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Preliminary estimates of wolverine density and abundance in Sweden, 2024/2025

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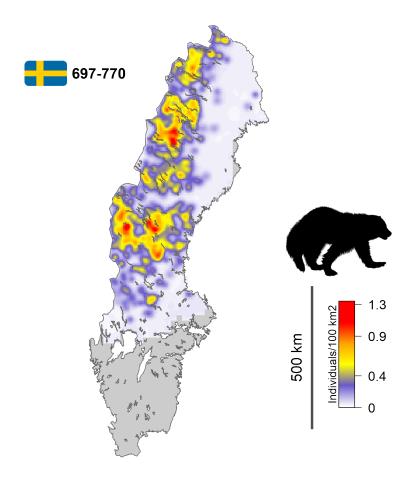
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Summary

Background Project RovQuant has produced density maps and abundance estimates for large carnivores (wolf, wolverine, and brown bear) throughout Scandinavia since 2019 based on non-invasive genetic sampling (NGS) and dead recovery data collected annually by Swedish and Norwegian authorities. In 2025, the Swedish Environmental Protection Agency (Naturvårdsverket) has requested preliminary wolverine abundance estimates for the Swedish portion of the wolverine population during winter 2024/2025, prior to the combined estimates provided annually for Sweden and Norway.

Approach Using NGS data and a single-season spatial capture-recapture (SCR) model, we estimated and mapped the density of wolverines in Sweden during the 2024/2025 winter. The method produced estimates of wolverine abundance for Sweden and also for Swedish counties in the current range of the species.

Results and Discussion The total number of wolverines in Sweden during winter 2024/2025 was likely (95% credible interval) between 697 and 770 individuals. We estimated that the proportion of females in the population was likely between 57% and 61%. The highest wolverine abundance was estimated in northern counties Jämtland (201-231 individuals), Norrrbotten (187-221) and Västerbotten (130-158).



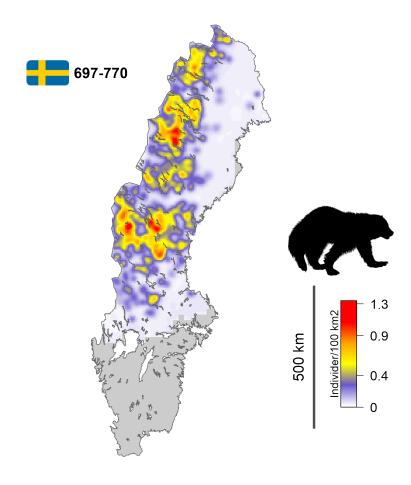
Density map and estimated wolverine abundance range in Sweden during winter 2024/25

Sammanfattning

Bakgrund Projekt RovQuant har sedan 2019 tagit fram täthetskartor och populationsuppskattningar för stora rovdjur (varg, järv och brunbjörn) i Skandinavien, baserat på icke-invasiv genetisk provtagning (NGS) och data från döda djur som samlas in årligen av svenska och norska myndigheter. År 2025 har Naturvårdsverket begärt preliminära populationsuppskattningar för järv inom den svenska delen av järvpopulationen under vintern 2024/2025, innan de samlade uppskattningarna för Sverige och Norge presenteras.

Metod Med hjälp av NGS-data och en single-season rumslig fångst-återfångstmodell (SCR) uppskattade och kartlade vi tätheten av järv i Sverige under vintern 2024/2025. Metoden gav uppskattningar av järvstammens storlek för hela Sverige samt för de svenska län som ingår i artens aktuella utbredningsområde.

Resultat och Diskussion Det totala antalet järvar i Sverige under vintern 2024/2025 uppskattades (95% konfidensintervall) till mellan 697 och 770 individer. Vi beräknade att andelen honor i populationen sannolikt låg mellan 57% och 61%. Den högsta tätheten av järv uppskattades i de nordliga länen Jämtland (201–231 individer), Norrbotten (187–221) och Västerbotten (130–158).



Täthetskarta och beräknad järvtäthet i Sverige under vintern 2024/25

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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 (nmbu.no) 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, 2020). The analytical framework developed by RovQuant is based on spatial capture-recapture (SCR) models (Efford, 2004; Royle et al., 2009). These models use the spatial information contained in the repeated genetic detections of individuals to estimate various population parameters, including spatially-explicit abundance (i.e., density). 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 counties or countries). The SCR method brings along several advantages, including the ability to map density, derive county-specific abundance, and yield tractable measures of uncertainty (Bischof et al., 2019a, 2020).

