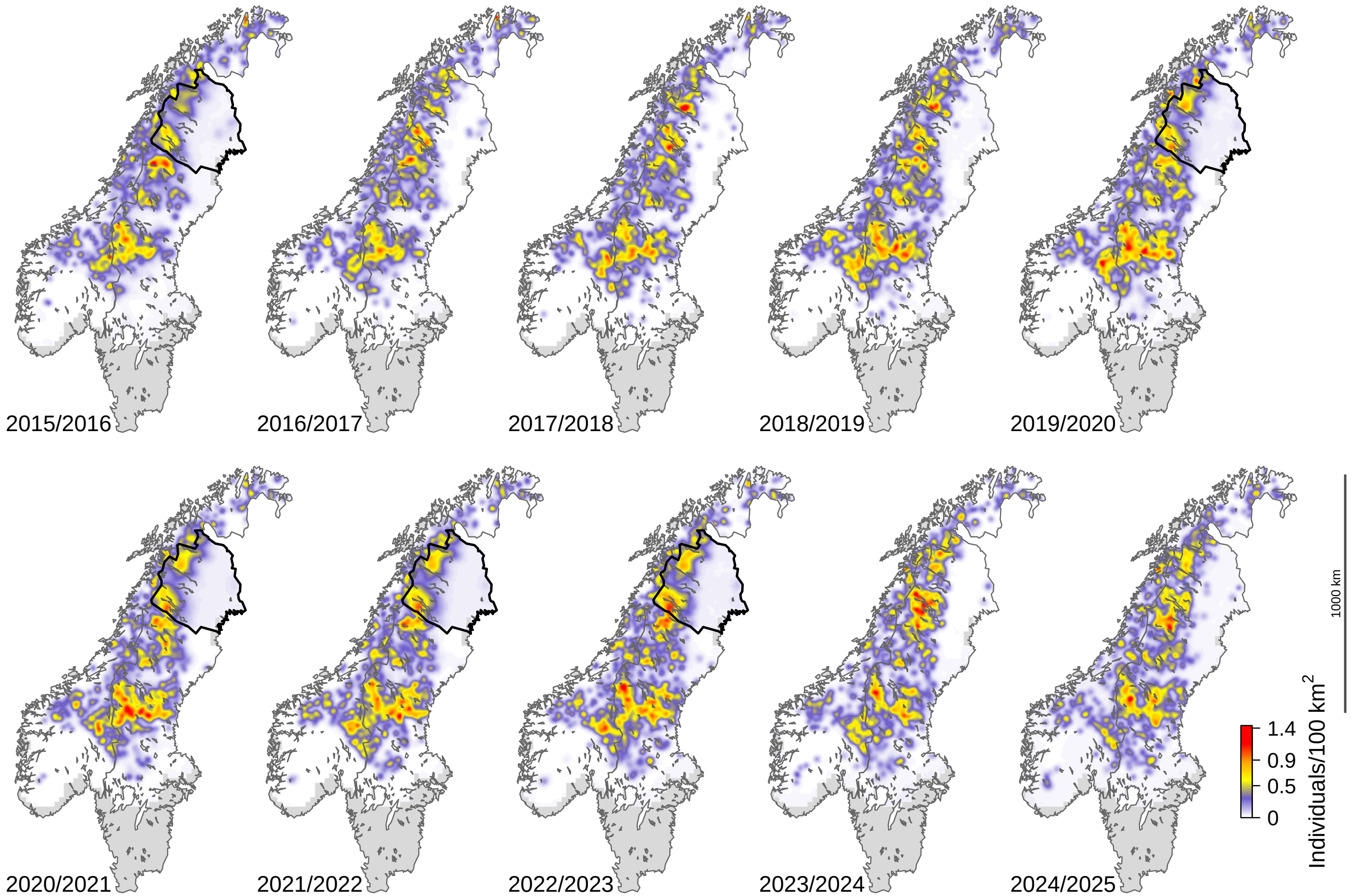

Figure A.3: Wolverine density based on individual utilization distributions in Scandinavia between 2015/16 and 2024/25. Estimates from 2015/2016-2023/2024 were obtained using the OPSCR model described and published in Milleret et al. (2024a). Estimates from 2024/2025 were obtained using the single-season SCR model described in this report. Note that no comprehensive NGS was conducted in Norrbotten (polygon outlined in black) in 2015/16 and from 2019/20 to 2022/23, which means that results in those years are solely based on the OPSCR model prediction and assumptions. The grey area represents areas that were considered not searched and therefore were not included in the analysis. These maps are available as geo-referenced raster files at https://github.com/richbi/RovQuantPublic.

