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Estimates of brown bear density, abundance, and population dynamics in Norway 2012 - 2021

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COVER PICTURE

Female brown bear with cubs, Staffan Widstrand.

NØKKELORD

Ursus arctos, brunbjørn, bestandstetthet, populasjonsdynamikk, oppdagbarhetssannsynlighet, ikke-invasiv innsamling av genetisk materiale, åpen populasjon romlig fangst-gjenfangst, rovdyrforvaltning

KEY WORDS

Ursus arctos, brown bear, population density, population dynamics, detection probability, non-invasive genetic sampling, open-population spatial capture-recapture, carnivore management

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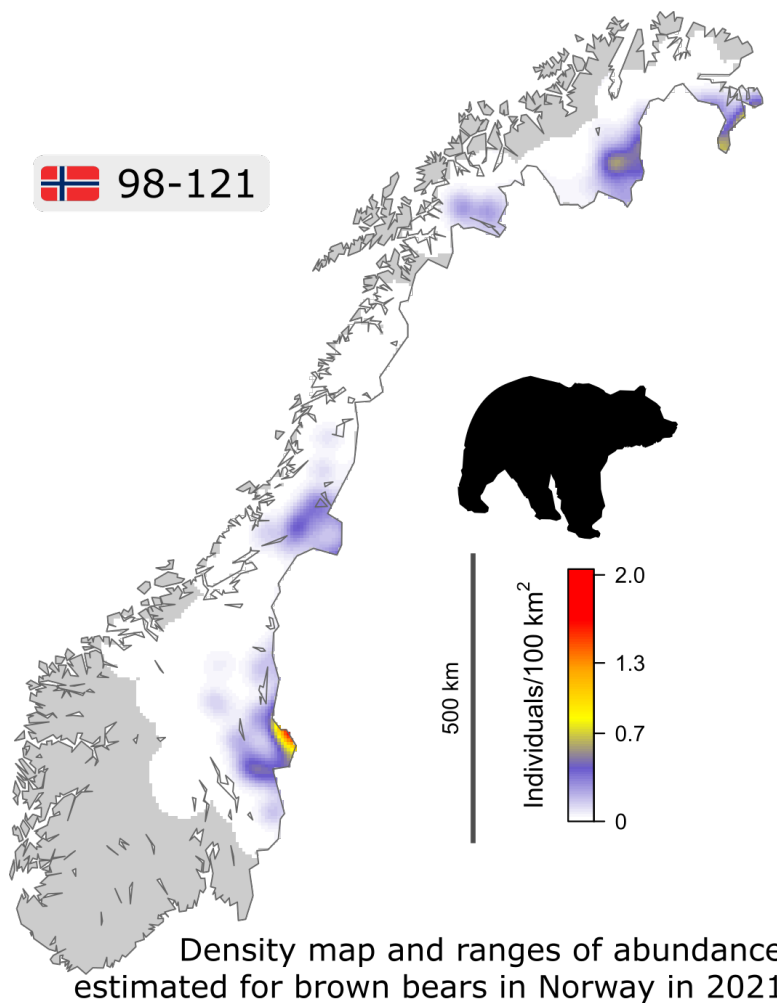
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Summary

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, we estimated annual density and vital rates of the Norwegian portion of the Scandinavian bear population between 2012 and 2021. Annual range-wide monitoring of bears in Norway allowed us to use the OPSCR model developed by RovQuant. Although NGS-based monitoring of bears is also conducted in Sweden, preliminary joint analysis of Norwegian and Swedish bear monitoring data revealed inconsistencies in the results which necessitate further investigation. Results and discussion of the analysis for Sweden will therefore be provided elsewhere.

Results We provide annual density maps and both total and jurisdiction-specific population size estimates for brown bears in Norway between 2012 and 2021. Based on the OPSCR model, the Norwegian brown bear population was likely (95% credible interval) between 98 and 121 individuals in 2021. Each year, between 19 (95% credible interval: 7-31) and 46 (34-57) individuals detected in Norway were attributed to Sweden, Finland or Russia. We further report annual estimates of cause-specific mortality, recruitment and detection probability. In order to facilitate joint analysis and reliable estimation of the bear population across Norway and Sweden, we recommend that Swedish monitoring switches from the current patchy and staggered sampling approach to regular range-wide sampling as is currently done for other large carnivore species, i.e. wolves (*Canis lupus*) and wolverines (*Gulo gulo*).

