Estimates of brown bear density, abundance, and population dynamics in Norway 2014 - 2023

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Summary

Background The Scandinavian brown bear (*Ursus arctos*) population is monitored annually in Norway using non-invasive genetic sampling (NGS) and recovery of dead individuals. DNA extracted from faeces, urine, hair, and tissue is used to identify the species, sex and individual from which each sample originated. These data are compiled annually in the Scandinavian large carnivore database Rovbase 3.0 (rovbase.no, rovbase.se).

Approach Using the Bayesian open-population spatial capture-recapture (OPSCR) model developed by RovQuant, we estimated the population dynamics of the Norwegian portion of the Scandinavian brown bear population between 2014 and 2023. We provide annual density maps, as well as estimates of jurisdiction-specific population sizes, cause-specific survival, recruitment, and detection probabilities. Associated uncertainties are reported with all estimates.

Results We estimated that, within its primary range (180 630 km^2), the Norwegian brown bear population was likely (95% credible interval) made up of between 122 and 154 individuals in 2023. Each year, a large proportion of bears detected in Norway can be attributed to neighbouring countries. Specifically, in 2023, between 47 and 63 (95% credible interval) of the individuals detected in Norway were attributed to neighbouring countries (Sweden = 21 to 32, Finland = 14 to 24, Russia = 6 to 14). The OPSCR results also highlight the ongoing recovery of the brown bear population in Norway, with an overall increase in population size, mostly driven by a comparatively steeper growth in the female portion of the population in recent years.
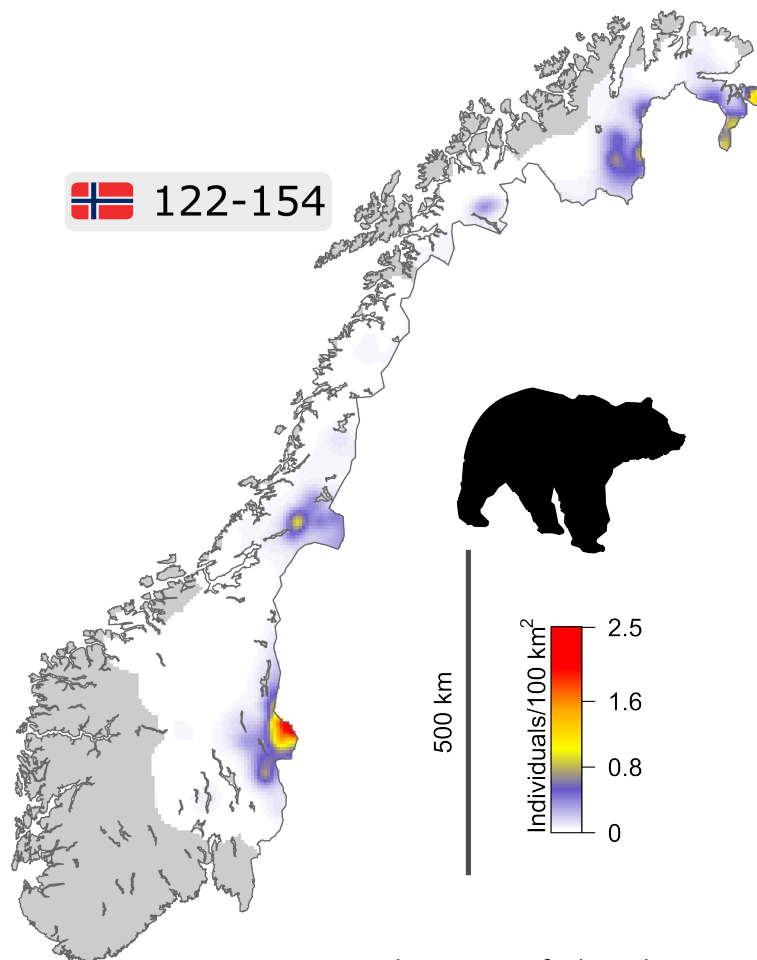
Density map and ranges of abundance
estimated for brown bears in Norway in 2023

Sammendrag

Bakgrunn Den skandinaviske bestanden av brunbjørn (*Ursus arctos*) blir overvåket årlig ved bruk av ikke-invasiv genetisk prøveinnsamling (NGS) og gjenfunn av døde individer. DNA ekstrahert fra skit, urin, hår og vev brukes til å identifisere art, kjønn og individ for hver enkelt prøve. Denne informasjonen samles og ivaretas i Rovbase 3.0 (rovbase.se, rovbase.no).

Tilnærming Ved bruk av en Bayesiansk åpen romlig fangst-gjenfangst modell (OPSCR) utviklet av RovQuant, estimerte vi bestandsdynamikken til den norske delen av den skandinaviske bjørnebestanden. Metoden gjør det mulig for oss å produsere årlige tetthetskart, områdespesifikke bestandsstørrelser, årsaksspesifikk dødelighet, rekrutterings og oppdagbarhets annsynligheter med tilhørende usikkerhet for brunbjørn i Norge mellom 2014 og 2023.

Resultater Basert på OPSCR-modellen var den norske brunbjørnbestanden sannsynligvis (95% kredibelt intervall) mellom 122 og 154 individer i sin primære rekkevidde ($180\,630$ km^2), i 2023. Årlig kan en stor andel av bjørnene påvist i Norge ha sitt aktivitetssentrum nabolandene. Nærmere bestemt, i 2023 ble mellom 47 og 63 (95% kredibelt intervall) bjørner påvist i Norge estimert å ha sitt aktivitetssentrum i Sverige (21-32), Finland (14-24) eller Russland (6-14). OPSCR-resultatene viser en pågående vekst av brunbjørnbestanden i Norge. Bestandsøkningen av bjørn er hovedsakelig drevet av en sterkere økning i hunner sammenlignet med hanner de siste 10 årene.
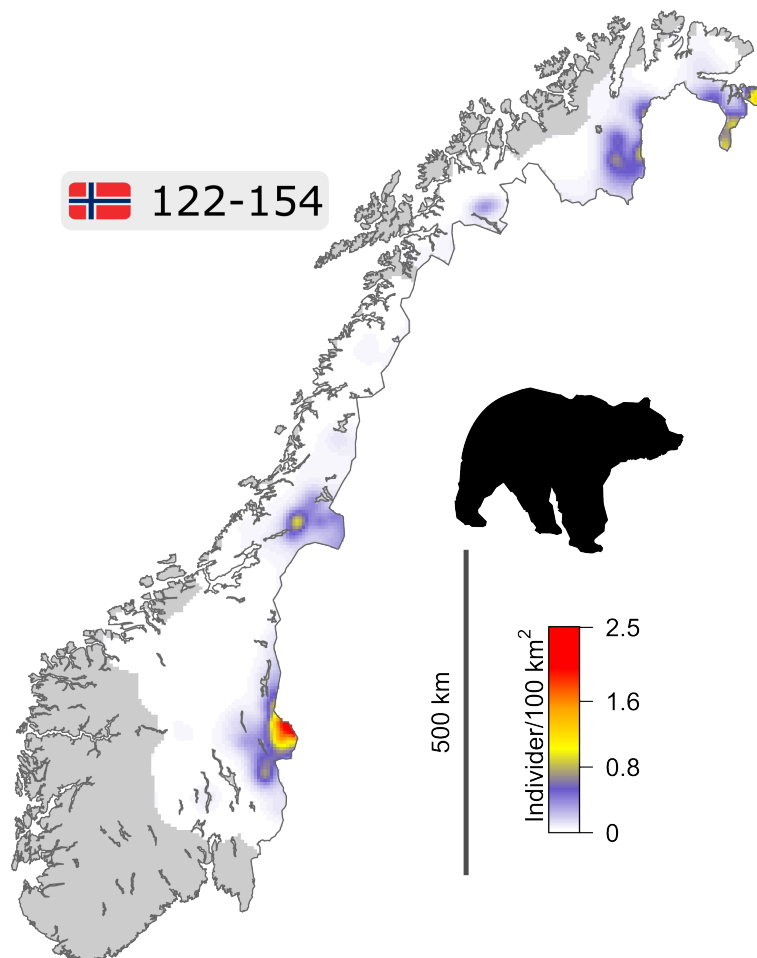
Kart som viser tetthet av brunbjørn med
intervaller for estimert antall brunbjørn i 2023

Contents

1   Introduction

Non-invasive genetic sampling (NGS) and dead recoveries are a centerpiece of national and regional large carnivore monitoring in Norway and Sweden. Over nearly two decades, both countries have accumulated one of the largest and most extensive individual-based data sets on large carnivores in the world, and plan to continue such transnational monitoring in the future. Each year, Rovdata (www.rovdata.no) compiles, analyzes, and reports monitoring data on the Eurasian lynx, wolverine, brown bear, wolf and golden eagle in Norway. NGS data and other sources of information are made publicly available and stored in the Scandinavian large carnivore database Rovbase 3.0 (www.rovbase.se,www.rovbase.no).

Since 2017, project RovQuant (www.nmbu.no) has been developing statistical methods to exploit the potential of this database and allow a comprehensive assessment of the population status and dynamics of three large carnivore species, namely the brown bear (*Ursus arctos*), wolf (*Canis lupus*), and wolverine (*Gulo gulo*). At the core of this analytical framework (Bischof et al., 2019b, 2020a) are Bayesian spatial capture-recapture (SCR) and open-population spatial capture-recapture (OPSCR) models (Ergon and Gardner, 2014; Bischof et al., 2016; Chandler et al., 2018; Dupont et al., 2021). SCR models use the spatial information contained in the repeated detection of individuals to estimate their location and population density. In addition, OPSCR models use the temporal information contained in data collected over multiple years to also estimate recruitment and survival probabilities, as well as inter-annual movements. Importantly, this approach accounts for imperfect detection, i.e., the probability that an individual present in the population remains undetected. The method ultimately generates density maps and vital rate estimates, from which abundance estimates can be derived for any spatial subunit (e.g., county or management region). Another crucial feature of this method is that all estimates are accompanied by their associated uncertainty, based on the model and data used (Bischof et al., 2019b, 2020b).

RovQuant first reported results based on the Rovbase data and OPSCR models for wolves in March 2019 (Bischof et al., 2019b), jointly for all three carnivore species in December 2019 (Bischof et al., 2019b, 2020b), and on an annual basis for wolves (Milleret et al., 2021, 2022a, 2023b, 2024b) and wolverines (Flagstad et al., 2021; Milleret et al., 2022b,c, 2023c) since 2021. Recently, RovQuant reported results about the status and population dynamics of the brown bear population in Norway for the period 2012-2022 (Dupont et al., 2023c). In the current report, we present an updated analysis of a 10-year time series (2014-2023) of the Norwegian portion of the Scandinavian brown bear population using the latest available bear monitoring data from Norway and the most recent version of the OPSCR model. We provide the following information:

- Annual and sex-specific estimates of the number of bears (with credible intervals) for Norway.

- Estimated proportion of individuals detected through NGS.

- Bear density maps throughout Norway.

- Annual estimates of mortality, recruitment, and population growth rate.