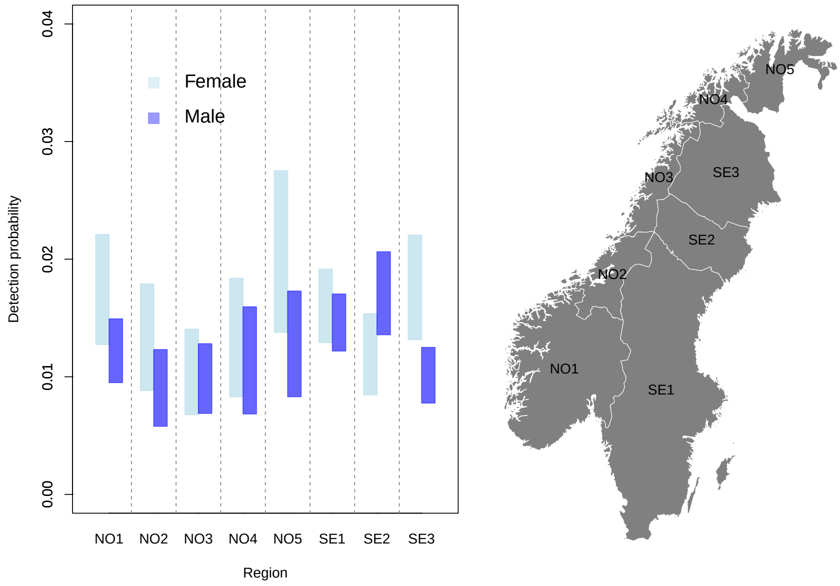

Figure A.4: Sex-specific baseline detection probabilities ($p_{0_{structured}}$) for the different Scandinavian jurisdictions during structured sampling in 2024/25 as estimated by the single-season spatial capture-recapture (SCR) model. Bars represent 95% credible intervals. Results are separated into 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 AC; it is not to be confused with detectability, i.e, the overall probability of detecting an individual.

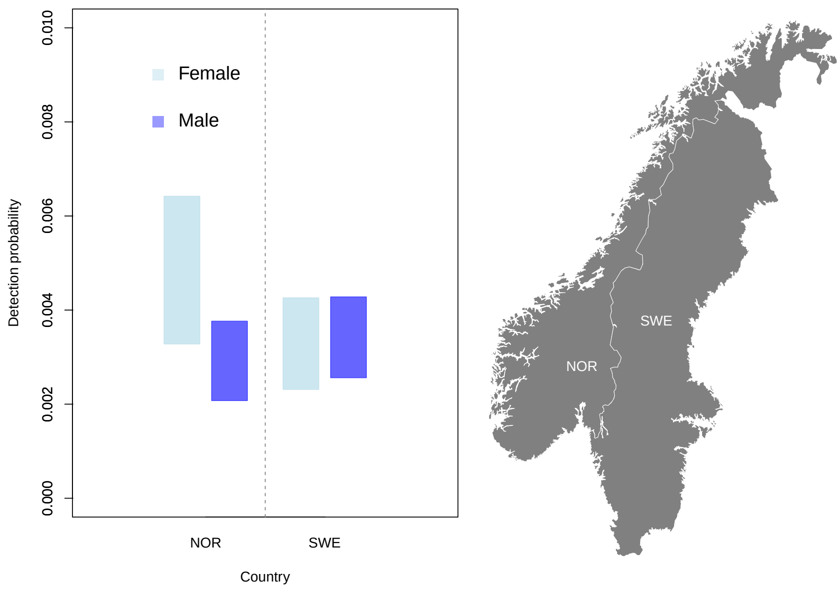

Figure A.5: Sex- and country-specific baseline detection probabilities ($p_{0_{unstructured}}$) of wolverines during unstructured sampling in 2024/25 as estimated by the single-season spatial capture-recapture (SCR) model. Bars represent 95% credible intervals. Estimates are shown for the mean values 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 wolverine 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 (Dec 1 - June 30) between 2015/16 and 2024/25.

