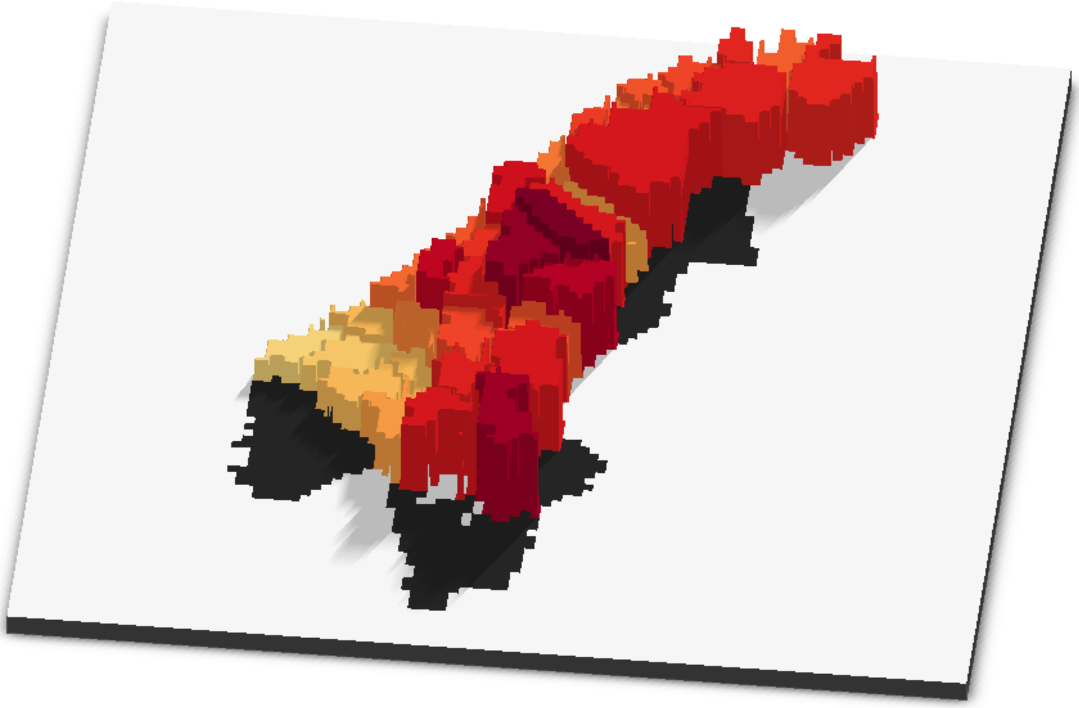
Norwegian University of Life Sciences
Faculty of Environmental Sciences and Natural Resource Management

2026
ISSN 2535-2806

MINA fagrapport 109

Spatial variation in wolverine mortality, 2019–2024

Cyril Milleret
Pierre Dupont
Richard Bischof



Milleret, C., Dupont, P., and Bischof, R., 2026. **Spatial variation in wolverine mortality, 2019–2024** - MINA fagrapport . 22 pp.

Ås, January 2026

ISSN: 2535-2806

AVAILABILITY

Open

PUBLICATION TYPE

Digital document (pdf)

QUALITY CONTROLLED BY

The Research committee (FU), MINA, NMBU

PRINCIPAL

Miljødirektoratet, Contact person: Veronica Sahlén

COVER PICTURE

Wolverine, Map of Norway and Sweden with height of extruded polygons indicating estimated wolverine mortality.

NØKKELORD

Gulo gulo, jerv, jerv, overlevelse, kryptisk dødelighet, romlig autokorrelasjon, ikke-invasiv genetisk prøvetaking, åpen-populasjon-romlig-fangst-gjenfangst, rovdyrforvaltning

KEY WORDS

Gulo gulo, wolverine, survival, cryptic mortality, spatial auto-correlation, non-invasive genetic sampling, open-population spatial capture-recapture, carnivore management

Cyril Milleret, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway

Pierre Dupont, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway

Richard Bischof (richard.bischof@nmbu.no), Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway

Summary

Background Wolverine mortality in Scandinavia is driven predominantly by humans. Human-caused mortality can occur legally (e.g., hunting and management culling), illegally (poaching), or accidentally (e.g. traffic collisions). Although rangewide annual mortality estimates for legal and all other causes have been available for the Scandinavian wolverine population since 2019, these sources of mortality are bound to vary throughout the landscape. Spatially explicit estimates of wolverine mortality and maps thereof could aid wolverine management, for example by identifying mortality hot spots. Of particular interest are maps displaying spatial variation in mortality due to causes other than legal removal, as this includes multiple causes of mortality that are difficult to detect and quantify, such as natural and illegal mortality.

Approach We used a Bayesian open-population spatial capture-recapture (OPSCR) model to analyze non-invasive genetic sampling (NGS) and dead recovery data of wolverines collected between 2019 and 2024 (Rovbase 3.0 ; www.rovbase.no). OPSCR models can generate spatially explicit estimates of mortality, while accounting for the fact that not all wolverine deaths are detected. We generated maps of mortality across the Scandinavian range of the wolverine, with a special focus on mortality that remains mostly undetected (i.e. mortality due to all causes other than legal removal).

Results We found substantial spatial variation in mortality among regions. Overall, legal mortality was higher in Norway than in Sweden, while all other combined causes of mortality were generally higher in Sweden than in Norway. Furthermore, the map of mortality due to all other causes revealed substantial spatial variation. In some regions, it was estimated that close to 1 in 2 wolverines died from causes other than legal mortality each year (mean = 0.44; 95% CrI:0.25; 0.68), while in others, less than 10% were estimated to have died from other causes of mortality (0.09 [0.04; 0.16]).

Discussion We detected substantial spatial variation in wolverine mortality due to causes other than legal removal (e.g., illegal, natural, accidents). Although illegal mortality is a known cause of mortality in the Scandinavian wolverine population, we cannot draw a direct link between mortality hot spots identified here and illegal activity. However, our findings and the resulting maps could help guide the allocation of resources by managers and law enforcement to investigate potential causes of elevated mortality. We discuss the implications of our findings and propose future developments of our approach to enhance its utility for wolverine management.