Although RovQuant aims to provide comprehensive analyses of large carnivore populations throughout their entire range in Norway and Sweden, we only analyzed and present results for the Norwegian monitoring data in this report. Previous analyses revealed multiple difficulties related to the Swedish brown bear non-invasive genetic monitoring data (Dupont et al., 2023a; Milleret et al., 2024a), leading among other things to inconsistent results across model permutations when the Scandinavian brown bear monitoring data were analyzed jointly for Norway and Sweden (Dupont et al., 2023b).

> **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 50 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.
> **Länsstyrelserna:** Swedish County Administrative Boards, in charge of the monitoring of large carnivores at the county level.
> **Legal culling**: Lethal removal of individuals by legal means, including licensed recreational hunting, management removals, and defense of life and property.
> **LLCC:** Local Large Carnivore Contact (Rovviltkontakt). A person in the local community that is employed by the Norwegian Nature Inspectorate on a limited basis. The role as a LLCC is primarily to carry out investigations, including necropsies of domestic animals in the field, to determine if a large carnivore is the primary cause of death or injury. LLCC are also employed to monitor large carnivores during winter.
> **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.
> **RCLC:** Regional Coordinator for Large Carnivore Monitoring and Documentation (Regionalt fagansvarlig rovviltdokumentasjon). A person in full employment in the Norwegian Nature Inspectorate with a coordinating function in the large carnivore monitoring at the regional level.
> **SCR:** Spatial capture-recapture.
> **SNO:** Statens naturoppsyn (Norwegian Nature Inspectorate) is the operative field branch of the Norwegian Environment Directorate (Miljødirektoratet).
> **Statsforvalteren:** Norwegian state's representative in the county, responsible for following up decisions, goals, and guidelines from the legislature and the government.
> **RovQuant:** Research project at the Norwegian University of Life Sciences (Ås, Norway) that develops and applies OPSCR models.

2 Methods

2.1 Data

For this analysis, we relied on data from multiple sources, the primary one being the Scandinavian large carnivore database Rovbase 3.0 (rovbase.se and rovbase.no; last extraction: 2024-05-26). This database is used jointly by Norway and Sweden to record detailed information associated with large carnivore monitoring, including, but not limited to, non-invasive genetic sampling (NGS) data and dead recoveries. In the following sections, we describe the various types of data used in the analysis.

Non-invasive genetic sampling The Norwegian Nature Inspectorate (Statens Naturoppsyn, SNO) has primary responsibility for the collection of bear scat and hair in Norway. This is often accomplished by the regional coordinators for large carnivore monitoring and documenta-

tion (RCLC) and a network of local large carnivore contacts (LLC) through targeted collection of samples via snow tracking, visits to recently used dens and in connection with depredation investigations and observation reports from the public. In addition, samples are collected by hikers, landowners and others throughout the year, as well as by hunters in the fall. All samples were analysed with 8 microsatellite markers and up to three markers for gender determination. Samples identified as bear were assigned an individual identity (individual ID) if 6–8 markers and gender were confirmed based on reliability thresholds for the given method: heterozygous loci must have 2 approved replicates, while homozygous loci must have 3 approved replicates. If an individual has been detected 3 or more times previously, only two approved replicates of homozygous result were required. For samples where 3-5 markers met the requirements, an individual ID was assigned if the DNA profile matched an already known individual in the database. For all new individuals, an additional 4 bear-specific microsatellite markers were used: G1D, G10B, Mu15 and G1A (Andreassen et al., 2012), so that the complete genetic profile consists of 12 STR markers. For further details on the DNA analysis procedure see Tobiassen et al. (2011), Andreassen et al. (2012) and Fløystad et al. (2019). Details about the bear non-invasive sampling data collected in Norway in 2023 and its DNA analysis can be found in Brøseth et al. (2024).

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

Observation reports in Skandobs We used all observation records in the Skandobs database that were recorded during the bear monitoring seasons since 2012 (skandobs.se, skandobs.no; last extraction: 2023-05-03). Skandobs is a web application developed in collaboration between Rovdata in Norway and Naturvårdsverket in Sweden, that allows anyone to register observations (e.g. visual, tracks, faeces, etc.) of bears, lynx (*Lynx lynx*), wolves, and wolverines in Scandinavia. This data set 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.

2.2 Open-population spatial capture-recapture model

We analysed the data collected between 2012 and 2023 using a Bayesian open-population spatial capture-recapture (OPSCR) model (Bischof et al., 2020b; Dupont et al., 2023d,c). Note that even if all the data available for the period 2012-2023 were used in the OPSCR analysis, we only report results for the most recent 10-year period (2014-2023) due to space limitations and to be consistent with previous RovQuant reports (Dupont et al., 2023c; Milleret et al., 2023b, 2024b).

OPSCR models allow the simultaneous analysis of NGS data from multiple years and provide estimates of vital rates and individual movements between monitoring seasons in addition to annual densities. OPSCR models can be extended to incorporate dead recovery data to improve inferences (Dupont et al., 2021). The Bayesian OPSCR model (Bischof et al., 2019b) we developed and used addresses three challenges associated with population-level wildlife inventories:

1. Detection is imperfect and sampling effort heterogeneous in space and time: not all individuals present in the study area are detected (Kéry and Schaub, 2011).
2. Individuals that reside primarily outside the surveyed area may be detected within it. This is especially true for the Norwegian bear population given the comparatively higher population densities on the Swedish side of the Norwegian-Swedish border (Bischof et al., 2016). Without this explicit link between population size and geographic area characteristic of the SCR framework, density cannot be estimated and population size is ill-defined (Efford, 2004).
3. Non-spatial population dynamic models (such as CR models) usually estimate "apparent" survival and recruitment, as these parameters include the probability of permanent emigration and immigration, respectively. By explicitly modelling movement of individuals between years, the OPSCR model can help return unbiased estimates of demographic parameters (Ergon and Gardner, 2014; Schaub and Royle, 2014; Gardner et al., 2018; Dupont et al., 2021; Efford and Schofield, 2022).

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

1. A model for the spatial distribution of individuals in the population and their movement between years (i.e. density and movement).
2. A model for population dynamics (i.e. recruitment and mortality) and population size.
3. A model for detection of individuals during DNA searches and dead recoveries.

Density and movement sub-model We used a Bernoulli point process to model the distribution of individual activity centers (ACs, Zhang et al., 2022). In the first year, individuals were located according to an intensity surface, which was a function of both the locations of all bears recovered dead throughout the 2012-2023 period (see Bischof et al., 2019b and Bischof et al., 2020b for more details), and the presence/absence of all bear observations registered in SkandObs during the 2012-2023 period. For all subsequent years ($t > 1$), the location of an individual's activity center was a function of the distance from its previous activity center (at time $t-1$) as well as the two spatial covariates mentioned above. As in previous analyses (Dupont et al., 2023b,c), we used an half-normal model to describe the movement propensity of individuals between years.

Population dynamics and population size sub-model We used a multi-state formulation (Lebreton and Pradel, 2002) where each individual life history is represented by a succession of 4 discrete states $z_{i,t}$: 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) "recovered" if it was legally killed in Norway between the start of the current and the start of the next monitoring period, and 4) "dead" if it died due to another mortality cause or if it was already dead in the previous monitoring season. We then modelled the transitions from one state to another between consecutive monitoring seasons (t to $t+1$) to estimate vital rates (recruitment and cause-specific mortality). More details are available in Bischof et al. (2019b), and Bischof et al. (2020b). In order to account for the fact that some individuals might never be detected, we used data augmentation (Royle and Dorazio, 2012), whereby additional, undetected individuals are available for inclusion in the population at each time step.

Detection sub-model SCR and OPSCR models account for the spatial variation in detectability by modelling individual detection probability as a function of the distance between the coordinates of a detection (i.e., a detector) and the individual's AC location (estimated by the density sub-model). A half-normal function is generally used to express the declining probability of detection with increasing distance between the AC and the detector. We accounted for

additional sources of spatial and temporal variation in individual detection probability by using several spatial covariates:

- Spatio-temporal variation in unstructured sampling (Figure A.4). For each detector grid cell and during each monitoring season (Apr 1 - Nov 30), we identified whether a) any carnivore sample had been registered in Rovbase and 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 could have been detected and submitted for genetic analysis.

- Spatial variation in accessibility measured as the average distance to the nearest road (Figure A.3).

- Spatio-temporal variation between aggregated counties (Figure A.6).

More details about the different model components can be found in Bischof et al. (2019a,b, 2020b).

Model fitting We fitted sex-specific Bayesian OPSCR models using Markov chain Monte Carlo (MCMC) simulation with NIMBLE version 0.13.1 (Turek et al., 2021; de Valpine et al., 2017; NIMBLE Development Team, 2019) and nimbleSCR version 0.2.1 (Bischof et al., 2021) in R version 4.1.0 (R Core Team, 2022). We ran 4 chains of 100 000 iterations each, including a 25 000-iterations burn-in period. Due to the computing challenge of post-processing large amounts of data, we thinned chains by a factor of 10 from which abundance estimates were derived. We considered models as converged when the Gelman-Rubin diagnostics (Rhat, Gelman and Rubin, 1992) was ≤1.1 for all parameters and by visually inspecting trace plots.

Abundance estimates and density maps Here, we report abundance based on AC locations (Box 2). 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, thus generating a posterior distribution of abundance for that area. In this fashion, abundance estimates and the associated uncertainty can be extracted for any spatial unit, including countries, counties or management regions (Figure A.1). 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 available on one side of the border. As a result, the probability of designating such individuals to either side of the border is integrated into jurisdiction-specific abundance estimates. This is especially relevant for bears detected along the Swedish and Norwegian border ("trans-boundary bears", Box 2) as individual bears can be partially designated to both countries (Bischof, 2015). To ensure that abundance estimates for spatial sub-units add up to overall abundance estimate, we used the mean and associated 95% credible interval to summarize posterior distributions of abundance. Combined (female/male) parameter estimates were obtained by merging posterior samples from the sex-specific models.

We also used both the posterior distribution of model-estimated AC positions and the scale parameter (σ) of the detection function to construct density maps based on individual space-use (Box 2). These maps are not only based on the position of the center of an individual's home range but also take into account the area (defined by σ, Royle et al. (2014)) over which that individual's activity is spread, i.e., its space use (Bischof et al., 2020b). To do so, we constructed individual space-use raster maps (5 km resolution), scaled values in each raster to sum to one, and then summed rasters across individuals to create a single population-level raster map. By repeating this procedure for each MCMC iteration, we obtained a posterior distribution of population space use. The overall density map was then derived by calculating the mean abundance across iterations in each cell (Bischof et al., 2020b). Abundance for any given region can also be derived from these maps (Box 2), but note that this approach relies on the assumption of

circular home ranges of identical size for all individuals of a given sex. In other words, it does not take into account individual variation in home-range size and shape.

Other derived parameters The overall average proportion of individuals detected each year, and the associated uncertainty, were obtained by dividing the total number of individuals detected through NGS sampling (Table A.1) by the abundance estimates for Norway and their associated credible intervals (Table A.3), respectively.

The average proportion of the Norwegian bear population that was detected each year, and the associated uncertainty, were obtained by dividing the number of individuals with their AC estimated in Norway that were detected through NGS sampling (Table A.1) by the abundance estimates from Norway for each iteration (Table A.3). This generated posterior distributions of the proportion of the Norwegian bear population detected, from which the mean and 95% credible intervals could be extracted. This procedure was used to calculate female, males and overall proportion of individuals detected.