		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024		2024/2025	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	Structured	349	421	433	486	320	529	427	554	433	495	443	547	458	563	748	806	479	576	428	568
	Unstructured	120	156	172	182	141	218	165	171	144	189	136	186	111	184	135	198	296	322	176	224
Sweden	Structured	150	177	330	382	403	603	407	529	277	396	325	399	375	531	383	494	786	877	605	855
	Unstructured	86	98	157	170	232	232	104	89	78	142	132	165	121	125	101	191	404	454	164	284
Total	Structured	499	598	763	868	723	1132	834	1083	710	891	768	946	833	1094	1131	1300	1265	1453	1033	1423
	Unstructured	206	254	329	352	373	450	269	260	222	331	268	351	232	309	236	389	700	776	340	508

Table A.2: Annual number of individual wolverines detected via non-invasive genetic sampling and included in the analysis. Numbers are reported by country, for females (F) and males (M). We included only individuals associated with samples collected within the study area during the primary monitoring period (Dec 1 - Jun 30) between 2015/16 and 2024/25. 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.

	2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024		2024/2025	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	179	123	182	131	170	123	192	149	195	151	185	134	194	137	216	154	210	161	190	144
Sweden	107	105	211	177	231	208	226	197	172	156	204	168	196	179	194	195	337	259	324	275
Total	283	224	377	287	390	313	409	333	361	301	383	296	389	307	400	341	526	395	503	391

Table A.3: Number of cause-specific dead recoveries of wolverines in Scandinavia between 2015/16 and 2024/25. Numbers are reported by country, for females (F) and males (M). Dead recovery data was only used to derive cause-specific mortality Table A.7.

	Country	2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021		2021/2022		2022/2023		2023/2024		2024/2025	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	3	1	3	2	7	1	3	4	6	5	4	4	1	0	3	4	2	5	1	3
	Sweden	0	2	0	2	1	2	1	2	0	1	2	1	3	4	3	3	2	1	0	1
Legal culling	Norway	42	43	47	61	27	31	57	37	50	62	44	44	42	46	47	48	53	54	36	34
	Sweden	6	9	5	2	1	5	6	3	7	19	3	10	10	3	14	11	14	17	9	7
Total	Total	51	55	55	67	36	39	67	46	63	87	53	59	56	53	67	66	71	77	46	45

Table A.4: Annual abundance estimates for wolverine 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 from the OPSCR model (from 2015/2016 to 2023/2024, Milleret et al. (2024a)) or the single-season SCR model (2024/25). Credible intervals (95%) are shown in parentheses. Small deviations between the total estimate and the sum of abundance estimates from the constituent sub-regions 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). As a consequence, especially at the local scale, the model-estimated number of wolverines based on DNA sampling can deviate from the number of wolverines inferred from ancillary observations (e.g., camera traps). Estimates for Norrbotten county in years without comprehensive NGS were derived solely using the prediction from the OPSCR model (shown in grey and marked with *). Total estimates in Sweden and for the entire study area that includes estimates from Norrbotten without comprehensive NGS are marked with **.