Sammendrag

Bakgrunn Dødelighet blant jerv i Skandinavia drives primært av mennesker. Menneskeskapt dødelighet kan være lovlig (f.eks. ved lisensfelling og ekstraordinære uttak), ulovlig (ved ulovlig jakt), eller skyldes uhell (som f.eks. trafikkollisjoner). Selv om årlige estimater for lovlig dødelighet og dødelighet grunnet andre årsaker har vært tilgjengelige for den skandinaviske jervebestanden siden 2019, så vil disse kildene til dødelighet variere over landskapet. Romlig-eksplisitte estimater av dødelighet blant jerv og kart over disse kan bistå i forvaltningen av jerv, for eksempel gjennom å identifisere områder med forhøyet dødelighet ("hot spots"). Av særlig interesse er kart som viser romlig variasjon i dødelighet grunnet andre årsaker enn lovlig uttaking, da dette inkluderer flere årsaker til dødelighet som er vanskelige å oppdage og kvantifisere, slik som naturlig og ulovlig dødelighet.

Tilnærming Vi benyttet en bayesiansk åpen-populasjon-romlig-fangst-gjenfangst-modell (OPSCR) for å analysere data fra ikke-invasiv genetisk prøvetaking (NGS) og data på funn av død jerv mellom 2019 og 2024 (Rovbase 3.0 ; www.rovbase.no). OPSCR-modeller kan produsere romlig-eksplisitte estimater av dødelighet samtidig som de tar i betraktning at ikke alle dødsfall blant jerv blir oppdaget. Vi produserer kart over dødelighet over det skandinaviske utbredelsesområdet til jerv, med et spesielt søkelys på dødelighet som er utfordrende å oppdage (dvs. dødelighet grunnet alle andre årsaker enn lovlig uttak).

Resultater Vi fant betydelig romlig variasjon i dødelighet mellom regioner. Lovlig dødelighet var høyere i Norge enn i Sverige, mens alle andre årsaker til dødelighet kombinert var høyere i Sverige enn i Norge. Kartet over dødelighet grunnet andre årsaker avslørte betydelig romlig variasjon. I noen regioner ble det estimert at nærmere 1 av 2 jerver dør av årsaker utenom lovlig dødelighet hvert år (gjennomsnitt = 0.44; 95% CrI:0.25; 0.68), mens i andre regioner ble det estimert at mindre enn 10% av dødelighet skyldtes andre årsaker (0.09 [0.04; 0.16]).

Diskusjon Vi fant betydelig romlig variasjon i dødelighet hos jerv grunnet andre årsaker enn lovlig uttaking (naturlig dødelighet, uhell osv.). Selv om ulovlig dødelighet er en kjent årsak til dødelighet i den skandinaviske jervepopulasjon så kan vi ikke trekke en direkte kobling mellom områder med forhøyet dødelighet ("hot spots") identifisert her og ulovlig aktivitet. Likevel kan våre funn og kartene vi har produsert kunne bistå i forvaltningens og politiets fordeling av ressurser i etterforskningen av mulige årsaker til forhøyet dødelighet. Vi diskuterer følgene av våre funn og foreslår framtidig utvikling av vår tilnærming for å forbedre dens nytteverdi i forvaltningen av jerv.

Contents

1 **Introduction** 6

2 **Methods** 8
  2.1 Data 8
    2.1.1 Non-invasive genetic sampling 8
    2.1.2 Dead recoveries 8
    2.1.3 Search effort (GPS tracks) 8
    2.1.4 Observation reports in Skandobs 9
  2.2 Open-population spatial capture-recapture model 9
    2.2.1 Density and movement sub-model 9
    2.2.2 Population dynamics sub-model 9
    2.2.3 Detection sub-model 11
    2.2.4 Model fitting 12

3 **Results** 13
  3.1 Non-invasive genetic samples and dead recoveries 13
  3.2 Spatial variation in mortality 13

4 **Discussion** 15

5 **Acknowledgements** 16

6 **Data availability** 16

References 18

Appendices 19

1 Introduction

Norway and Sweden are strongholds of Europe's wolverine (*Gulo gulo*) population, containing approximately 70% of European wolverines (Kaczensky et al., 2024). Although protection status and management approaches differ between Norway and Sweden, both countries conduct coordinated monitoring using non-invasive genetic sampling and dead recoveries (Kleven et al., 2024). All collected data are stored in the Scandinavian large carnivore database Rovbase (www.rovbase.se, www.rovbase.no). The data obtained during this large scale monitoring program are analyzed with modern statistical approaches (Bischof et al., 2020) to assess the status and trajectory of the wolverine population. As a result, Swedish and Norwegian management agencies have access to annual population density maps and abundance estimates, as well as annual estimates of vital rates (recruitment and survival; Milleret et al. (2024a)).

The Norwegian Nature Inspectorate (SNO), recently expressed interest in identifying spatial differences in wolverine mortality across the Norwegian range of the species. Specifically, authorities are interested in quantifying spatial variation in mortality that is not attributable to legal removals. The goal is to detect areas with elevated mortality, which could possibly be linked with illegal activity or other - including natural - factors influencing population vital rates locally. Thus far, only population size estimates are provided on a regional basis, while vital rates are estimated annually for the entire population (Milleret et al., 2024a).

Although wolverine monitoring in Scandinavia is intensive, not all individuals are detected and not all mortality events are discovered. This means that the estimation of population size and demographic parameters such as survival must take into-account imperfect detection. The analytical framework developed by RovQuant is based on Bayesian open-population spatial capture-recapture (OPSCR) models (Ergon and Gardner, 2014; Bischof et al., 2016; Chandler et al., 2018; Bischof et al., 2020). These models use the spatial and temporal information contained in the repeated genetic detections of individuals to estimate spatially-explicit abundance (i.e., density) and vital rates (e.g., recruitment and survival), while accounting for imperfect detection during sampling. Recently, we have extended open-population spatial capture recapture (OPSCR) models to allow estimation and mapping of spatial variation in cause-specific mortality (Milleret et al., 2023a, 2025). This new class of OPSCR models can yield valuable information about the landscape-level drivers of mortality and holds potential for informing management about mortality hotspots.