The numbers of bears detected in Norway that could be attributed to other countries were obtained by summing the number of individuals detected in Norway that had their activity center located in Sweden, Finland or Russia for each iteration of the MCMC chains. With this procedure, we were able to generate posterior distributions of the number of individuals detected in Norway that could be attributed to neighbouring countries, from which the mean and 95% credible intervals could be extracted. The proportion of the individuals detected in Norway that could be attributed to each country was then obtained by dividing these numbers by the total number of individuals detected through NGS sampling.

We derived the proportion of females in the population and the associated uncertainty by dividing the posterior distribution representing the number of females by the combined abundance estimate for males and females (Table A.1). Yearly population growth rates were calculated as $\lambda_t = N_{t+1}/N_t$.

Focus on uncertainty Although we reported median (or mean for abundance; see above) estimates for all parameters in the tables, we intentionally focused the main results of this report on the 95% credible interval limits of the estimates. We did so with the aim of drawing the reader's attention to the uncertainty around population size estimates, rather than a single point estimate (Milleret et al., 2022c).
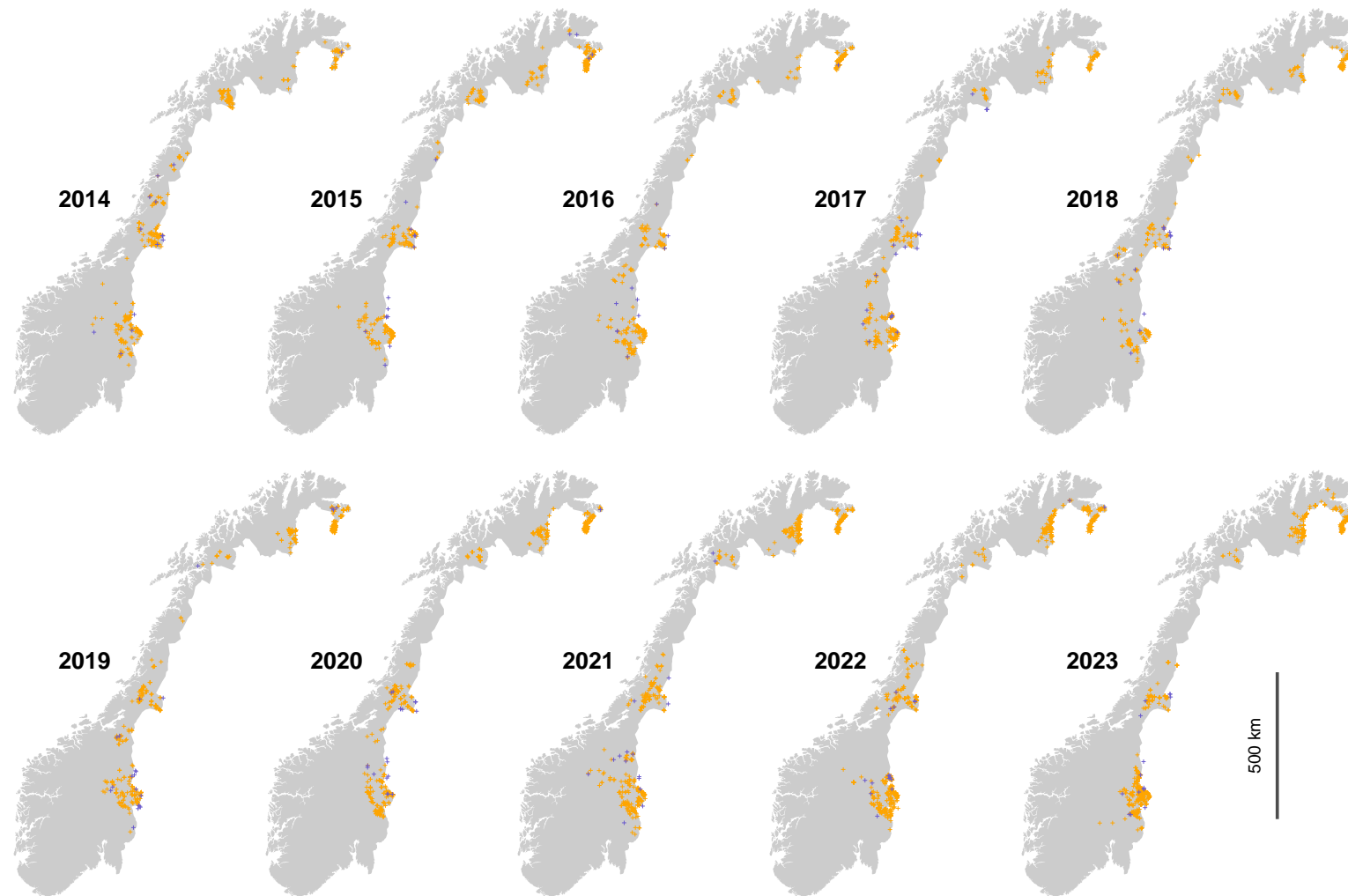
Figure 1: Annual distribution of brown bear non-invasive genetic samples (NGS, yellow crosses) and dead recoveries (purple crosses) between 2014 and 2023 and included in the OPSCR analyses. We included only samples collected within the study area during the primary monitoring period (Apr 1 - Nov 30).

3   Results

3.1   Non-invasive genetic samples and dead recoveries

A total of 5 864 (2 423 female; 3 441 male) genotyped bear genetic samples collected in Norway between 2014 and 2023 were included in the analysis (Figure 1). These samples were associated with 592 (208 female; 384 male) individuals. We also included 134 bears recovered dead in Norway or at the border area with Sweden in the OPSCR model, of which 115 (28 female; 87 male) were due to legal culling and 19 (7 female; 12 male) due to other causes of mortality. Annual tallies of NGS samples and associated individuals, as well as dead recoveries included in the analysis for the period 2014-2023 are provided in the Appendices (NGS samples and individuals: Table A.1, dead recoveries: Table A.2).

3.2   Density and abundance

Brown bear abundance for the entire study area in Norway (180 630 km^2, excluding the buffer area) was estimated (95% credible interval) to be between 122 and 154 individuals in 2023, based on the estimated locations of individual activity centers (Table 1, Figure 2). Estimates refer to the status of the population at the start of the annual sampling period (April 1). The Norwegian bear population slightly increased over the 10-year period with yearly population growth rates λ_t ranging from 0.77-1.05 (95% credible interval) in 2014/2015 and 1.00-1.37 in 2016/2017 Table A.6. The proportion of females in the Norwegian bear population increased slightly over the years (Table A.4) and was likely between 39% and 50% in 2023 compared with 35%-46% in 2014.

This overall pattern hides variable population trajectories in the different large carnivore regions of Norway (Figure 5), with a stable population in large carnivore regions 3 (Oppland), 6 (Trøndelag, Møre og Romsdal) and 7 (Nordland) and a slowly increasing population in region 8 (Troms and Finnmark). By contrast, population size has doubled in region 5 (Hedmark), increasing from 21-32 individuals in 2014 to 44-58 in 2023. The evolution of the population sex-ratio also varied spatially (Table A.4), with the strongest increase in the proportion of females observed in region 5.

We provide annual abundance estimates for the entire study area and by large carnivore region between 2014 and 2023 (Table A.3). The analysis also yielded annual density maps, which reveal changes in the distribution of bears over time, most visibly the expansion and increase in density in region 5 and a decline in the southern part of region 8 (Figure 3, Figure A.5).

Table 1: Bear population size estimates in 2023 by sex and large carnivore management region within the main Norwegian population range. Only 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 last column. 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 bears. 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.

	Females	Males	Total	% Area included
Region 2	0.1 (0-1)	0.4 (0-2)	0.5 (0-2)	7
Region 3	0.5 (0-2)	1.3 (0-3)	1.7 (0-5)	80
Region 4	0 (0-0)	0 (0-0)	0 (0-0)	23
Region 5	22.3 (18-27)	28.5 (24-34)	50.8 (44-58)	100
Region 6	10.2 (8-13)	15.9 (11-22)	26.1 (20-33)	82
Region 7	0.8 (0-3)	4.9 (2-9)	5.8 (2-10)	84
Region 8	24.5 (18-32)	28.2 (20-37)	52.7 (42-64)	69
TOTAL	58.5 (49-68)	79.2 (67-92)	137.7 (122-154)	56
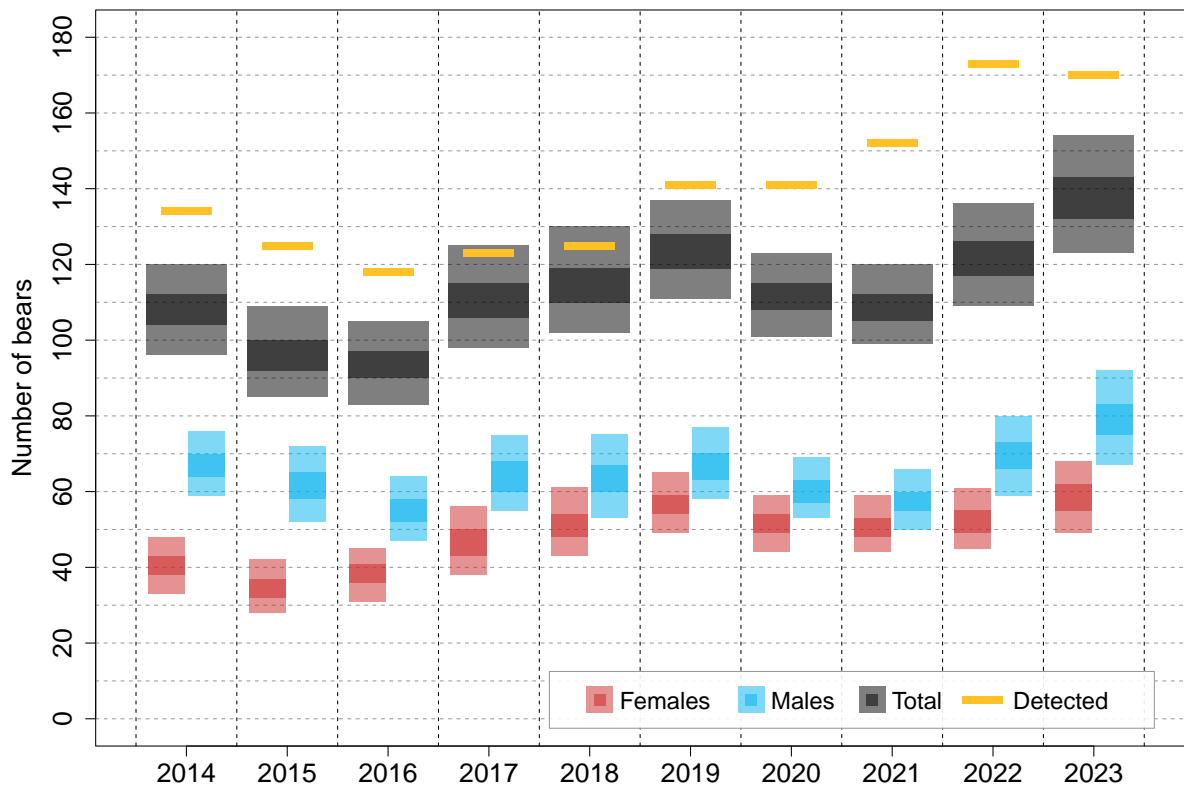
Figure 2: Total (black) and sex-specific (blue: males, red: females) annual bear population size estimates within the main Norwegian population range between 2014 and 2023 derived from the open-population spatial capture-recapture model. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Yellow bars show the number of individuals detected in Norway each year. The number of individuals detected in Norway exceeds the estimated population size, as individuals with activity centers in neighboring countries, near the Norwegian border, may be detected inside Norway.