RovQuant publishes abundance estimates for wolves, wolverines, and bears for different geographic units annually. Joint estimates for wolves and wolverines in Norway and Sweden have been available since 2019 (last reports: Milleret et al. 2023, 2024a); estimates for bears in Norway since 2023 (last reports: Dupont et al. 2024, 2025); and in 2024 estimates for wolverines in administrative entities associated with the Sámi reindeer herding areas in Norrbotten County (Sweden) were reported (Milleret et al., 2024b).

Here, as requested by the The Swedish Environmental Protection Agency (Naturvårdsverket), we performed a preliminary analysis of the wolverine NGS data collected across the species' entire range in Sweden during the winter of 2024/2025 using a single-season SCR model. We provide the following information:

- Sex-specific estimates of the number of wolverines in 2024/2025 in Sweden.
- Sex-specific estimates of the number of wolverines in 2024/2025 for each Swedish county intersecting the species range.
- Map of wolverine density for Sweden.
- Estimated proportion of individuals detected through non-invasive genetic sampling in Sweden.

All estimates are accompanied by their 95% Bayesian credible intervals as a measure of uncertainty. All estimates presented in this report are preliminary and will be replaced by those generated through the joint Swedish-Norwegian analysis scheduled for completion at the end of 2025.

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.

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 84 km buffer around all NGS data collected during the period considered.

Habitat buffer: Buffer surrounding the searched area that is considered potentially suitable habitat but was not searched (60km in this report).

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.

 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.

RovQuant: Project at the Norwegian University of Life Sciences (Ås, Norway) that develops and applies SCR models.

SCR: Spatial capture-recapture.

Skandobs: Web application (skandobs.se, skandobs.no) that allows anyone to register observations (e.g., visual, tracks, faeces, etc.) of wolverines, bears, wolves and lynx in Sweden and Norway.

2 Methods

2.1 Data

We used data from the Scandinavian large carnivore database Rovbase 3.0 (rovbase.se and rovbase.no; last extraction: 2025-09-15). 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 in Sweden during the 2024/2025 winter.

Non-invasive genetic sampling In Sweden, the collection of scat and hair is managed by Länsstyrelserna at the regional level and carried out by field officers from Länsstyrelserna. Although samples may be collected throughout the year, the official survey period for the 2024/2025 season was Oct 1 – June 2. Therefore, we used data from that period for the analysis. In addition, samples suspected to be from cubs were not included in the analysis meaning 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 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. (2023).

GPS search tracks Government employees involved in structured searches for wolverine DNA (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 SCR model to account for spatial variation in search effort during NGS.

2.2 Spatial capture-recapture model

We analysed the data collected in Sweden in the winter 2024/2025 using a Bayesian single-season spatial capture-recapture (SCR) model (Bischof et al., 2019b), which addresses two challenges associated with population-level wildlife inventories:

- 1. Detection is imperfect and sampling effort is heterogeneous in space: 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).

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 We used data augmentation to estimate population size (Royle et al., 2014). Individual state z_i follows a Bernoulli distribution with probability ψ . Individual state z_i takes the value 1 if the individual is considered as part of the population and 0 otherwise.

Density sub-model We used a Bernoulli point process to model the distribution of individual ACs (Zhang et al., 2022). Individual ACs were located according to an intensity surface, which was a function of the locations of all known dens recorded between 2009 and 2023 (see Bischof et al., 2019b and Bischof et al., 2020 for more details).

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).

DNA material was collected following two main processes: 1) Authorities collected genetic samples and recorded the corresponding search effort during official searches ("structured sampling" hereafter); 2) DNA material was collected by members of the public or by the authorities in a more or less opportunistic manner, which means that search effort is not directly available ("unstructured sampling" hereafter). In the past, it was 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 it 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", "Länsstyrelsen", "SNO" or "Fylkesmannen" 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.

We assumed that both sampling processes could in theory occur throughout Sweden 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 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 and individual heterogeneity in detectability during **structured sampling** using:

- Spatial variation in search effort represented by the length of GPS search tracks in each 10 × 10 km detector grid cell.
- Spatial 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 monitoring regimes between counties.
- Individual variation linked with a detection during the previous occasion (2023/24 monitoring season) that could be expected to influence the probability of being detected at the next occasion.