Here, we used non-invasive genetic sampling data from six recent monitoring seasons (2019-2024) and a newly developed OPSCR model to estimate regional variation in wolverine mortality in Scandinavia with a special focus on mortality due to causes other than legal mortality. These causes include natural deaths, vehicle collisions and illegal mortality, which may sometimes be reported but remain mostly undetected, contrary to legal mortality events which are always reported.

In this report, we provide the following information:

- A map and estimates of mortality due to causes other than legal removal across fine regional subdivision of the Scandinavian wolverine range.
- Estimates of mortality due to legal removal across a coarse regional subdivision of the Scandinavian wolverine range.

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 mortality: Lethal removal of individuals by legal means, including licensed recreational hunting, management removals, and defense of life and property.
Other mortality: All causes of mortality that are not attributed to "legal mortality" such as natural, traffic-related, or illegal mortality.
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 Agency (Miljødirektoratet).
RovQuant: Research project at the Norwegian University of Life Sciences (Ås, Norway) that focuses on the development and application of OPSCR models.

2 Methods

2.1 Data

We included data from multiple sources in the analysis, the primary one being the Scandinavian large carnivore database Rovbase 3.0 (rovbase.se and rovbase.no; last extraction: 2024-10-23). This database is used jointly by Norway and Sweden to record detailed information associated with large carnivores 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 six consecutive monitoring seasons from 2019/2020 to 2023/2024.

2.1.1 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 NGS in Norrbotten county during 2023/2024 was performed between October 1 and May 15, although, the vast majority of samples were obtained after December 1 (Milleret et al., 2024b). For consistency with previous estimations (Milleret et al., 2024a), 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), Flagstad et al. (2021), and Kleven et al. (2024).

2.1.2 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 causes (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 used for non-invasive genetic samples. In this study, we focused primarily on identifying spatial variation in the mortality due to the combination of causes other than legal removals.

2.1.3 Search effort (GPS 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 model to account for spatial and temporal variation in search effort during NGS.

2.1.4 Observation reports in Skandobs

We used all observation records in the Skandobs database that were recorded during the wolverine monitoring seasons since 2019 (skandobs.se, skandobs.no; last extraction: 2024-09-30). Skandobs is a web application that allows anyone to anonymously register observations (visual, tracks, feces, etc.) of bears (*Ursus arctos*), lynx (*Lynx lynx*), wolves (*Canis lupus*), and wolverines in Scandinavia. This data currently consists of more than 100 000 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 Open-population spatial capture-recapture model

To estimate spatial variation in cause-specific mortality, we modified the Bayesian open-population spatial capture-recapture (OPSCR) model used to estimate yearly population size and dynamics (Bischof et al., 2019b; Milleret et al., 2024a). The model addressed three challenges associated with population-level wildlife inventories:

1. Detection of individuals and mortality events are imperfect and sampling effort is heterogeneous in space and time (Kéry and Schaub, 2012).
2. Individuals that reside primarily outside the surveyed area may be detected within it (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 can help return unbiased estimates of demographic parameters (Ergon and Gardner, 2014; Schaub and Royle, 2014; Gardner et al., 2018).

The OPSCR model is composed of three sub-models:

1. A model for individual distribution and movement.
2. A model for population dynamics and spatial mortality.
3. A model for detection during DNA searches and dead recoveries.

2.2.1 Density and movement sub-model

In SCR models, the location of individuals is represented by the center of their activity ; Royle et al. (2014)). 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 (see Bischof et al., 2019b and Bischof et al., 2020 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. (2023b), 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).

2.2.2 Population dynamics sub-model

In contrast to the OPSCR models used to obtain annual population size estimates (Bischof et al., 2020; Milleret et al., 2024a), and because the focus of this analysis was the estimation of mortality rates rather than density and abundance, we used an OPSCR model conditioned on the first detection of individuals. This approach is traditionally used to estimate survival in capture recapture models such as the Cormack-Jolly-Seber model (Lebreton et al., 1992). This choice allowed us to simplify the model assumptions and speed up computation. As a consequence, the approach does not allow true population-level estimation and only reflects survival estimates associated with detected individuals.

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) “alive” if the individual was alive; (2) “dead legal” if the individual was recovered dead caused by legal mortality; (3) "dead" if the individual died from other causes of mortality. This is the absorbing state in which all individuals ultimately transition to after dying regardless of the mortality cause. We then modeled the transition from one state to another between consecutive monitoring seasons (t to $t+1$) to estimate the different mortality probabilities.

Spatial variation in mortality We parameterized the model to account for demographic (sex), temporal (year) and spatial variation in cause-specific mortality (i.e., legal and other causes of mortality). Specifically, we followed the modeling approach described in Milleret et al. (2023a) that uses the location of individual activity centers to model spatial variation in mortality. We accounted for competing risk (i.e., an individual that died from one cause of mortality cannot die from another cause) using mortality hazard rates (Ergon et al., 2018). We considered two mortality causes: 1) "legal" that grouped all reported legal mortality events in Norway and Sweden ("Lisensfelling", "Nødverge tamdyr", "Oppdrag SNO", "Skadefelling"); 2) "other" that grouped all other mortality events. Nearly all deaths falling into the "other" category remained undetected, despite their large contribution to overall mortality (Milleret et al., 2024a).

Although our focus was on the estimation of the spatial variation in mortality due to causes other than legal mortality, we also accounted for temporal, sex-specific, and spatial variation in legal mortality. We divided Scandinavia in 4 regions using the E14 highway that separates the northern and the southern portions of the Swedish and Norwegian wolverine populations (Gervasi et al., 2015). We assumed legal mortality to be sex and year-specific in the two regions of Norway. However, we did not consider year-specific legal mortality rates in Sweden due to the very low number of legal mortality events. In addition, we accounted for a sex-specific effect of wolverine density on legal mortality. Wolverine density maps (available in Milleret et al. (2024a)) at year $t-1$ were used to estimate its effect on mortality during the transition from year $t-1$ to t.