	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022	2022/2023	2023/2024	2024/2025
TOTAL	943.8 (881-1016)**	913.1 (881-948)	948.3 (920-979)	1079.7 (1042-1121)	1115.7 (1071-1164)**	1093.7 (1051-1140)**	1120.1 (1075-1168)**	1168.9 (1127-1214)**	1040.9 (1012-1072)	1076.9 (1040-1118)
NORWAY	384 (359-414)	355.8 (341-372)	356.6 (341-374)	411.5 (394-431)	408.9 (391-429)	370.3 (354-388)	385.8 (369-403)	393.2 (378-410)	375.8 (360-393)	374.7 (352-400)
Region 1	9.6 (5-15)	7.3 (4-12)	5.7 (3-10)	5.7 (2-10)	5.6 (2-10)	5.9 (2-11)	8.3 (4-13)	7.3 (3-12)	8.9 (5-14)	16 (10-23)
Region 2	4.1 (1-8)	3 (1-6)	2 (0-5)	2.4 (0-6)	2.4 (0-6)	3.8 (1-7)	3.9 (1-7)	5.1 (2-9)	9.7 (6-14)	14 (9-20)
Region 3	27.6 (23-33)	23.3 (19-28)	22.3 (18-27)	27.8 (23-33)	30.3 (26-35)	32 (27-37)	26.5 (22-32)	32.5 (29-37)	27 (23-31)	26.9 (22-33)
Region 4	0.9 (0-3)	0.6 (0-3)	0.4 (0-2)	0.6 (0-2)	0.9 (0-3)	0.7 (0-3)	0.6 (0-3)	0.9 (0-3)	2.1 (0-5)	2.8 (1-6)
Region 5	64 (57-71)	63.2 (57-70)	75.7 (69-83)	91.4 (84-99)	90.7 (84-98)	83.5 (76-91)	88.7 (82-96)	85.6 (79-93)	81.3 (74-89)	66 (59-74)
Region 6	78.6 (68-91)	80 (73-88)	89.8 (82-98)	103.2 (95-112)	89.2 (81-99)	83.4 (75-92)	99.5 (92-108)	95.3 (88-103)	76.9 (69-85)	84.7 (74-98)
Region 7	83.6 (76-92)	70 (64-76)	67.1 (61-73)	78 (71-85)	88.5 (81-96)	69.4 (63-76)	69.8 (64-76)	77.7 (72-84)	85.9 (80-92)	80.6 (74-88)
Region 8	115.6 (105-127)	108.3 (101-116)	93.6 (86-102)	102.4 (94-112)	101.3 (93-110)	91.6 (84-100)	88.4 (80-97)	88.8 (82-97)	84.1 (78-91)	83.7 (76-93)
SWEDEN	559.7 (514-610)**	557.4 (530-587)	591.7 (568-616)	668.1 (637-701)	706.8 (669-748)**	723.4 (686-763)**	734.3 (695-775)**	775.7 (739-815)**	665.1 (642-690)	702.2 (675-731)
Norra	496.6 (455-541)**	488.8 (465-515)	509.9 (488-532)	568.6 (540-598)	600.8 (566-638)**	618.5 (584-655)**	618.8 (582-656)**	643.5 (609-680)**	553.9 (535-575)	588.4 (564-615)
Jämtland	178.7 (161-198)	176.9 (163-192)	190.8 (178-204)	217.5 (202-233)	225.3 (210-241)	229.5 (215-245)	215.6 (202-230)	223.3 (209-239)	174.8 (162-188)	209.3 (195-226)
Norrbotten	168.5 (146-192)	168.2 (157-181)	173 (163-185)	178.4 (162-195)	194.1 (171-219)	200.9 (177-226)	211.4 (186-237)	230.5 (207-255)	219.7 (211-230)	194.6 (181-210)
Västerbotten	128.4 (114-144)	118.7 (108-130)	112.1 (101-124)	132.8 (121-145)	135.8 (125-147)	138.3 (128-150)	125.5 (113-139)	132.5 (120-146)	119.6 (111-130)	138 (126-151)
Västernorrland	21 (14-29)	25 (18-32)	33.9 (27-41)	40 (33-48)	45.7 (38-54)	49.8 (42-58)	66.3 (59-74)	57.2 (49-66)	39.7 (33-47)	46.5 (40-54)
Mellersta	62.8 (51-76)	68.3 (58-79)	81.6 (73-91)	99.2 (89-110)	105.7 (94-118)	104.6 (94-116)	115.2 (105-126)	131.8 (122-143)	110.8 (100-122)	113.5 (103-124)
Dalarna	30.8 (24-38)	35.3 (29-42)	45.3 (39-51)	47.8 (41-56)	50.2 (43-58)	52.7 (45-61)	58.1 (51-65)	66.3 (60-73)	54.8 (48-62)	52.5 (47-59)
Gävleborg	16.2 (10-23)	17.5 (12-24)	21.3 (16-27)	34.9 (29-41)	34.9 (29-41)	33.4 (28-39)	33.6 (28-39)	41 (36-47)	33.1 (28-39)	39.1 (34-44)
Örebro	1.8 (0-5)	1.2 (0-4)	1.6 (0-4)	1.1 (0-4)	2 (0-5)	1.9 (0-5)	2 (0-5)	2.5 (0-6)	2.9 (0-6)	3.8 (1-7)
Stockholm	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)
Uppsala	1.9 (0-5)	1.4 (0-4)	1.1 (0-4)	1.5 (0-4)	1.7 (0-5)	1.3 (0-4)	1.2 (0-4)	2.1 (0-5)	2.6 (0-6)	2.7 (0-6)
Värmland	10.3 (6-15)	11.4 (7-16)	11.1 (8-14)	12.6 (9-16)	15.1 (11-20)	14 (10-19)	19 (15-23)	18.2 (14-23)	15.4 (11-20)	13.1 (8-18)
Västmanland	1 (0-3)	0.7 (0-3)	0.5 (0-2)	0.7 (0-3)	0.9 (0-3)	0.7 (0-3)	0.6 (0-3)	0.9 (0-3)	1.1 (0-3)	1.2 (0-4)
Västra Götaland	0.9 (0-3)	0.7 (0-3)	0.6 (0-2)	0.6 (0-3)	0.7 (0-3)	0.6 (0-3)	0.6 (0-2)	0.9 (0-3)	1 (0-3)	0.9 (0-3)
Södra	0.3 (0-2)	0.3 (0-2)	0.2 (0-2)	0.3 (0-2)	0.3 (0-2)	0.3 (0-2)	0.3 (0-2)	0.4 (0-2)	0.4 (0-2)	0.3 (0-2)
Östergötland	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	0.2 (0-1)	0.2 (0-1)
Södermanland	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	0.2 (0-2)	0.2 (0-1)