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

• Spatial distribution of ancillary samples and samples not successfully genotyped. For each detector grid cell and during each monitoring season (Oct 1 - Jun 2), we identified whether a) any carnivore sample had been registered in Rovbase (excluding successfully genotyped wolverine samples already used in the SCR analysis), b) any observation of carnivores had been registered in Skandobs. 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.

- Spatial 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.
- 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.

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

Model fitting We fitted sex-specific Bayesian SCR models using MCMC simulation with NIM-BLE version 1.2.1 (de Valpine et al., 2017; Turek et al., 2021; de Valpine et al., 2022) and R package nimbleSCR version 0.2.1 (Bischof et al., 2021) in R version 4.3.3 (R Core Team, 2021). We ran 4 chains each with 25 000 iterations, including a 5 000-iterations burn-in period. Due to the computing challenge associated with post-processing large amounts of data, we thinned chains by a factor of 5 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.

Abundance estimates To obtain an estimate of abundance for any given area, we summed the number of predicted AC locations of live individuals that fell within that area for each iteration of the MCMC chains. 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 or counties (Figure 1). Individuals detected near a border (e.g., a county 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 county-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 (counties) 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.

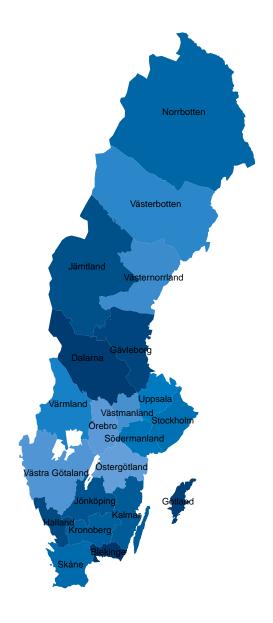


Figure 1: Counties in Sweden.

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 AC 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., 2020). To do so, we constructed raster maps (5 km resolution) of individual utilization distributions, scaled values in each raster to sum to one, and then summed rasters across individuals to create a single population-level raster map for each iteration. An overall density map was derived by calculating the mean across iterations in each cell (Bischof et al., 2020). 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.

Other derived parameters The average proportion of individuals detected, and the associated uncertainty, was obtained by dividing the number of individuals with their AC estimated in Sweden that were detected through NGS sampling by the corresponding mean abundance estimates for Sweden for each MCMC iteration. This generated a posterior distribution of the

proportion of the Swedish wolverine population that had been detected, from which the mean and associated 95% credible interval could be extracted.

The number of wolverines detected in Sweden that could be attributed to other countries was obtained by summing the number of individuals detected in Sweden that had their AC located in Norway or Finland for each MCMC sample. With this procedure, we were able to generate posterior distributions of the number of individuals detected in Sweden that could be attributed to neighboring countries, from which the means and associated 95% credible intervals could be extracted.

Focus on uncertainty Although we reported mean estimates in the abundance estimates table, 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., 2022).

3 Results

3.1 Non-invasive genetic samples and dead recoveries

A total of 1954 (789 female; 1165 male) genotyped wolverine genetic samples were collected in Sweden in the winter 2024/2025. These samples were associated with 609 (330 female; 279 male) individuals. Among all genotyped samples, 1502 (624 female; 878 male) were assigned to structured sampling and 452 (165 female; 287 male) to unstructured sampling.

3.2 Density and abundance

In the winter 2024/2025, we estimated that wolverine abundance in Sweden was likely (95% credible interval) between 697 and 770 (Figure 2) individuals (Females: 401-468; Males: 285-314). Estimates refer to the status of the population at the start of the annual sampling period (October 1). Abundance estimates of wolverines extracted for the different counties are provided in Table 1.

Between 74 and 82% of the wolverines estimated to have their AC in Sweden were detected during this study. In addition, between 12 and 22 individuals detected during NGS were estimated to have their activity center outside of Sweden (i.e., in Norway or Finland), presumably because these individuals occasionally spend time inside of Sweden. In other words, it is possible to detect more individuals in an area than are estimated to live within that area. This is also the case for the brown bear in Norway, where a significant number of detections in Norway are attributed to individuals that likely have their activity center in Sweden (for further explanations see Bischof et al. 2016 and Dupont et al. 2025).