For other causes of mortality, we focused on estimating finer-scale regional variation in mortality. The definition of the regions was suggested by SNO based on administrative units and was slightly adjusted to ensure that a sufficient number of wolverines was detected in each of the regions Figure A.1. We then used an intrinsic Gaussian conditional autoregressive (CAR) model to estimate region-specific mortality (de Valpine et al., 2024). CAR models are specifically designed to estimate unknown spatial processes with spatial dependence. This modeling framework fits well with our study, as we did not have apriori knowledge about which regions may have lower or higher mortality rates. However, we expected mortality to be spatially autocorrelated, with neighbouring regions having more similar mortality estimates than non-adjacent regions. Since our goal was to estimate fine-scale spatial variation in mortality due to causes other than legal mortality, we prioritized spatial resolution over temporal resolution in our analysis. In other words, the sample size available did not allow us to estimate sex, year and region-specific mortality rates. This means that our estimates of spatial variation in other causes of mortality represent aggregate values across sex and years. Nonetheless, and as for legal mortality, we accounted for a sex-specific effect of wolverine density on other causes of mortality.

2.2.3 Detection sub-model

Non-invasive genetic sampling 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 "Statsforvalteren" or "SNO" in Rovbase) and located within 500 m of a GPS search track recorded the same day. All remaining samples were assigned to the unstructured sampling. In 2024 in Norrbotten, 66 DNA samples were obtained using hair traps, these samples were considered as being a 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., 2020). 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. Compared to the annual population size estimation (Milleret et al., 2024b), we considered that the entire Norwegian and Swedish countries were searched. The only area where individuals could be located but not detected was located within a 60km buffer of study area in Finland and Russia. This was performed to limit potential edge effect issues related to the use of a buffer when estimating survival with OPSCR models (Gardner et al., 2018; Efford and Schofield, 2022).

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 2024-10-11).
- Spatio-temporal variation in monitoring regimes between jurisdictions (groups of counties in Sweden, carnivore management regions in Norway).
- 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. 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.

- 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 2024-10-11).

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

- Spatio-temporal variation between countries.

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

For years and areas without comprehensive sampling effort (i.e., Norrbotten county in Sweden in all years except 2017, 2018, 2019, and 2024), 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. (2020).

Dead recoveries We used the location of the legal dead recoveries of individuals to estimate the probability to recover an individual dead due to legal mortality, conditional on its AC location and its space used (σ) (Dupont et al., 2021). Contrary to the observation model used for NGS data, dead recovery of individuals can only occur at a single location, but multiple individuals can be detected at the same location simultaneously (Dupont et al., 2021). To model this process, we used a Bernoulli point process with a bivariate normal model (Zhang et al., 2023). We assumed that dead recovery could occur anywhere in the habitat.

2.2.4 Model fitting

We fitted the Bayesian OPSCR model 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 25 000 iterations, including a 10 000-iterations burn-in period. Due to the computing challenge associated with post-processing large amounts of data, we thinned chains by a factor of 10 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.

3 Results

3.1 Non-invasive genetic samples and dead recoveries

A total of 16 578 (7 409 female; 9 169 male) genotyped wolverine genetic samples were collected between 2019 and 2024, of which 47% originated from Sweden. These samples were associated with 2 272 (1221 female; 1051 male) individuals. A total of 634 (335 female; 356 male) individuals were recovered dead due to legal mortality. A total of 57 (26 female; 31 male) individuals were recovered dead due to other causes. Deaths from other causes consisted of 23 individuals dead from unknown causes, 16 from natural causes, 14 from traffic collisions, 2 from confirmed illegal killing and 2 for animal welfare reasons ("Dyrevelferdshensyn"). 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)

3.2 Spatial variation in mortality

Mortality due to legal removal Legal mortality was higher in Norway than in Sweden (Figure 1). Legal mortality was also higher in the south compared to the north of Norway, especially for females. We detected a negative effect of wolverine density on the legal mortality of both females ($\beta_{h_{Female}} = -0.53$; 95% CrI $[-0.78; -0.30]$) and males ($\beta_{h_{Male}} = -0.57$; 95% CrI $[-0.82; -0.33]$) .