Box 2: On the definition of population size

Population size can be defined in different ways and the interpretation of the estimates will depend on the chosen definition. Bear population size in Norway can for example be defined as the total number of bears that spent any time within Norwegian boundaries, i.e., that can potentially be detected in Norway. However, this definition is problematic for different reasons. Most importantly, trans-boundary bears, i.e., bears that spend time on both sides of a border, will potentially be double-counted, which leads to overestimation of the total population size when adding-up estimates from multiple regions. In the spatial capture-recapture framework, population size is usually defined as the number of individuals that have their activity center within the borders of the region of interest. Because the activity center of an individual can not be located on both sides of a border, this resolves the issue of double counting. Note that while the AC of an individual can not be located on both sides of the border, the uncertainty about its exact location and therefore the probability that an individual has its AC located in a given region, are directly integrated in the credible interval (see the **Abundance estimates** section). However, large carnivores have large home ranges and their influence extends beyond their activity center location. Because SCR models also estimate average individual space-use, it is possible to derive the proportion of time each individual spends in a given region. From this, population size can be defined as the sum of the individual space use distributions within a given region (see the **Density maps** section). This definition also avoids double-counting. Contrary to AC-based abundance, abundance based on space use does not assign an individual to one of several regions but instead attributes the presence of a single individual to all regions proportionally to its use of that region.

Table 2: Brown bear population size estimates by sex in Norway in 2023 based on individual activity center locations.

|	Females	Males	Total
Region 2	0.1 (0-1)	0.4 (0-2)	0.5 (0-2)
Region 3	0.5 (0-2)	1.3 (0-3)	1.7 (0-5)
Region 4	0 (0-0)	0 (0-0)	0 (0-0)
Region 5	22.3 (18-27)	28.5 (24-34)	50.8 (44-58)
Region 6	10.2 (8-13)	15.9 (11-22)	26.1 (20-33)
Region 7	0.8 (0-3)	4.9 (2-9)	5.8 (2-10)
Region 8	24.5 (18-32)	28.2 (20-37)	52.7 (42-64)
TOTAL	58.5 (49-68)	79.2 (67-92)	137.7 (122-154)

Table 3: Brown bear population size estimates by sex in Norway in 2023 based on individual space use distributions.

	Females	Males	Total
Region 2	0.1 (0-1)	0.4 (0-1)	0.5 (0-1)
Region 3	0.5 (0-2)	1.3 (0-3)	1.9 (0-4)
Region 4	0 (0-0)	0 (0-0)	0.1 (0-0)
Region 5	23.2 (21-26)	28.7 (26-32)	52 (48-56)
Region 6	10.6 (8-14)	16.4 (12-22)	27 (22-33)
Region 7	1 (0-3)	5.1 (3-8)	6.1 (3-10)
Region 8	26 (21-31)	28.4 (23-35)	54.4 (47-63)
TOTAL	61.4 (54-69)	80.4 (71-90)	141.8 (130-154)

In the case of the Norwegian bear population, the higher population densities in Sweden imply that many individuals will have their AC estimated to be located in Sweden while their space use distribution will extend into Norway. Consequently, population size estimates for Norway based on individual space-use tend to be slightly higher than estimates based on activity center locations.
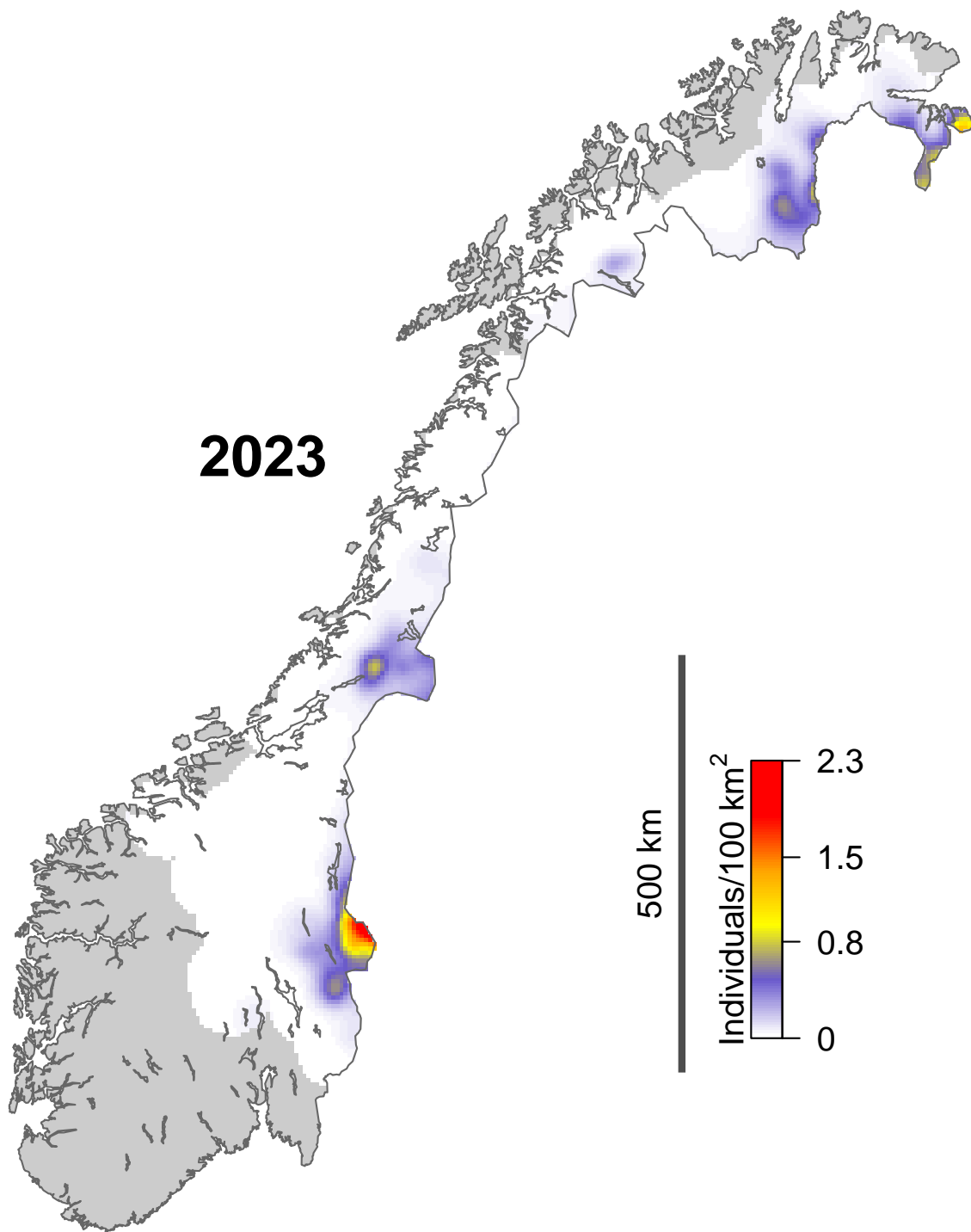
Figure 3: Brown bear density based on individual space use distributions throughout the study area (white background) in Norway in 2023. Density was estimated with an open-population spatial-capture recapture model fitted to NGS and dead recovery data collected between 2012 and 2023. See the 'Methods' section for further detail.

3.3 Vital rates

The OPSCR model produced annual estimates of legal hunting mortality and mortality associated with all other causes (Figure 4), as well as estimates of the average per capita recruitment rates over the 10-year period (Table A.5).
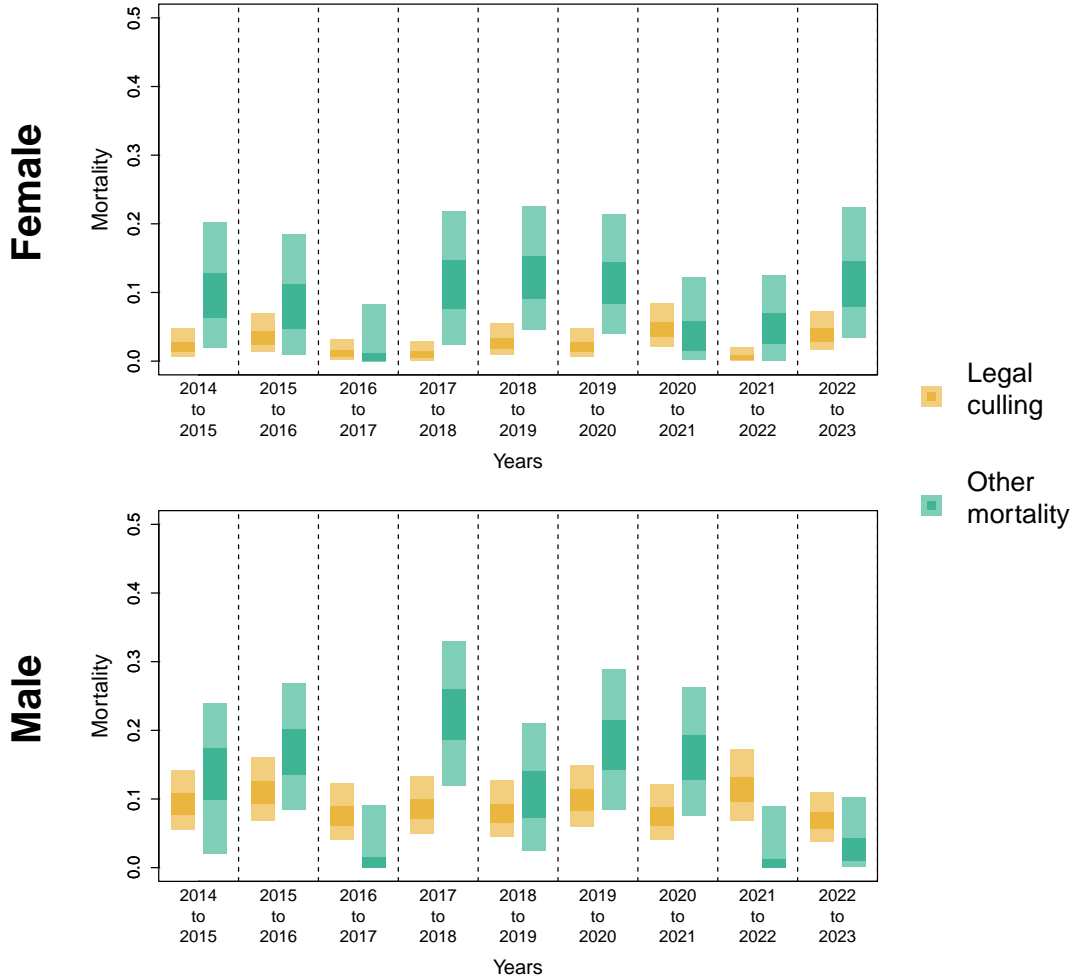

Figure 4: Mortality probabilities due to legal culling and all other causes for female and male brown bears. Shown are overall estimates throughout the study area in Norway, based on the sex-specific OPSCR models. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Estimates refer to deaths occurring between the start of one sampling season and the start of the next one. Consequently, estimates for mortality between 2023 and 2024 are not yet available for this analysis.