Table A.5: Annual abundance estimates for wolverine at the county level in Norway; 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 from the OPSCR model (from 2015/2016 to 2023/2024, Milleret et al. (2024a)) or the single-season SCR model (2024/25). Credible intervals (95%) are shown in parentheses. Small deviations between the total estimate and the sum of abundance estimates from the constituent sub-regions 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). As a consequence, especially at the local scale, the model-estimated number of wolverines based on DNA sampling can deviate from the number of wolverines inferred from ancillary observations (e.g., camera traps).

	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022	2022/2023	2023/2024	2024/2025
NORWAY	384 (359-414)	355.8 (341-372)	356.6 (341-374)	411.5 (394-431)	408.9 (391-429)	370.3 (354-388)	385.8 (369-403)	393.2 (378-410)	375.8 (360-393)	374.7 (352-400)
Østfold	0.4 (0-2)	0.3 (0-2)	0.2 (0-1)	0.2 (0-1)	0.4 (0-2)	0.3 (0-2)	0.3 (0-2)	0.4 (0-2)	0.6 (0-3)	0.7 (0-3)
Akershus/Oslo	0.6 (0-2)	0.4 (0-2)	0.2 (0-1)	0.4 (0-2)	0.5 (0-2)	0.4 (0-2)	0.4 (0-2)	0.5 (0-2)	1.4 (0-4)	2.1 (0-5)
Aust-Agder	0.9 (0-3)	1.6 (1-3)	0.9 (0-3)	0.7 (0-3)	0.8 (0-3)	2.3 (1-4)	2.1 (1-4)	2.5 (1-5)	3.4 (2-6)	7.2 (5-10)
Buskerud	1.3 (0-4)	0.7 (0-3)	0.5 (0-2)	0.8 (0-3)	0.8 (0-3)	0.8 (0-3)	0.9 (0-3)	1.4 (0-4)	2.5 (1-5)	2.7 (0-6)
Finnmark	68.7 (61-77)	62.7 (58-68)	50.9 (45-57)	54.1 (47-61)	56.5 (52-62)	52.4 (47-58)	50.7 (45-57)	47.3 (42-53)	43 (40-47)	43.4 (38-49)
Hedmark	64 (57-72)	63.2 (57-70)	75.7 (69-83)	91.4 (84-99)	90.7 (84-98)	83.5 (76-91)	88.7 (82-96)	85.6 (79-93)	81.3 (74-89)	66 (59-74)
Hordaland	2.5 (1-5)	0.8 (0-3)	0.6 (0-3)	0.9 (0-3)	0.8 (0-3)	0.8 (0-3)	0.8 (0-3)	1.1 (0-4)	1.4 (0-4)	2.4 (0-6)
Møre og Romsdal	17.3 (12-23)	16.4 (13-21)	18.5 (15-23)	20.3 (17-24)	18.7 (15-23)	18.3 (14-23)	18.2 (15-22)	17.5 (14-22)	19.7 (16-24)	18.9 (14-24)
Nord-Trøndelag	31.8 (25-39)	35.3 (31-40)	37.7 (33-43)	43 (38-49)	42.6 (37-49)	40.9 (36-47)	50.4 (46-56)	49.9 (45-55)	38.8 (34-44)	45.6 (39-54)
Nordland	83.6 (76-92)	70 (64-76)	67.1 (61-73)	78 (71-85)	88.5 (81-96)	69.4 (63-76)	69.8 (64-76)	77.7 (72-84)	85.9 (80-92)	80.6 (74-88)
Oppland	27.6 (23-33)	23.3 (19-28)	22.3 (18-27)	27.9 (23-33)	30.3 (26-35)	32 (27-37)	26.6 (22-32)	32.5 (29-37)	27 (23-31)	27 (22-33)