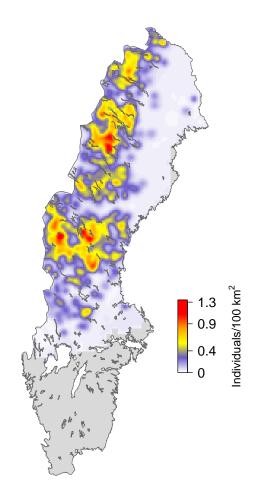


Figure 2: Wolverine density based on individual utilization distributions in Sweden during winter 2024/2025 based on a single-season spatial capture recapture model. This map can be accessed as a geo-referenced raster file at https://github.com/richbi/RovQuantPublic

 $\begin{tabular}{ll} \textbf{Table 1:} Wolverine abundance estimates for the different counties in Sweden in 2024/2025. Numbers are based on estimated AC locations of wolverines. Combined female-male estimates were obtained by joining sex-specific posterior estimates. Credible intervals (95%) are shown in parentheses. Sex-specific AC-based estimates are provided in https://github.com/richbi/RovQuantPublic.$

	F	M	Total
SWEDEN	432.8 (401-468)	298.8 (285-314)	731.6 (697-770)
Dalarna	30.2 (24-37)	24.8 (21-29)	55 (48-63)
Gävleborg	21 (17-26)	21 (18-25)	42 (36-48)
Jämtland	131.9 (120-146)	83.7 (77-91)	215.6 (201-231)
Norrbotten	129.2 (116-145)	74.4 (67-83)	203.6 (187-221)
Stockholm	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)
Uppsala	1.9 (0-5)	1.9 (0-4)	3.8 (1-8)
Värmland	7.8 (4-13)	6.4 (3-10)	14.3 (9-20)
Västerbotten	88.3 (76-102)	54.5 (50-60)	142.8 (130-158)
Västernorrland	18.5 (13-25)	29.8 (26-35)	48.3 (41-56)
Västmanland	1.2 (0-4)	0.7 (0-3)	1.8 (0-5)
VästraGötaland	0.4 (0-2)	0.2 (0-1)	0.6 (0-2)
Örebro	2.4 (1-5)	1.4 (0-4)	3.8 (1-7)

4 Discussion

We estimated that the Swedish wolverine population during the 2024/2025 winter was between 697 and 770 individuals. These estimates are higher than those reported during the previous season (642-690 individuals, Milleret et al. (2024a)). The proportion of females in the population was likely between 57% and 61%. We also provided county-specific estimates for counties in which NGS samples were collected during the 2024/2025 season (i.e., the searched area), which represents the current range of the species. Abundance was estimated to be highest in Northern counties such as Jämtland (201-231), Norrbotten (187-221) and Västerbotten (130-158)

It is important to note that the estimates presented in this report should be considered preliminary. They will be superseded by the final estimates from the annual joint RovQuant wolverine report for Norway and Sweden, scheduled for the end of 2025. The preliminary numbers reported here and the final numbers may differ for three main reasons. First, whereas the present report only uses Sweden's NGS data, the joint report will use data from both the Swedish and Norwegian ranges of this trans-boundary population. Second, whereas the present report used a single-season SCR model and only data collected during winter 2024/25, the final joint report will use an open-population spatial capture-recapture (OPSCR) model (Bischof et al., 2020; Milleret et al., 2024a) and data from the last 10 monitoring seasons. As a consequence, the joint report for 2025 will be based on more information and will provide additional key estimates, such as vital rates and inter-annual movements, not included in this preliminary analysis. Finally, in this report we used data from 1 October to 2 June, which corresponds to the current official monitoring season in Sweden. This differs from the monitoring season in Norway, which extends from December 1 to June 30. The joint RoyQuant reports use data from 1 December to 30 June (as it includes Norway and Sweden), meaning that fewer samples will be included in the analysis.

5 Acknowledgments

This work was made possible by the large carnivore monitoring programs and the extensive monitoring data collected by Swedish wildlife management authorities (Länstyrelsena). Our study relied on genetic analyses conducted by the laboratory personnel at the DNA laboratories at the Swedish University of Agricultural Sciences. This work was funded by Naturvårdsverket (NV-02444-23). 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 the raster map (Figure 2) are available at https://github.com/richbi/RovQuantPublic.

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