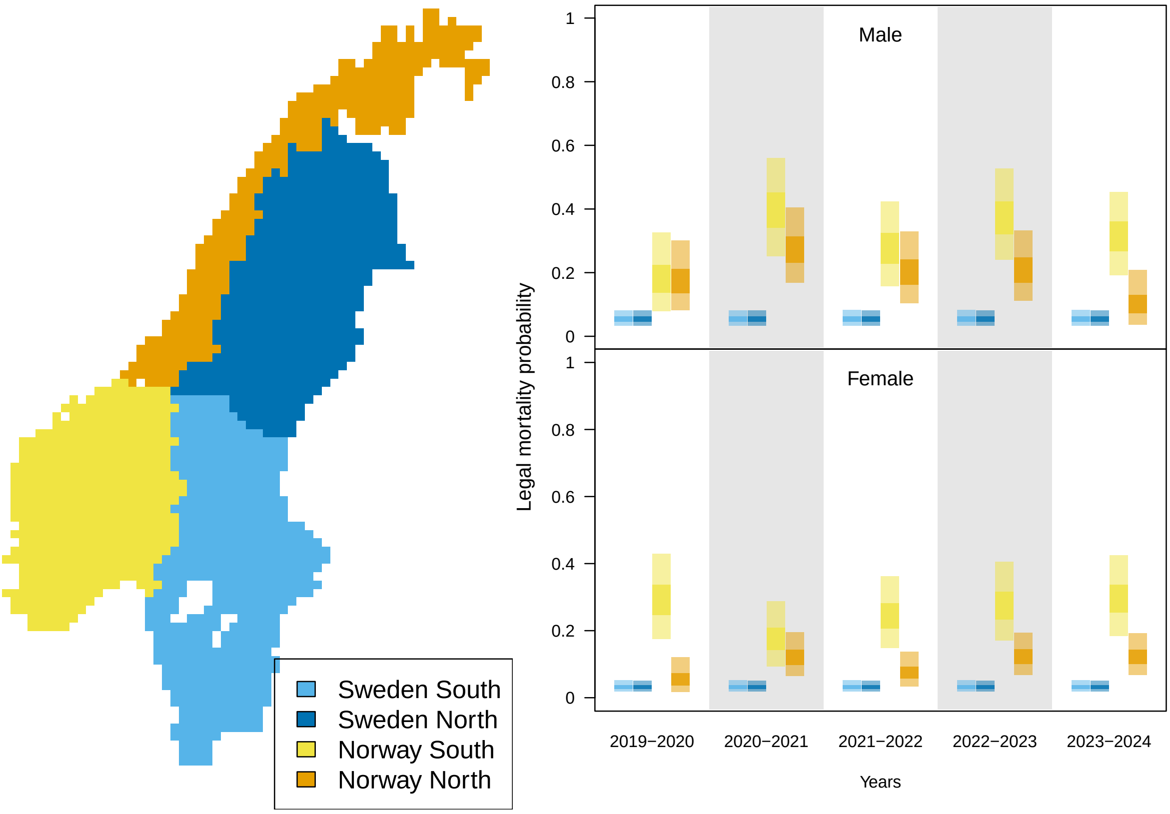


Figure 1: Estimates of mortality due to legal removal of wolverines within 4 regions of Scandinavia from 2019-2024. Region and sex-specific mortality estimates are represented by vertical bars, where the darker and lighter bars show the 50% and 95% credible intervals, respectively. Note that whereas mortality due to legal removal was estimated on an annual basis for the two regions in Norway, an overall estimate was generated for Sweden, with mortality assumed to be constant during the study period to cope with the low number of legal removal events in this country.

Mortality due to causes other than legal removal We detected substantial variation in other causes of mortality (Figure 2). The region with the lowest predicted mean mortality due to other causes was region 41 (Norway) with 0.09 (0.04-0.16), while the highest were region 15 and 17 (Sweden) with a probability of 0.44 (0.25-0.68) and 0.39 (0.32-0.47; Table A.4). However, region 15 was not displayed in the figure due to the low number of detected individuals located in this region (Figure 2). The seven regions with the highest mortality were located in Sweden, and 13 out of the 14 regions with the lowest estimated mortality due to other causes were located in Norway. Among the Norwegian regions, regions 31, 16, 3, 1, 4, 20, and 9 had the highest mean estimates of mortality due to other causes ($\geq$0.26; Table A.4). We also found a negative effect of wolverine density on other mortality for females ($\beta_{h_{Female}} = -0.23$; 95% CrI $[-0.33; -0.13]$) but no evidence of such an effect for males ($\beta_{h_{Male}} = -0.03$; 95% CrI $[-0.12; 0.07]$).

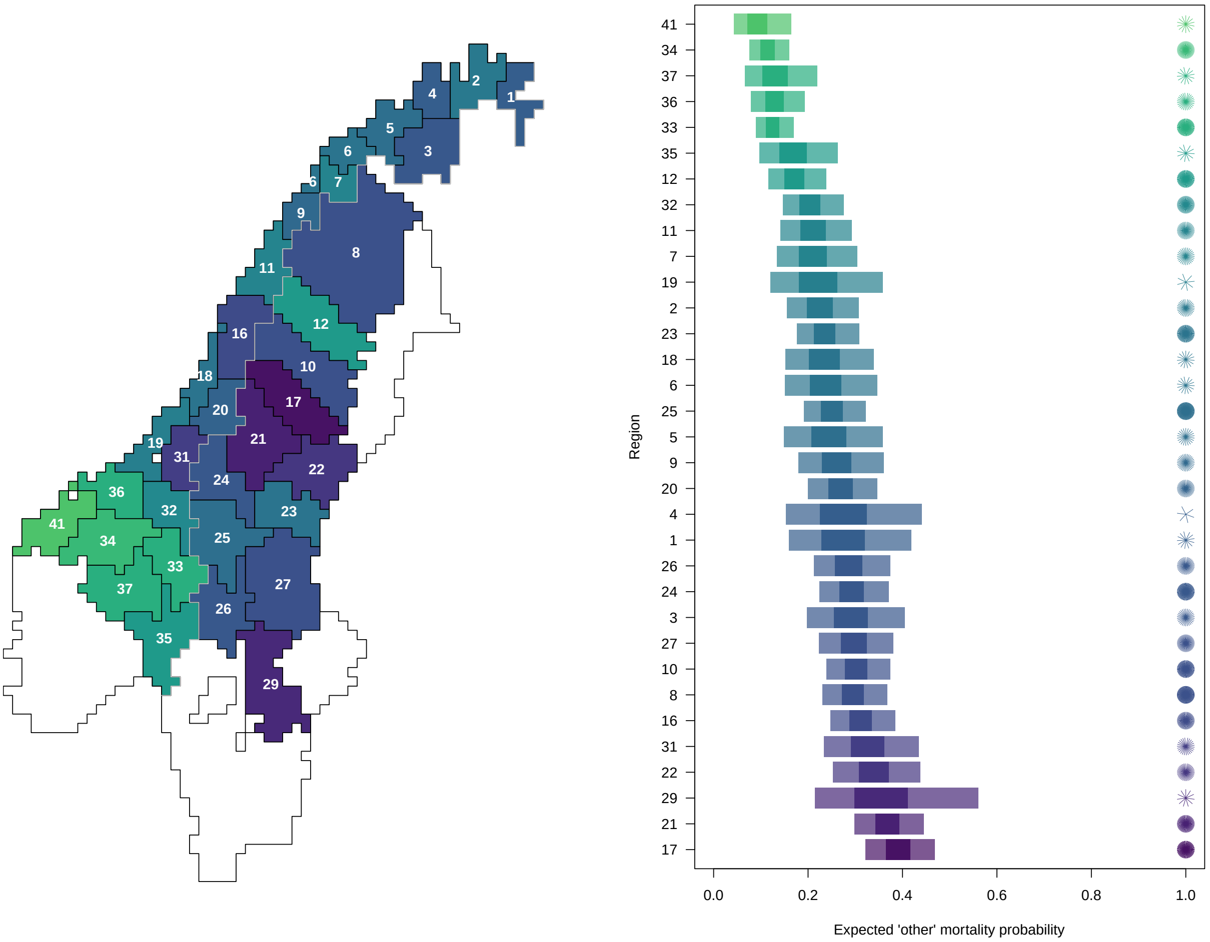


Figure 2: Map displaying the mean predicted mortality of wolverines during the period 2019-2024 due to causes other than legal mortality in Scandinavia (left panel; regions shown with numbered ID). Region-specific mortality estimates are also represented by the horizontal bars (right panel), where the darker and lighter bars show the 50% and 95% credible intervals, respectively. Only results for regions with more than 10 wolverines detected are displayed (33 out of the 41 regions used to estimate spatial variation in other causes mortality) because mortality in regions with few detected individuals and on the edge of the main population range is challenging to estimate. Sample sizes for each region are shown as sunflower symbols on the right size of the plot, where each "leaf" represents 2 detected individuals. Detailed values for all 41 regions are provided in Table A.4 and details on the regions used in Figure A.1.