3.4 Detection probability

Every year, more bears were detected through NGS in Norway than the estimated population size. This is due to the detection of individuals with estimated activity centers located in neighboring countries (Figure 2, see also explanation in Bischof et al. 2016). In other words, the model estimated that between 47 and 63 individuals detected through NGS in Norway in 2023 had their activity center located in either Sweden (21 to 32 individuals), Finland (14 to 24) or Russia (6 to 14), which corresponds to between 28% and 37% of the individuals detected in Norway that year.

When it comes to detectability in the Norwegian bear population, in 2023, the model estimated that between 61% and 75% of the Norwegian bear population were detected through NGS. Detectability was higher for males compared to females and varied between years, from 0.53-0.67 in 2015 to 0.70-0.84 in 2020 (Table A.8).

Baseline detection probability (p_0) varied between jurisdictions and was always higher for females compared to males (Figure A.6). Detection probability decreased with the distance to the nearest road (Figure A.3, Table A.7) and strongly increased with the proxy for search effort derived from the observation data in Skandobs and Rovbase (Figure A.4, Table A.7).

4   Discussion

Our analysis revealed a positive population trajectory for the bear population in Norway during the last 10 years (Figure 2). We observed the most pronounced increase in the female portion of the population, which led to an increasingly balanced sex-ratio in more recent years. This is consistent with the expected pattern for a bear population during a re-colonization phase. Male bears, who disperse more frequently and further than females (Støen et al., 2006; Zedrosser et al., 2007), can recolonize areas at a higher pace, leading to a higher proportion of males at the beginning of the recolonization phase (2012-2017) and at larger distances from the female core areas (Kindberg et al., 2011). Being philopatric, recolonizaton of females is slower (Zedrosser et al., 2007; Kindberg et al., 2011; Støen et al., 2006), but their proportion will slowly catch up as population density increases, due in part to the higher estimated survival rate of females compared to males (Figure 4, Table A.5). These life-history differences between sexes create a situation where the Scandinavian brown bear population expands from its core areas in Sweden, with males moving outwards first and females subsequently "catching-up".

The spatially-explicit nature of our analysis also allowed us to highlight regional differences in the brown bear recolonization pattern in Norway (Figure 5). The overall population increase in the Norwegian brown bear population seems mainly driven by increasing bear numbers in carnivore management region 5 (Hedmark) and, to a lesser extent, region 8 (Troms and Finnmark), whereas it remained stable in regions 3 (Oppland), 6 (Møre og Romsdal, Trøndelag), and 7 (Nordland). The increase in the proportion of females also varied between management regions and was most visible in region 5. By contrast, the sex ratio has been relatively balanced and stable in region 8 throughout the 2014-2024 period. This may reflect the fact that this region is more advanced in the recolonization process as it is closer to areas of potentially high bear population density in Finland and Russia, compared to regions at the edge of the brown bear range like Oppland where the population is still mostly composed of a few males (Table A.4).

5   Suggestions for future improvements

As RovQuant continues to work on improving the functionality and efficiency of OPSCR models, we intend to test and potentially implement the following developments in future analyses of the Scandinavian bear monitoring data:

1. Further explore possibilities to use the NGS data collected in Sweden to derive reliable population size estimates jointly for Sweden and Norway.

2. Review and adjust spatial covariates on density to better reflect habitat selection by bears and therefore population density. This may involve the addition of land cover and topographic variables.

3. Distinguish between dispersing and non-dispersing individuals, for example by using a finite-mixture approach.

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., 2022a).

5. Account for unknown sources of spatial variation in detectability through the use of spatially autocorrelated random effects (Dey et al., 2022b).

Figure 5: Total (black) and sex-specific (blue: males, red: females) annual bear population size estimates in the different carnivore management regions in Norway (Figure A.1) between 2014 and 2023. Abundance estimates were derived from the locations of individual activity centers estimated by sex-specific open-population spatial capture-recapture models. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Here, we only present carnivore regions with a mean estimated population size > 1 in at least one year during the study period.
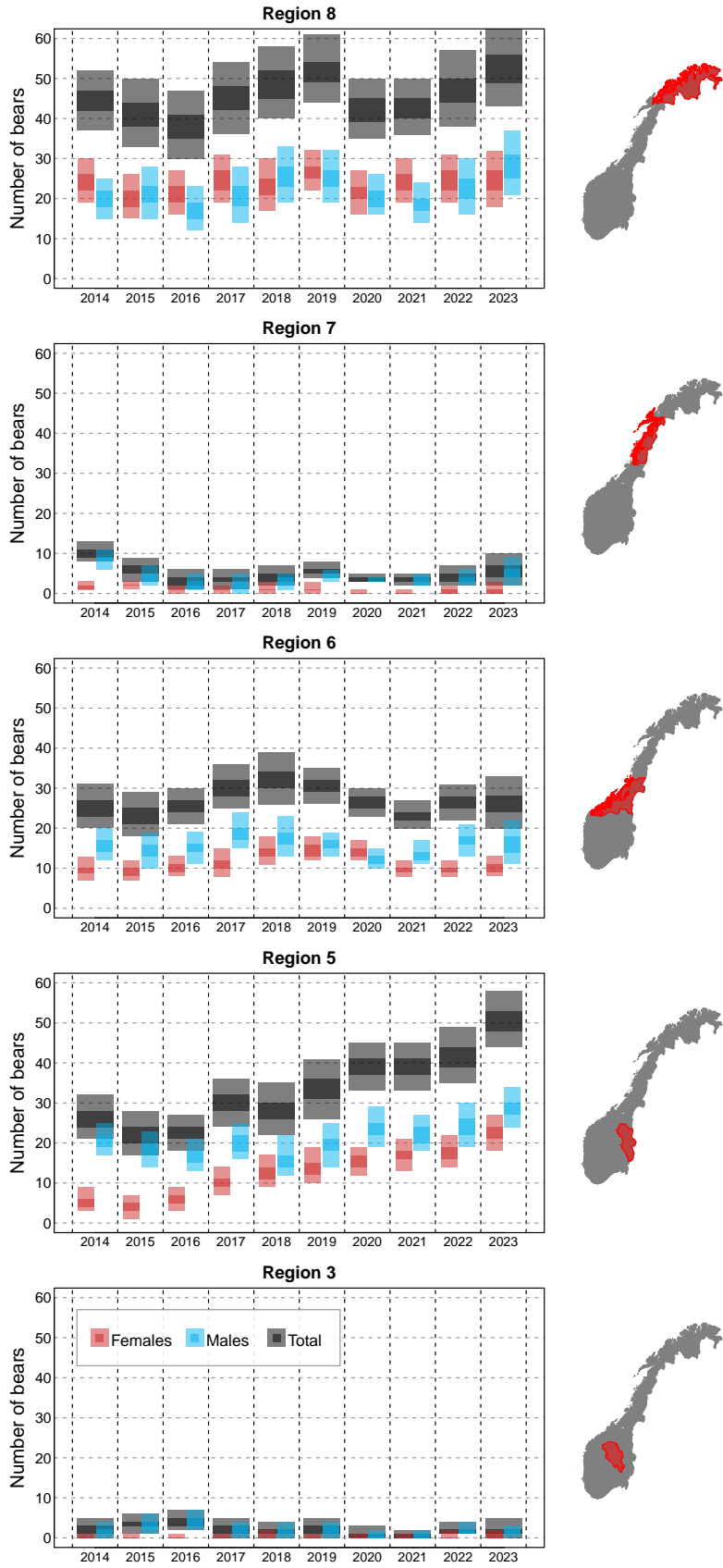
6. Account for spatial variation in survival and other vital rates (Milleret et al., 2023a).

6 Acknowledgements

7 Data availability

Data, R code to reproduce the analysis, as well as figures, tables, and raster maps (Figure A.5) are available on GitHub (https://github.com/richbi/RovQuantPublic)