Rogaland	1.2 (0-4)	0.9 (0-3)	1 (0-3)	0.8 (0-3)	0.9 (0-3)	1 (0-3)	1.1 (0-3)	1.4 (0-4)	1.6 (0-5)	2.5 (0-6)
Sør-Trøndelag	29.5 (24-36)	28.3 (23-34)	33.6 (28-40)	39.9 (34-46)	27.9 (22-35)	24.2 (19-30)	30.9 (25-37)	27.9 (23-33)	18.4 (13-24)	20.1 (15-27)
Sogn og Fjordane	5.3 (3-9)	5.2 (3-8)	3.8 (2-7)	3.6 (1-7)	3.4 (1-7)	3.6 (1-7)	5.9 (3-9)	4.2 (2-7)	5 (3-8)	9.7 (6-14)
Telemark	1.9 (0-5)	0.7 (0-3)	0.6 (0-2)	0.8 (0-3)	0.8 (0-3)	0.8 (0-3)	0.8 (0-3)	1.2 (0-4)	3.8 (2-7)	4.1 (1-8)
Troms	46.9 (41-54)	45.6 (41-51)	42.6 (38-48)	48.3 (43-54)	44.8 (39-51)	39.2 (34-45)	37.7 (32-44)	41.5 (37-47)	41.1 (36-47)	40.3 (35-47)
Vest-Agder	0.6 (0-2)	0.4 (0-2)	0.3 (0-2)	0.4 (0-2)	0.4 (0-2)	0.4 (0-2)	0.4 (0-2)	0.6 (0-2)	0.8 (0-3)	1.2 (0-3)
Vestfold	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)	0 (0-1)

Table A.6: Annual population growth rate estimates for the wolverine population in Scandinavia ("Total") and separately for Norway and Sweden. Estimates were derived using the posterior distributions of annual abundance estimates (Table A.4). Credible intervals (95%) are shown in parentheses.

	2016-2017	2017-2018	2018-2019	2019-2020	2020-2021	2021-2022	2022-2023	2023-2024	2024-2025
Norway	0.93 (0.85-1.00)	1.00 (0.95-1.06)	1.15 (1.09-1.23)	0.99 (0.94-1.05)	0.91 (0.85-0.96)	1.04 (0.98-1.11)	1.02 (0.96-1.08)	0.96 (0.90-1.01)	1.00 (0.92-1.08)
Sweden	1.00 (0.91-1.09)	1.06 (1.00-1.13)	1.13 (1.07-1.20)	1.06 (0.99-1.13)	1.02 (0.96-1.09)	1.02 (0.95-1.08)	1.06 (0.99-1.12)	0.86 (0.81-0.91)	1.06 (1.00-1.11)
Total	0.97 (0.90-1.04)	1.04 (0.99-1.09)	1.14 (1.09-1.19)	1.03 (0.98-1.09)	0.98 (0.93-1.03)	1.02 (0.97-1.08)	1.04 (0.99-1.10)	0.89 (0.85-0.93)	1.03 (0.94-1.11)

Table A.7: Estimates of the demographic parameters obtained from the sex-specific wolverine open-population spatial capture-recapture (OPSCR) models. Parameters represent transition rates from Dec 1 to Nov 30 in the following year. Median estimates and 95% credible intervals (in parentheses) for per capita recruitment rate (ρ), survival (ϕ), mortality due to legal culling (h), and mortality due to other causes (w) are presented for males (M) and females (F). Note that cause-specific mortality (h and w) was not estimated directly in the model, but derived from the recorded number of dead recoveries.