4 Discussion

In this study, we were able to quantify fine-scale spatial variation in mortality of wolverines in Scandinavia during a 6-year period. This was made possible by the intensive transnational monitoring (Bischof et al., 2020) and the use of recent methodological advances allowing spatially-explicit estimation of cause-specific mortality (Milleret et al., 2023a, 2025). We focused primarily on estimating fine-scale variation in mortality due to causes other than legal mortality. Such estimates are particularly challenging to obtain as most mortality events remain undetected. Estimation methods must thus be able to disentangle the probability that an individual died from the probability that it was still alive but not detected. To do so, we used the open population spatial capture recapture (OPSCR) framework.

We found substantial variation in both legal (Figure 1) and all other sources of mortality (Figure 2 in wolverines in Scandinavia. We detected a higher risk of legal mortality in Norway compared to Sweden, which is readily explained by the difference in national policies (Milleret et al., 2023a).

The main focus of this investigation was mortality due to other than legal causes (e.g., natural deaths, road kills, poaching). We found substantial variation of mortality due to other causes across the 41 regions considered. Regions with the highest mortality due to other causes were located in Sweden, whereas most of the regions with the lowest mortality were located in Norway. The interpretation of the region-specific mortality estimates should take into account that the number of individuals detected, and therefore the sample size, was particularly low in some of the regions (Figure 2, Table A.4), particularly along the edge of the main population range. Due to the low number of individuals detected, it is challenging to estimate detection probability in these areas, and therefore to distinguish between the probability of detection, mortality, and movement (Gardner et al., 2018). For this reason, we did not display mortality estimates in regions with less than 10 individuals detected Figure 2.

Being observational in nature, our study does not allow us to explain the causes behind spatial variation in mortality. Mortality due to causes other than legal mortality entails traffic collision and several other causes of death that remain mostly undetected (natural mortality, illegal hunting). While we cannot ascertain illegal mortality as the main cause for the apparent mortality hot spots, our maps and quantitative results could aid management authorities and law enforcement by guiding investigative efforts.

By explicitly accounting for the imperfect detection, survival and movement of individuals, we aimed at obtaining unbiased estimates of mortality. The robustness of inferences from the model depend on whether the aforementioned processes are adequately represented (Efford and Schofield, 2022). Unfortunately, robust tools to assess the fit of OPSCR models are still missing (Dey et al., 2022).

We focused our analysis on estimating spatial variation in other causes of mortality (that remained mostly undetected) without considering other potential sources of variation in mortality such as temporal and individual differences. In the future, the model could be improved by accounting for these additional factors. The novel method used in this study is promising as we were able to quantify hidden spatial patterns of mortality from non-invasive genetic monitoring.

5 Acknowledgements

This work was made possible by the large carnivore monitoring programs and the extensive monitoring data collected by Swedish (Länstyrelsena) and Norwegian (SNO) wildlife management authorities, as well as the public in both countries. Our analyses relied on genetic analyses conducted by the laboratory personnel at the DNA laboratories at the Swedish University of Agricultural Sciences, and the Norwegian Institute for Nature Research. We also thank Swedish and Norwegian wildlife managers for feedback provided during project RovQuant. We are grateful to Wei Zhang for his help with the modeling aspects, and Nina Rosita Hansen for the Norwegian translations. This work was funded by Miljødirektoratet, and partially by the Research Council of Norway (NFR 286886: project WildMap, NFR 345279: project PopFlow). Computation was performed on resources provided by NMBU's computing cluster Orion. J. Vermaat provided helpful comments on a draft of this report.

6 Data availability

Data, R code to reproduce the analysis, as well as figures, tables, and raster map (Figure 2) are available at https://github.com/richbi/RovQuantPublic.

References

Bischof, R., Brøseth, H., and Gimenez, O. (2016). Wildlife in a Politically Divided World: Insularism Inflates Estimates of Brown Bear Abundance. *Conservation Letters*, 9(2):122–130.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Åkesson, M., Brøseth, H., and Kindberg, J. (2019a). Estimating the size of the scandinavian wolf population with spatial capture recapture and conversion factors. *MINAfagrapport57*, 80pp.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Brøseth, H., and Kindberg, J. (2019b). Estimating density, abundance and population dynamics of bears, wolverines, and wolvesin scandinavia. *MINAfagrapport63*, 79pp.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., Ordiz, A., de Valpine, P., Turek, D., Royle, J. A., Gimenez, O., Flagstad, Ø., Åkesson, M., Svensson, L., Brøseth, H., and Kindberg, J. (2020). Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. *Proceedings of the National Academy of Sciences*, 117(48):30531–30538.

Bischof, R., Turek, D., Milleret, C., Ergon, T., Dupont, P., Dey, S., and de Valpine, P. (2021). *nimbleSCR: Spatial Capture-Recapture (SCR) Methods Using 'nimble'.* R package version 0.1.2.

Chandler, R. B., Hepinstall-Cymerman, J., Merker, S., Abernathy-Conners, H., and Cooper, R. J. (2018). Characterizing spatio-temporal variation in survival and recruitment with integrated population models. *The Auk*, 135(3):409–426.

de Valpine, P., Paciorek, C., Turek, D., Michaud, N., Anderson-Bergman, C., Obermeyer, F., Wehrhahn Cortes, C., Rodrìguez, A., Temple Lang, D., and Paganin, S. (2022). *NIMBLE User Manual.* R package manual version 0.12.2.

de Valpine, P., Paciorek, C., Turek, D., Michaud, N., Anderson-Bergman, C., Obermeyer, F., Wehrhahn Cortes, C., Rodrìguez, A., Temple Lang, D., and Paganin, S. (2024). *NIMBLE User Manual.* R package manual version 1.3.0.