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Appendices
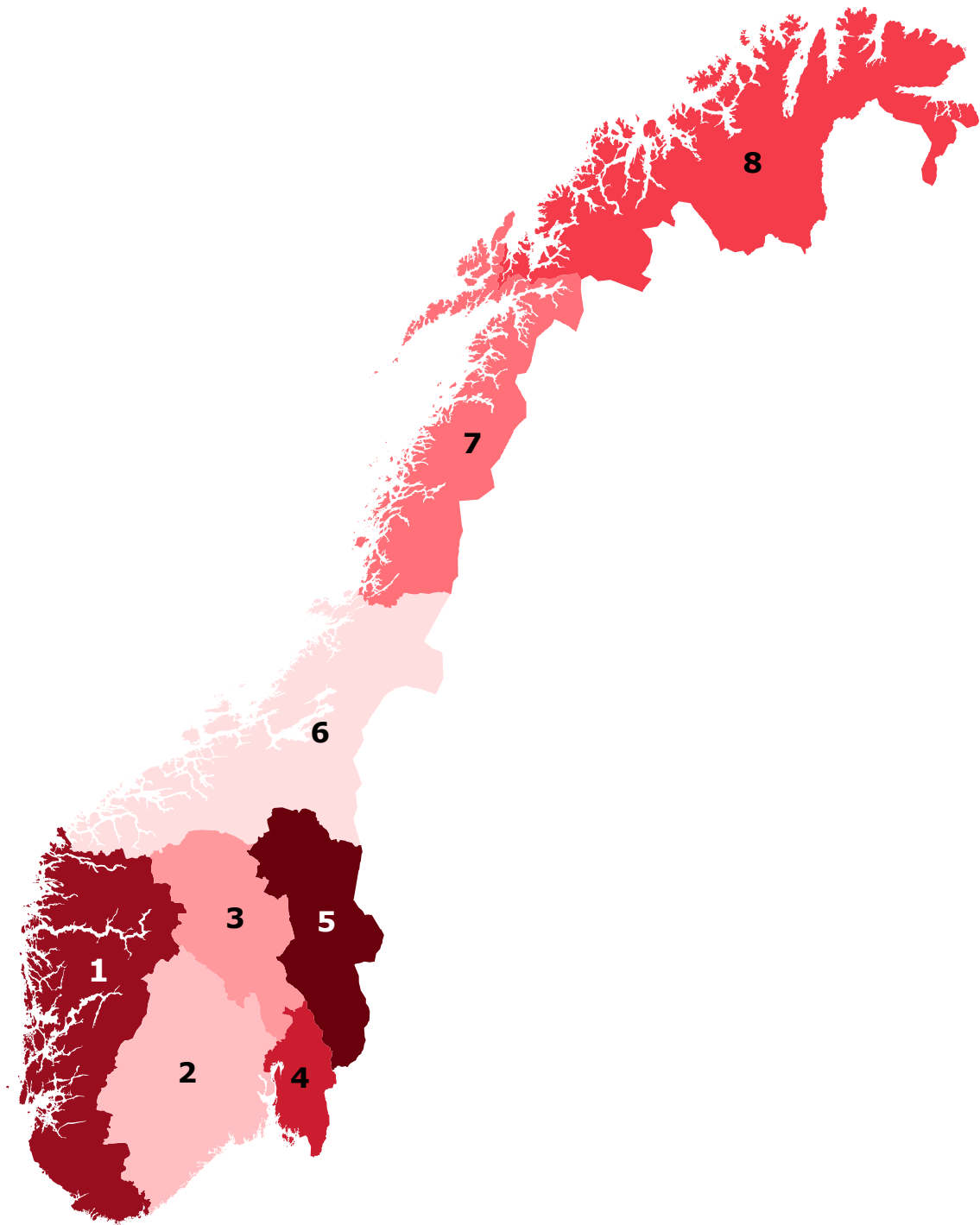
Figure A.1: Carnivore management regions (forvaltningsregioner for rovvilt) in Norway.
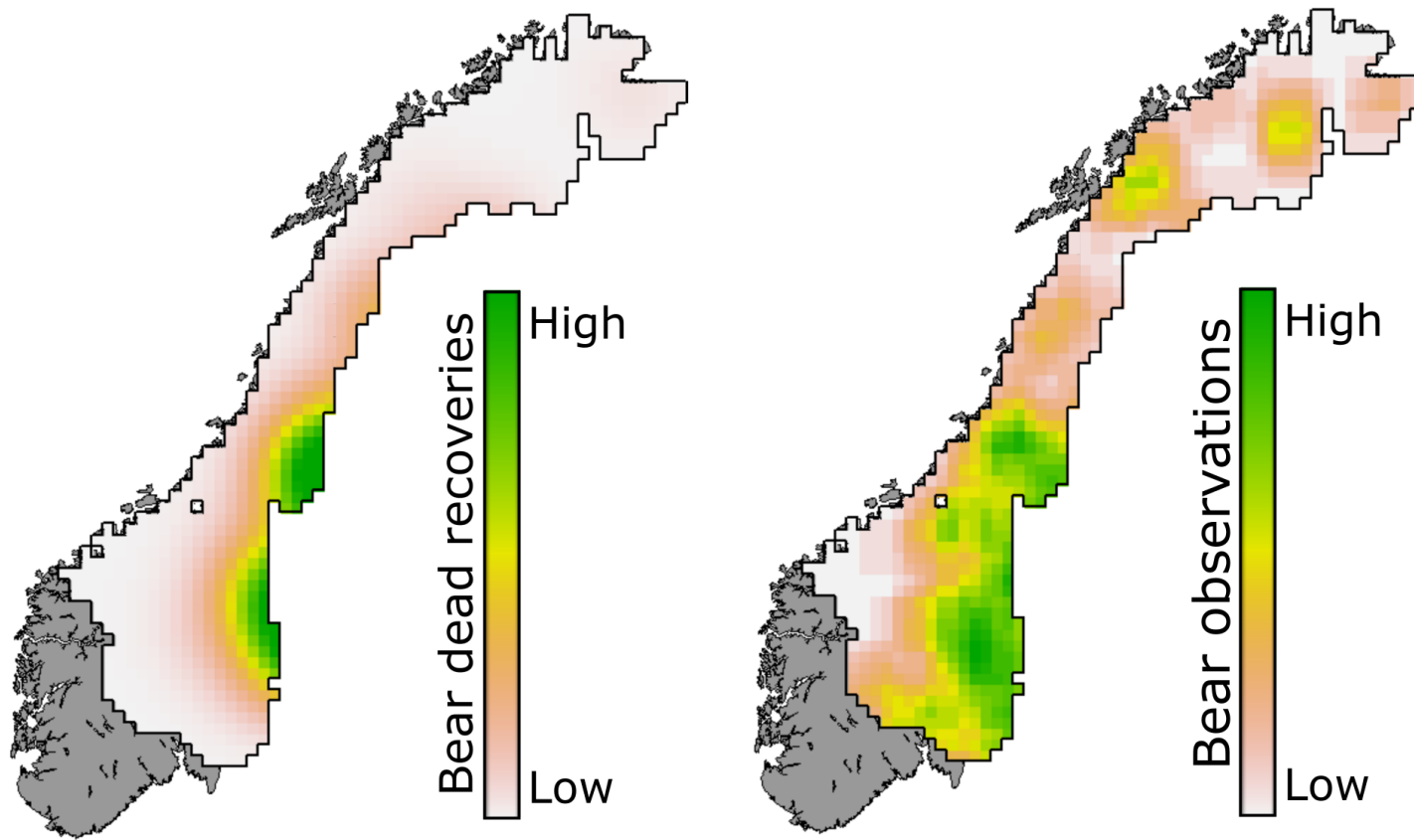
Figure A.2: Spatial covariates denoting the scaled density of brown bear dead recoveries (left) and brown bear observations recorded in Skandobs (right) in Norway. These covariates were used in the density and movement sub-models of the open-population spatial capture-recapture model.
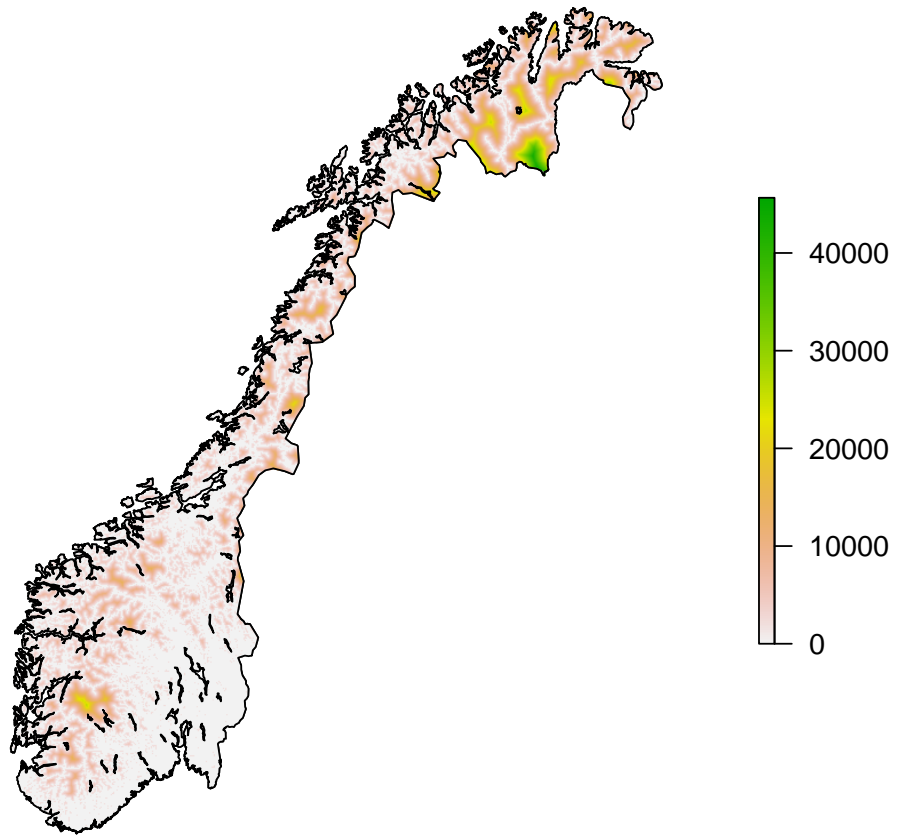
Figure A.3: Spatial covariate denoting the distance to the nearest road (in meters) in Norway. This covariate was used in the detection sub-model of the open-population spatial capture-recapture model.
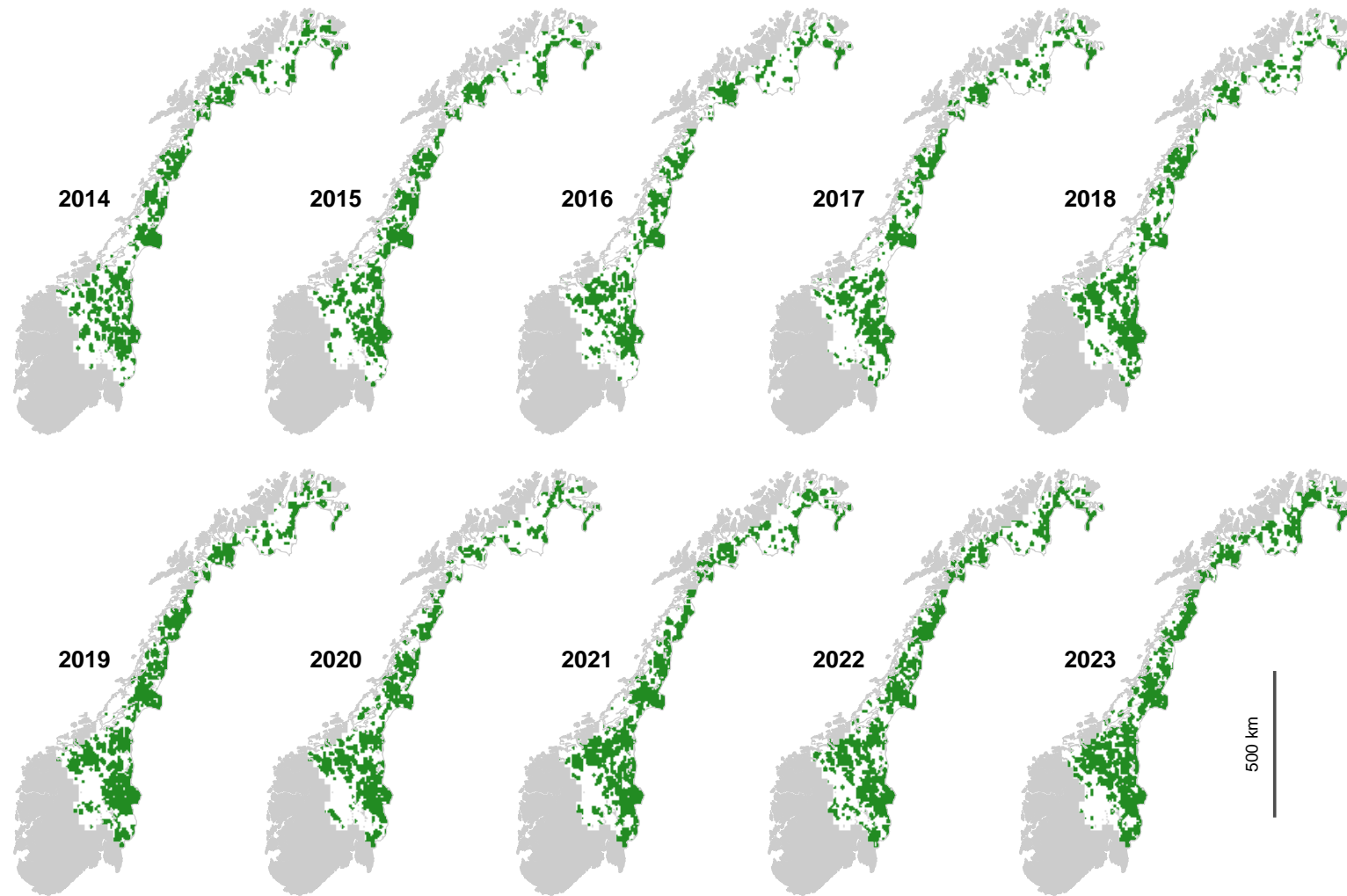
Figure A.4: Spatial covariate denoting the presence (green cells) of at least one carnivore observations between 2014 and 2023 for each 5 x 5km detector grid cell. This covariate was used in the detection sub-model of the open-population spatial capture-recapture model.
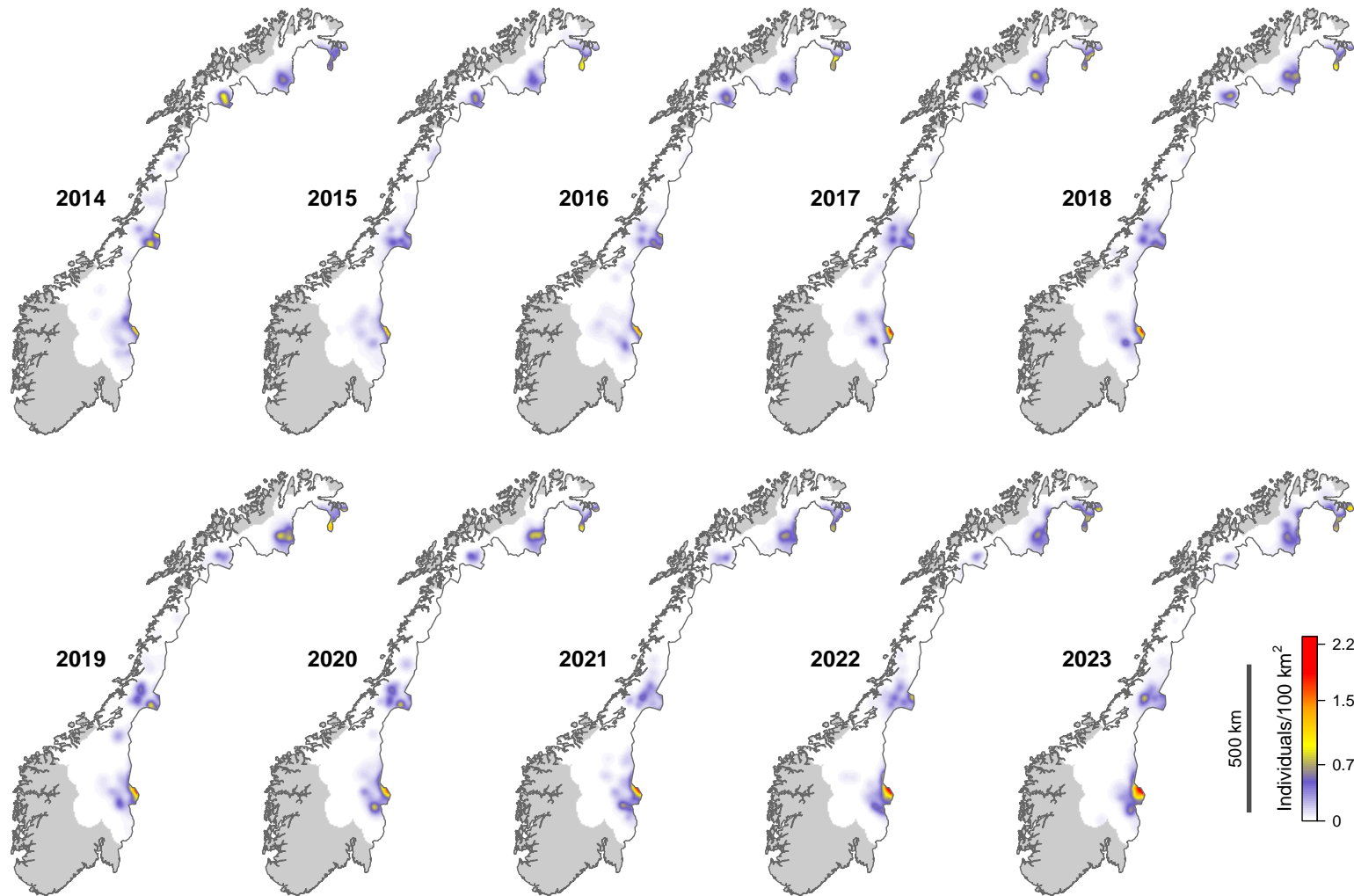
Figure A.5: Annual brown bear density based on individual space-use throughout Norway between 2014 and 2023. Density was estimated using the open-population spatial capture-recapture model.
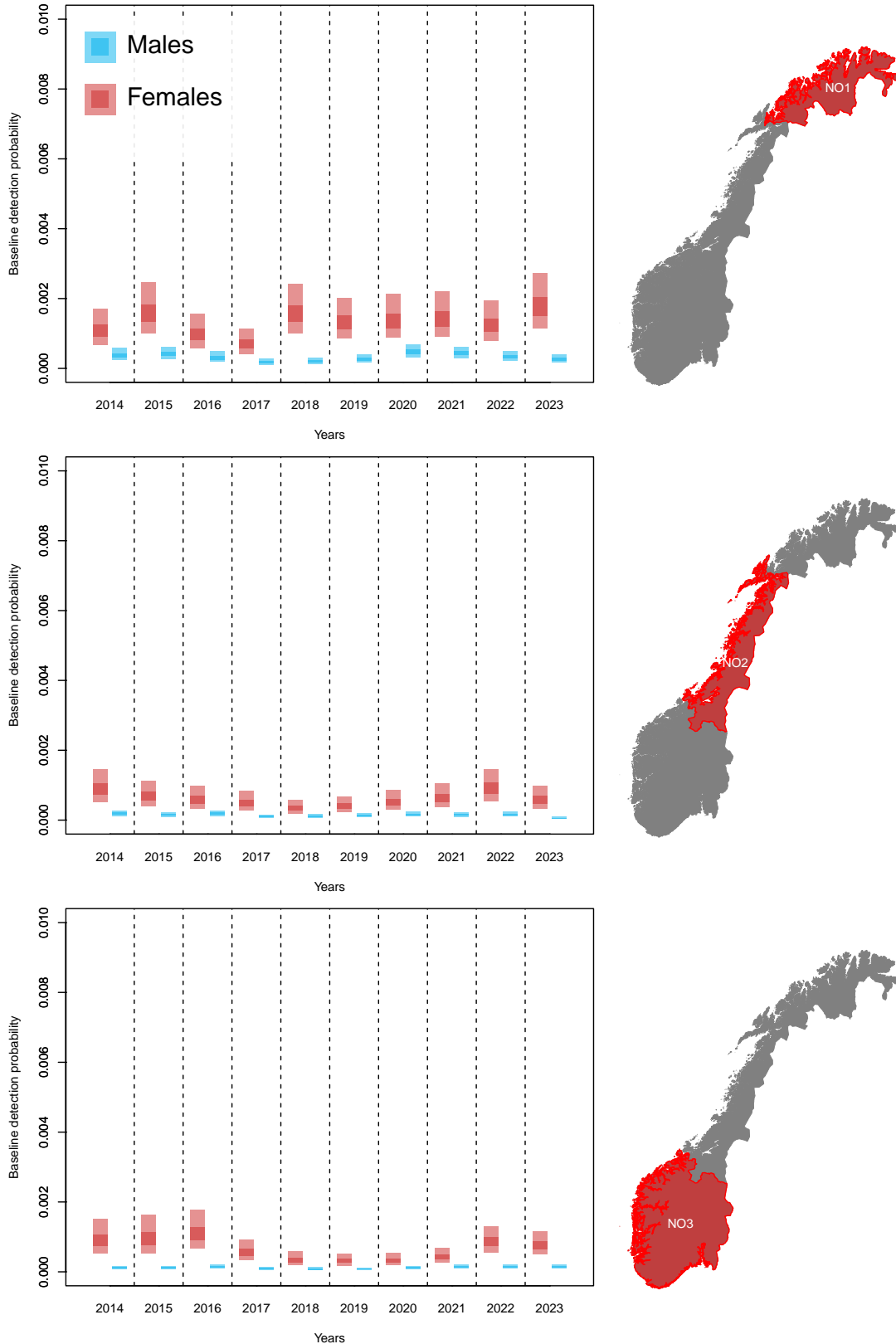
Figure A.6: Sex-specific baseline detection probability (p_0) estimated by the open-population spatial capture recapture models (females in red and males in blue). Results are separated into panels based on regions (each combining multiple counties). Estimates are shown for the mean values of the detection covariates. Darker and lighter bars show the 50% and 95% credible intervals, respectively. 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 brown bear non-invasive genetic samples collected and individuals detected in Norway and included in the OPSCR analyses for females (F) and males (M). In the analysis, we included samples collected within the study area during the primary monitoring period (Apr 1 - Nov 30) between 2012 and 2023. In the table, only sample sizes from monitoring seasons since 2014 are shown.