	2016-2017		2017-2018		2018-2019		2019-2020		2020-2021	
	M	F	M	F	M	F	M	F	M	F
ρ	0.28 (0.17-0.38)	0.15 (0.05-0.26)	0.40 (0.34-0.46)	0.22 (0.16-0.29)	0.43 (0.36-0.50)	0.31 (0.24-0.38)	0.36 (0.30-0.41)	0.27 (0.20-0.33)	0.34 (0.29-0.41)	0.21 (0.16-0.28)
ϕ	0.64 (0.58-0.71)	0.73 (0.67-0.79)	0.65 (0.59-0.70)	0.76 (0.71-0.81)	0.70 (0.64-0.75)	0.83 (0.79-0.88)	0.62 (0.57-0.68)	0.79 (0.74-0.84)	0.61 (0.55-0.66)	0.78 (0.73-0.82)
h	0.11 (0.09-0.12)	0.06 (0.05-0.06)	0.13 (0.12-0.13)	0.06 (0.06-0.07)	0.09 (0.08-0.09)	0.04 (0.04-0.05)	0.08 (0.08-0.08)	0.07 (0.06-0.07)	0.16 (0.15-0.17)	0.06 (0.06-0.06)
w	0.25 (0.20-0.30)	0.21 (0.15-0.26)	0.22 (0.19-0.25)	0.17 (0.14-0.21)	0.21 (0.18-0.25)	0.12 (0.08-0.16)	0.30 (0.26-0.33)	0.14 (0.10-0.18)	0.23 (0.20-0.26)	0.16 (0.12-0.20)

	2021-2022		2022-2023		2023-2024		2024-2025	
	M	F	M	F	M	F	M	F
ρ	0.38 (0.33-0.45)	0.21 (0.16-0.27)	0.44 (0.38-0.51)	0.26 (0.21-0.31)	0.32 (0.27-0.37)	0.19 (0.14-0.23)	0.36 (0.33-0.40)	0.25 (0.22-0.29)
ϕ	0.64 (0.58-0.69)	0.81 (0.76-0.86)	0.72 (0.66-0.77)	0.74 (0.70-0.79)	0.63 (0.58-0.68)	0.73 (0.69-0.78)	0.57 (0.52-0.62)	0.68 (0.63-0.74)
h	0.10 (0.10-0.11)	0.05 (0.05-0.05)	0.09 (0.08-0.09)	0.06 (0.06-0.07)	0.09 (0.09-0.10)	0.07 (0.07-0.08)	0.12 (0.12-0.13)	0.08 (0.07-0.08)
w	0.26 (0.22-0.29)	0.14 (0.09-0.18)	0.20 (0.16-0.23)	0.19 (0.15-0.23)	0.28 (0.25-0.30)	0.19 (0.16-0.23)	0.31 (0.28-0.33)	0.24 (0.19-0.28)

Table A.8: Average proportion of individuals detected via non-invasive genetic sampling (NGS) in Sweden and Norway for males (M) and females (F). 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 single-season SCR model (2024/25) and open-population spatial capture-recapture (OPSCR) model (2015/16 - 2023/24) (Table A.4). Credible intervals (95%) are shown in parentheses. Note that in some years in Norway, male wolverines detected exceeded the estimated number of wolverines. This is possible when wolverine detection probability was very high and wolverines with activity centers in Sweden were detected on the Norwegian side of the border.

	2015/2016		2016/2017		2017/2018		2018/2019		2019/2020	
	F	M	F	M	F	M	F	M	F	M
Norway	0.71 (0.63-0.77)	0.95 (0.88-1.02)	0.78 (0.74-0.82)	1.06 (0.99-1.13)	0.74 (0.69-0.78)	0.98 (0.92-1.04)	0.74 (0.69-0.79)	0.97 (0.91-1.03)	0.76 (0.71-0.82)	0.99 (0.93-1.04)
Sweden	0.29 (0.25-0.32)	0.51 (0.46-0.57)	0.63 (0.58-0.68)	0.79 (0.74-0.83)	0.65 (0.62-0.69)	0.85 (0.81-0.89)	0.56 (0.53-0.60)	0.74 (0.69-0.79)	0.39 (0.36-0.42)	0.60 (0.56-0.64)
Total	0.46 (0.41-0.50)	0.67 (0.62-0.72)	0.66 (0.63-0.70)	0.82 (0.79-0.86)	0.67 (0.64-0.70)	0.85 (0.81-0.88)	0.62 (0.59-0.65)	0.79 (0.75-0.83)	0.51 (0.48-0.55)	0.73 (0.69-0.76)