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., and Bodik, R. (2017). Programming with models: writing statistical algorithms for general model structures with nimble. *Journal of Computational and Graphical Statistics*, 26(2):403–413.

Dey, S., Bischof, R., Dupont, P. P. A., and Milleret, C. (2022). Does the punishment fit the crime? consequences and diagnosis of misspecified detection functions in bayesian spatial capture–recapture modeling. *Ecology and Evolution*, 12(2):e8600.

Dupont, P., Milleret, C., Tourani, M., Brøseth, H., and Bischof, R. (2021). Integrating dead recoveries in open-population spatial capture–recapture models. *Ecosphere*, 12(7):e03571.

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 106(3):598–610.

Efford, M. G. and Schofield, M. R. (2022). A review of movement models in open population capture–recapture. *Methods in Ecology and Evolution*, 13(10):2106–2118.

Ergon, T., Borgan, O., Nater, C. R., and Vindenes, Y. (2018). The utility of mortality hazard rates in population analyses. *Methods in Ecology and Evolution*, 9(10):2046–2056.

Ergon, T. and Gardner, B. (2014). Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution*, 5(12):1327–1336.

Flagstad, O., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., SegerstrOm, P., and Ellegren, H. (2004). Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology*, 18(3):676–688.

Flagstad, O., Kleven, O., Brandsegg, H., Spets, M., Eriksen, L., Andersskog, I., Johansson, M., Ekblom, R., Ellegren, H., and Brøseth, H. (2021). Dna-basert overvåking av den skandinaviske jervebestanden 2020. *Norsk institutt for naturforskning(NINA), Trondheim*, NINA Rapport nr 1956.

Gardner, B., Sollmann, R., Kumar, N. S., Jathanna, D., and Karanth, K. U. (2018). State space and movement specification in open population spatial capture–recapture models. *Ecology and Evolution*, 8(20):10336–10344.

Gelman, A. and Rubin, D. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7:457–511. `http://www.stat.columbia.edu/~gelman/research/published/itsim.pdf`.

Gervasi, V., Broseth, H., Nilsen, E. B., Ellegren, H., Flagstad, O., and Linnell, J. D. C. (2015). Compensatory immigration counteracts contrasting conservation strategies of wolverines (Gulo gulo) within Scandinavia. *Biological Conservation*, 191:632–639.

Kaczensky, P., Ranc, N., Hatlauf, J., Payne, et al. (2024). Large carnivore distribution maps and population updates 2017–2022/23.

Kéry, M. and Schaub, M. (2012). *Bayesian population analysis using WinBUGS: a hierarchical perspective.* Academic Press, Waltham, MA.

Kleven, O., Berg, S., Bischof, B., Dupont, P., Königsson, H., Milleret, C., Spets, M. H., Spong, G., and Brøseth, H. (2024). DNA-basert overvå-king av den skandinaviske jervebestanden 2024. *Norsk institutt for naturforskning(NINA)*, NINA Rapport nr 2535.

Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals - a unified approach with case-studies. *Ecological Monographs*, 62(1):67–118.

Lebreton, J.-D. and Pradel, R. (2002). Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*, 29:353–369.

Milleret, C., Dey, S., Dupont, P., Brøseth, H., Turek, D., de Valpine, P., and Bischof, R. (2023a). Estimating spatially variable and density-dependent survival using open-population spatial capture–recapture models. *Ecology*, 104(2):e3934.

Milleret, C., Dupont, P., Brøseth, H., Flagstad, O., Kleven, O., Königsson, H., Spong, G., Kindberg, J., and Bischof, R. (2024a). Estimates of wolverine density, abundance, and population dynamics in scandinavia, 2015–2024. *MINAfagrapport 101*, 34pp.

Milleret, C., Dupont, P., Brøseth, H., Øystein, F., Kindberg, Jonas Svensson, L., , and Bischof, R. (2023b). Estimates of wolf density, abundance, and population dynamics in Scandinavia, 2013–2022. *MINAfagrapport 85*, 34pp.

Milleret, C., Dupont, P., Dey, S., Brøseth, H., Kindberg, J., Turek, D., de Valpine, P., Åkesson, M., Wabakken, P., Zimmermann, B., and Bischof, R. (2025). Map of death: spatially explicit mortality of the grey wolf. *Proceedings of the Royal Society B: Biological Sciences*, 292(2053):20250948.

Milleret, C., Dupont, P., Winiger, A., Spong, G., Königsson, H., and Bischof, R. (2024b). Estimates of wolverine density and abundance in norrbotten county in sweden and associated reindeer herding areas. *MINAfagrapport 100*, 20pp.

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J. A., Chandler, R. B., Sollmann, R., and Gardner, B. (2014). *Spatial Capture-Recapture*. Academic Press.

Schaub, M. and Royle, J. A. (2014). Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods in Ecology and Evolution*, 5(12):1316–1326.

Turek, D., Milleret, C., Ergon, T., Brøseth, H., Dupont, P., Bischof, R., and de Valpine, P. (2021). Efficient estimation of large-scale spatial capture–recapture models. *Ecosphere*, 12(2):e03385.

Zhang, W., Chipperfield, J. D., Illian, J. B., Dupont, P., Milleret, C., de Valpine, P., and Bischof, R. (2023). A flexible and efficient bayesian implementation of point process models for spatial capture–recapture data. *Ecology*, 104(1):e3887.