	2014		2015		2016		2017		2018		2019		2020		2021		2022		2023	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
number of NGS samples	163	301	236	334	198	265	165	267	184	206	240	344	216	423	265	463	337	404	419	434
number of NGS individuals	53	81	54	71	48	70	55	68	57	68	57	84	62	79	64	88	76	97	76	94

Table A.2: Number of cause-specific dead recoveries of bears included in the OPSCR analysis between 2014 and 2023. Numbers are reported by country, for females (F) and males (M). Note that i) bears recovered dead in Sweden inside the 50 km habitat buffer were included in the analysis, and ii) dead recovery data from the final season (2023) were not used in this analysis because survival is modeled as part of the transition from one season to the next.

	Country	2014		2015		2016		2017		2018		2019		2020		2021		2022		2023	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	0	0	1	0	0	0	0	0	1	1	2	0	1	3	0	0	2	1	0	3
	Sweden	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Legal culling	Norway	1	9	1	6	0	7	0	7	2	4	2	8	1	4	1	9	1	9	1	3
	Sweden	3	2	0	3	2	1	1	4	2	3	1	3	6	1	0	4	3	0	0	0
TOTAL	Total	4	11	2	9	2	8	1	12	5	8	5	11	8	8	1	13	6	10	1	9

Table A.3: Annual abundance estimates for Norway and by large carnivore management regions (Figure A.1). Estimates are based on activity center locations estimated by the open-population spatial capture-recapture (OPSCR) model. Credible intervals (95%) are shown in parentheses. Small deviations between the total estimate and the sum of abundance estimates from the constituent subregions may arise due to rounding. See Methods section for further detail.