	2020/2021		2021/2022		2022/2023		2023/2024		2024/2025	
	F	M	F	M	F	M	F	M	F	M
Norway	0.79 (0.74-0.84)	0.98 (0.92-1.05)	0.78 (0.73-0.83)	1.00 (0.95-1.06)	0.87 (0.82-0.92)	1.04 (0.97-1.10)	0.95 (0.89-1.01)	1.04 (0.98-1.10)	0.86 (0.79-0.92)	1.01 (0.94-1.08)
Sweden	0.44 (0.41-0.47)	0.64 (0.59-0.69)	0.42 (0.39-0.45)	0.67 (0.62-0.72)	0.42 (0.39-0.45)	0.62 (0.58-0.66)	0.84 (0.80-0.89)	0.95 (0.91-0.99)	0.79 (0.74-0.84)	0.98 (0.95-1.02)
Total	0.55 (0.52-0.58)	0.74 (0.70-0.78)	0.54 (0.51-0.58)	0.76 (0.72-0.80)	0.56 (0.53-0.59)	0.74 (0.70-0.77)	0.85 (0.81-0.88)	0.93 (0.89-0.95)	0.80 (0.76-0.84)	0.93 (0.89-0.95)

Table A.9: Estimates of the density and scale parameters obtained from the single-season spatial capture-recapture model in 2024/2025 for males (M) and females (F). . β_{dens} represents the effect of the number of known wolverine dens on activity center locations (Bischof et al., 2020b). The scale parameter σ of the detection function is expressed in kilometers and estimated separately for each year. Credible intervals (95%) are shown in parentheses. Parameters that were not estimated separately each year are marked with *.

	2024/2025	
	M	F
β^*_{dens}	0.63 (0.48-0.76)	0.67 (0.55-0.77)
σ	8.54 (8.28-8.81)	6.28 (6.04-6.54)

Table A.10: Estimates of the detection process parameters for the structured sampling from the single-season spatial capture-recapture model in 2024/2025 for males (M) and females (F). $\beta_{1Structured}$ corresponds to the effect of previous detection of an individual, $\beta_{2Structured}$ to the effect of search-effort (track length), and $\beta_{3Structured}$ to the effect of average snow cover during the monitoring period on baseline detection probability ($p_{0Structured}$). Coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	2024/2025	
	M	F
$\beta_{1_{Structured}}$	0.40 (0.25-0.54)	0.04 (-0.14-0.22)
$\beta_{2_{Structured}}$	0.40 (0.35-0.45)	0.39 (0.33-0.45)
$\beta_{3_{Structured}}$	0.13 (0.02-0.24)	0.12 (-0.01-0.24)

Table A.11: Estimates of the detection process parameters for the unstructured sampling from the single-season spatial capture-recapture model in 2024/2025 for males (M) and females (F). $\beta_{1Unstructured}$ corresponds to the effect of previous detection, $\beta_{2Unstructured}$ to the effect of average snow cover during the monitoring period, $\beta_{3Unstructured}$ to the effect of distance to the nearest road, and $\beta_{4Unstructured}$ to the effect of spatio-temporal heterogeneity in unstructured sampling derived using the observation data (from Skandobs, Rovbase and hair trap samples) on baseline detection probablity ($p_{0Unstructured}$). Coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	2024/2025	
	M	F
$\beta_{1_{Unstructured}}$	0.66 (0.44-0.89)	0.46 (0.19-0.74)
$\beta_{2_{Unstructured}}$	0.57 (0.42-0.72)	0.27 (0.09-0.44)
$\beta_{3_{Unstructured}}$	-0.19 (-0.32–0.06)	-0.07 (-0.21-0.06)
$\beta_{4_{Unstructured}}$	0.66 (0.44-0.88)	0.48 (0.23-0.74)