Appendices

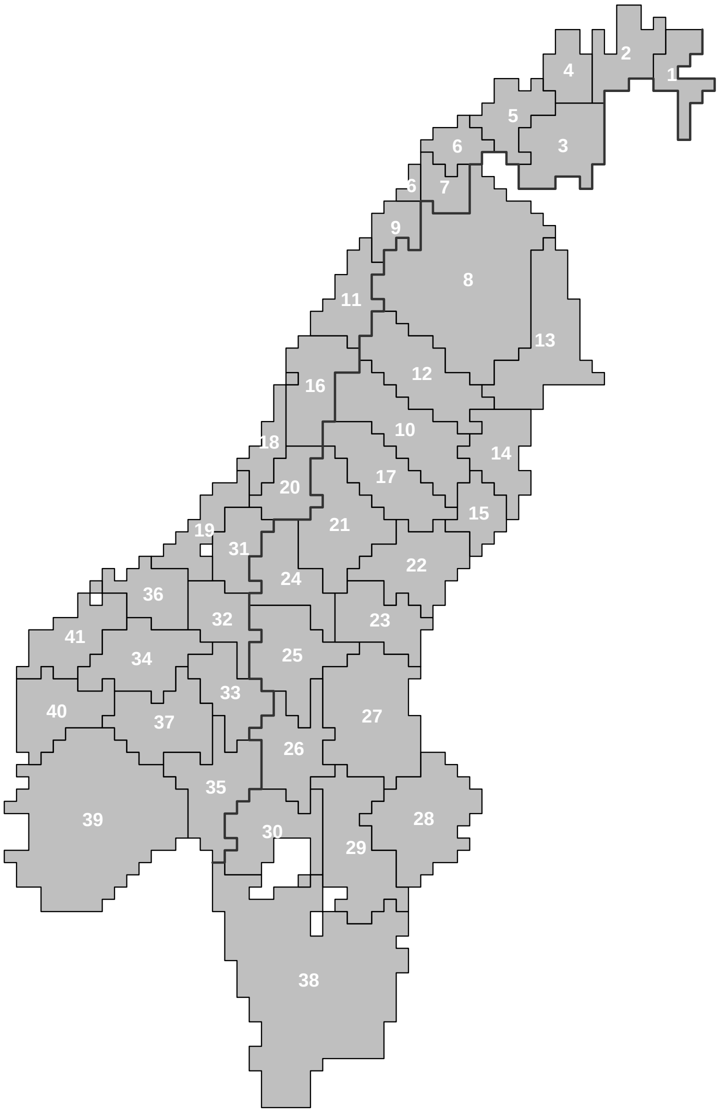


Figure A.1: Map of the 41 Scandinavian regions used to estimate spatial variation in wolverine mortality due causes other than legal mortality. Each region was attributed a number

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 2019 and 2024.

		2019		2020		2021		2022		2023		2024	
		F	M	F	M	F	M	F	M	F	M	F	M
Norway	Structured	426	554	431	495	443	547	458	563	745	802	478	575
	Unstructured	165	171	142	188	136	187	111	185	135	198	296	321
Sweden	Structured	407	529	277	396	325	399	375	531	383	494	782	878
	Unstructured	89	87	78	142	110	164	119	125	101	189	397	449
Total	Structured	833	1083	708	891	768	946	833	1094	1128	1296	1260	1453
	Unstructured	254	258	220	330	246	351	230	310	236	387	693	770

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 2019 and 2024. Some individuals were detected in both countries during the same year, hence the sum of the national counts can exceed the total number of unique individuals detected in Scandinavia.

	2019		2020		2021		2022		2023		2024	
	F	M	F	M	F	M	F	M	F	M	F	M
Norway	191	149	195	151	185	134	194	138	215	152	210	161
Sweden	225	197	172	156	202	167	196	179	194	194	331	259
Total	407	333	361	301	381	295	389	308	399	338	520	395

Table A.3: Number of cause-specific dead recoveries of wolverines in Scandinavia between 2019 and 2024. Numbers are reported by country, for females (F) and males (M).

	Country	2019		2020		2021		2022		2023		2024	
		F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	1	3	6	5	4	4	1	0	3	3	2	5
	Sweden	1	1	0	1	2	1	3	4	2	3	1	1
Legal culling	Norway	57	37	50	62	44	44	42	45	47	48	28	36
	Sweden	6	3	7	19	3	10	10	3	13	12	2	6
Total	Total	65	44	63	87	53	59	56	52	65	66	33	48

Table A.4: Mean mortality estimates (sorted in descending order) and 95% credible interval (95% CrI) of wolverines during the period 2019-2024 due causes other than legal mortality in 41 regions of Scandinavia (see Figure A.1). The total number of individuals detected in each region during the entire period is also provided.

RegionID	Country	Mean	95%CrI	N Detected
15	Sweden	0.44	0.25-0.68	2
17	Sweden	0.39	0.32-0.47	157
21	Sweden	0.37	0.30-0.45	129
29	Sweden	0.36	0.21-0.56	22
14	Sweden	0.34	0.17-0.56	1
22	Sweden	0.34	0.25-0.44	79
28	Sweden	0.33	0.13-0.64	1
31	Norway	0.33	0.23-0.43	53
16	Norway	0.31	0.25-0.38	121
8	Sweden	0.30	0.23-0.37	208
10	Sweden	0.30	0.24-0.37	167
13	Sweden	0.30	0.14-0.53	4
27	Sweden	0.30	0.22-0.38	98
30	Sweden	0.30	0.16-0.48	10
3	Norway	0.29	0.20-0.40	60
24	Sweden	0.29	0.22-0.37	174
26	Sweden	0.29	0.21-0.37	79
1	Norway	0.28	0.16-0.42	27
4	Norway	0.28	0.15-0.44	13
20	Norway	0.27	0.20-0.35	83
9	Norway	0.26	0.18-0.36	64
38	Sweden	0.26	0.12-0.50	0
5	Norway	0.25	0.15-0.36	44
25	Sweden	0.25	0.19-0.32	236
6	Norway	0.24	0.15-0.35	31
18	Norway	0.24	0.15-0.34	30
23	Sweden	0.24	0.18-0.31	146
2	Norway	0.23	0.15-0.31	63
19	Norway	0.22	0.12-0.36	17
7	Norway	0.21	0.13-0.30	56
11	Norway	0.21	0.14-0.29	83
32	Norway	0.20	0.15-0.27	116
12	Sweden	0.17	0.12-0.24	155
35	Norway	0.17	0.10-0.26	23
39	Norway	0.14	0.06-0.26	7
33	Norway	0.13	0.09-0.17	159
36	Norway	0.13	0.08-0.19	55
37	Norway	0.13	0.07-0.22	27
40	Norway	0.12	0.05-0.23	3
34	Norway	0.11	0.08-0.16	104
41	Norway	0.09	0.04-0.16	28