	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023
Region 2	0.2 (0-1)	0.2 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.5 (0-2)
Region 3	1.8 (0-4)	3.5 (1-6)	4.3 (2-7)	2.2 (0-5)	1.6 (0-4)	2.2 (0-5)	0.8 (0-3)	0.5 (0-2)	1.8 (1-4)	1.6 (0-4)
Region 4	0.2 (0-1)	0.2 (0-1)	0 (0-1)	0 (0-1)	0.1 (0-1)	0.1 (0-1)	0 (0-0)	0.1 (0-1)	0 (0-0)	0 (0-0)
Region 5	25.9 (21-32)	22 (16-28)	22.3 (18-28)	29.6 (24-36)	28.2 (22-35)	33.2 (26-41)	39 (33-45)	38.9 (33-45)	41.9 (35-49)	50.7 (44-58)
Region 6	25 (20-30)	23 (18-29)	25.1 (20-31)	30 (25-36)	32.1 (26-39)	30.4 (26-35)	26.5 (23-31)	23.1 (20-27)	26.8 (22-31)	26.7 (20-34)
Region 7	10 (8-13)	5.9 (3-9)	3.1 (1-6)	3.4 (1-6)	4 (2-7)	5.6 (4-8)	3.4 (3-5)	3.3 (2-6)	4.2 (2-7)	6.2 (3-11)
Region 8	43.9 (36-52)	41.2 (33-50)	38.4 (30-47)	45 (36-55)	48.8 (40-59)	52.3 (44-61)	41.8 (34-50)	42.4 (35-50)	46.9 (38-56)	52.5 (43-63)
TOTAL	107 (96-119)	95.9 (84-109)	93.5 (82-105)	110.5 (97-124)	115 (101-130)	123.9 (112-137)	111.5 (101-123)	108.4 (98-119)	121.6 (108-135)	138.1 (123-154)

Table A.4: Annual proportion of female in the brown bear population of Norway. Estimates were derived using the posterior distributions of sex-specific annual abundance estimates. Grey font is used for large carnivore regions with a mean estimated population size <= 5 in at least one year, to emphasize the small sample size (number of individuals) associated with these sex ratio estimates. Credible intervals (95%) are shown in parentheses.

	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023
Region 2	0.31 (0.00-1.00)	0.25 (0.00-1.00)	0.26 (0.00-1.00)	0.32 (0.00-1.00)	0.45 (0.00-1.00)	0.43 (0.00-1.00)	0.58 (0.00-1.00)	0.47 (0.00-1.00)	0.46 (0.00-1.00)	0.39 (0.00-1.00)
Region 3	0.13 (0.00-0.67)	0.06 (0.00-0.40)	0.04 (0.00-0.33)	0.19 (0.00-1.00)	0.22 (0.00-1.00)	0.18 (0.00-1.00)	0.39 (0.00-1.00)	0.49 (0.00-1.00)	0.16 (0.00-0.67)	0.25 (0.00-1.00)
Region 4	0.13 (0.00-1.00)	0.05 (0.00-1.00)	0.12 (0.00-1.00)	0.15 (0.00-1.00)	0.10 (0.00-1.00)	0.14 (0.00-1.00)	0.53 (0.00-1.00)	0.24 (0.00-1.00)	0.21 (0.00-1.00)	0.33 (0.00-1.00)
Region 5	0.29 (0.19-0.39)	0.27 (0.14-0.40)	0.31 (0.21-0.42)	0.36 (0.27-0.46)	0.45 (0.33-0.57)	0.42 (0.32-0.52)	0.42 (0.33-0.50)	0.45 (0.38-0.53)	0.42 (0.35-0.50)	0.43 (0.37-0.49)
Region 6	0.40 (0.32-0.50)	0.40 (0.31-0.50)	0.44 (0.35-0.52)	0.43 (0.34-0.52)	0.48 (0.39-0.58)	0.48 (0.40-0.56)	0.56 (0.48-0.63)	0.43 (0.35-0.50)	0.37 (0.29-0.46)	0.40 (0.29-0.52)
Region 7	0.16 (0.08-0.30)	0.28 (0.00-0.50)	0.39 (0.00-0.67)	0.44 (0.14-0.80)	0.21 (0.00-0.60)	0.07 (0.00-0.33)	0.08 (0.00-0.40)	0.05 (0.00-0.33)	0.08 (0.00-0.40)	0.15 (0.00-0.50)
Region 8	0.55 (0.47-0.64)	0.50 (0.40-0.60)	0.52 (0.42-0.62)	0.56 (0.45-0.67)	0.47 (0.39-0.57)	0.52 (0.45-0.60)	0.55 (0.47-0.63)	0.56 (0.49-0.64)	0.54 (0.46-0.63)	0.50 (0.41-0.59)
TOTAL	0.40 (0.35-0.46)	0.39 (0.33-0.45)	0.42 (0.36-0.49)	0.46 (0.40-0.52)	0.46 (0.40-0.52)	0.46 (0.41-0.51)	0.49 (0.44-0.54)	0.48 (0.43-0.53)	0.44 (0.39-0.50)	0.44 (0.39-0.50)

Table A.5: Estimates of the demographic parameters obtained from the bear OPSCR model and data collected in Norway between 2014 and 2024. 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 survival and mortality do not always sum to 1 because the posterior median is presented (not the mean).

	2014 to 2015		2015 to 2016		2016 to 2017		2017 to 2018		2018 to 2019	
	F	M	F	M	F	M	F	M	F	M
ρ	0.04 (0.00-0.14)	0.30 (0.16-0.45)	0.13 (0.06-0.25)	0.15 (0.04-0.26)	0.12 (0.03-0.25)	0.20 (0.09-0.36)	0.11 (0.03-0.23)	0.31 (0.17-0.47)	0.14 (0.06-0.24)	0.17 (0.06-0.31)
ϕ	0.88 (0.78-0.96)	0.77 (0.66-0.89)	0.89 (0.78-0.96)	0.72 (0.62-0.82)	0.98 (0.91-1.00)	0.92 (0.82-0.96)	0.88 (0.77-0.97)	0.69 (0.58-0.80)	0.85 (0.75-0.93)	0.81 (0.71-0.90)
h	0.02 (0.01-0.05)	0.09 (0.05-0.14)	0.03 (0.01-0.07)	0.11 (0.07-0.16)	0.01 (0.00-0.03)	0.07 (0.04-0.12)	0.01 (0.00-0.03)	0.08 (0.05-0.13)	0.02 (0.01-0.05)	0.08 (0.04-0.13)
w	0.09 (0.02-0.20)	0.14 (0.02-0.24)	0.08 (0.01-0.19)	0.17 (0.08-0.27)	0.00 (0.00-0.08)	0.00 (0.00-0.09)	0.11 (0.02-0.22)	0.22 (0.12-0.33)	0.12 (0.05-0.23)	0.10 (0.02-0.21)

	2019 to 2020		2020 to 2021		2021 to 2022		2022 to 2023	
	F	M	F	M	F	M	F	M
ρ	0.06 (0.01-0.15)	0.20 (0.09-0.33)	0.12 (0.05-0.23)	0.17 (0.08-0.29)	0.06 (0.00-0.15)	0.39 (0.25-0.55)	0.15 (0.08-0.24)	0.24 (0.12-0.38)
ϕ	0.87 (0.76-0.94)	0.72 (0.61-0.82)	0.92 (0.83-0.97)	0.76 (0.66-0.86)	0.95 (0.87-0.99)	0.88 (0.79-0.93)	0.85 (0.74-0.93)	0.91 (0.82-0.95)
h	0.02 (0.01-0.05)	0.10 (0.06-0.15)	0.04 (0.02-0.08)	0.07 (0.04-0.12)	0.00 (0.00-0.02)	0.11 (0.07-0.17)	0.04 (0.02-0.07)	0.07 (0.04-0.11)
w	0.11 (0.04-0.21)	0.18 (0.08-0.29)	0.03 (0.00-0.12)	0.16 (0.07-0.26)	0.04 (0.00-0.13)	0.00 (0.00-0.09)	0.11 (0.03-0.22)	0.02 (0.00-0.10)

Table A.6: Annual population growth rate estimates for the bear population in Norway. Estimates were derived using the posterior distributions of annual abundance estimates (Table A.3). Credible intervals (95%) are shown in parentheses.

	2014 to 2015	2015 to 2016	2016 to 2017	2017 to 2018	2018 to 2019	2019 to 2020	2020 to 2021	2021 to 2022	2022 to 2023
λ	0.90 (0.76-1.04)	0.98 (0.83-1.14)	1.19 (1.02-1.38)	1.04 (0.89-1.23)	1.08 (0.93-1.24)	0.91 (0.80-1.03)	0.97 (0.85-1.10)	1.12 (0.98-1.29)	1.13 (0.98-1.31)

Table A.7: Parameter estimates for the spatial and detection processes of the OPSCR models for male (M) and female (F) bears in Norway. The inter-annual movement parameter (τ) and the scale parameter of the detection function (σ) are expressed in kilometers. β_{dead1} and β_{dead2} correspond to the effect of the locations of all bears recovered dead throughout the 2012-2023 period on the initial and subsequent AC locations, respectively. $\beta_{skandobs1}$ and $\beta_{skandobs2}$ correspond to the effect of the presence of bear observations registered in SkandObs on the initial and subsequent AC locations, respectively (Bischof et al., 2020b). β_{roads} corresponds to the effect of the average distance to the nearest road and β_{obs} corresponds to the effect of the presence of any large carnivore observation registered in Rovbase or SkandObs on the baseline detection probability. All coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	Parameters	F	M
Spatial process	τ	8.12 (7.31-9.11)	35.30 (33.49-37.06)
	β_{dead_1}	0.62 (0.49-0.76)	0.47 (0.32-0.59)
	$\beta_{skandobs_1}$	-0.22 (-0.41-(-)0.06)	-0.15 (-0.30-0.02)
	β_{dead_2}	-0.19 (-0.50-0.10)	0.38 (0.31-0.46)
	$\beta_{skandobs_2}$	1.24 (0.83-1.69)	0.56 (0.44-0.68)
Detection process	σ	8.86 (8.57-9.17)	12.87 (12.52-13.23)
	β_{roads}	-0.77 (-0.87-(-)0.67)	-0.75 (-0.84-(-)0.67)
	β_{obs}	2.18 (1.83-2.53)	3.21 (2.92-3.51)

Table A.8: Average proportion of the Norwegian bear population detected via non-invasive genetic sampling (NGS) in Norway. Values were calculated as the proportion of individuals with their activity center estimated in Norway by the OPSCR models (Table A.3) that were detected with NGS (Table A.1). Credible intervals (95%) are shown in parentheses.

	2014	2015	2016	2017	2018
F	0.58 (0.47-0.69)	0.53 (0.42-0.64)	0.54 (0.44-0.65)	0.54 (0.44-0.64)	0.56 (0.47-0.67)
M	0.78 (0.70-0.87)	0.65 (0.56-0.75)	0.71 (0.62-0.79)	0.71 (0.62-0.81)	0.70 (0.60-0.80)
Total	0.70 (0.63-0.77)	0.60 (0.53-0.67)	0.63 (0.56-0.70)	0.63 (0.56-0.70)	0.63 (0.56-0.71)

	2019	2020	2021	2022	2023
F	0.62 (0.53-0.71)	0.69 (0.59-0.80)	0.67 (0.58-0.78)	0.64 (0.55-0.74)	0.66 (0.56-0.77)
M	0.81 (0.72-0.89)	0.84 (0.76-0.92)	0.87 (0.80-0.93)	0.80 (0.72-0.88)	0.69 (0.61-0.79)
Total	0.71 (0.65-0.78)	0.77 (0.70-0.84)	0.77 (0.70-0.83)	0.73 (0.66-0.79)	0.68 (0.61-0.75)