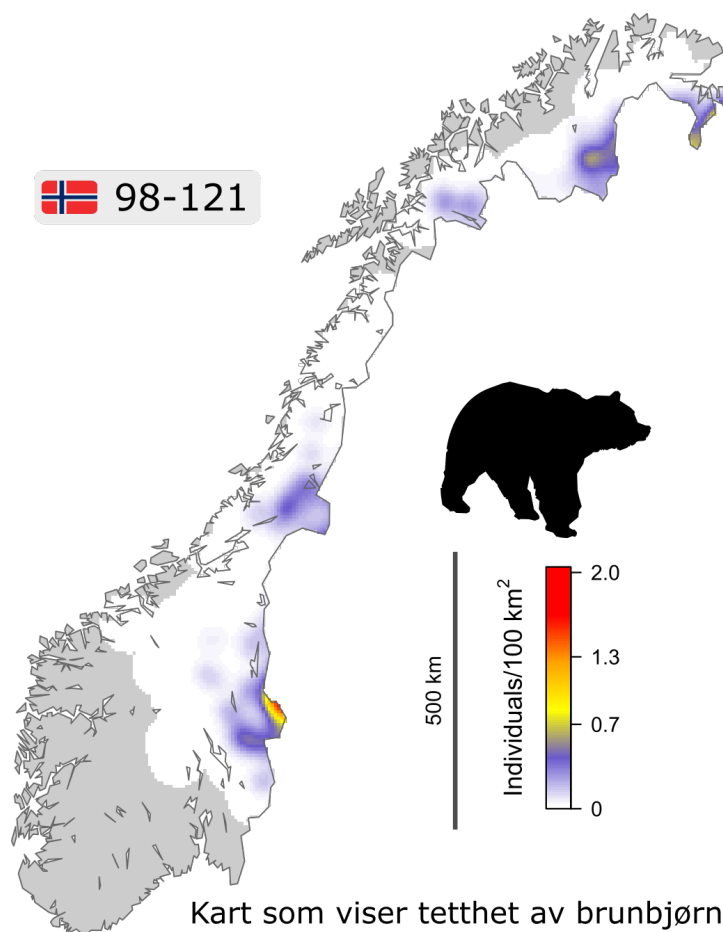


Sammendrag

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), estimerte vi årlige tettheter og demografiske rater hos den norske delen av den skandinaviske brunbjørnbestanden fra 2012 til 2021. Årlig landsdekkende overvåking av brunbjørn i Norge tillot oss å bruke OPSCR-modellen utviklet av RovQuant. NGS-basert overvåking av brunbjørn gjennomføres også i Sverige, men innledende felles analyse av norske- og svenske overvåkingsdata avdekket inkonsekvente resultater som gjør det nødvendig med videre undersøkelser. Resultater og diskusjon omkring analysene av det svenske overvåkingsmaterialet fra 2012 til 2021 vil bli gitt i en egen rapport.

Resultater Vi laget årlige kart med tetthet av brunbjørn fra 2012 til 2021, hvor bestandsstørrelsen både totalt og innenfor ulike administrative enheter kunne avledes. Basert på OPSCR modellen var den norske bestanden av brunbjørn mellom 98 og 121 individer i 2021 (95% kredibelt intervall). Årlig ble mellom 19 (95% kredibelt intervall: 7-31) og 46 (34-57) av individene påvist i Norge tilskrevet Sverige, Finland eller Russland. I tillegg til årlige tettheter og områdespesifikke bestandsestimater, gir rapporten estimater på årsaksspesifikke dødlighetsfaktorer, rekruttering og oppdagbarhet. For å legge til rette for en felles analyse og pålitelig estimering av brunbjørn bestanden på tvers av Norge og Sverige, så anbefaler vi at den svenske overvåkingen bytter fra dagens prøveinnsamling som er flekkvis og forskjøvet til en som er landsdekkende og jevnlig, slik som det i dag gjøres for ulv og jerv.



Kart som viser tetthet av brunbjørn med intervaller for estimert antall brunbjørn i 2021

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1 Introduction

Non-invasive genetic sampling (NGS) and dead recoveries are a centerpiece of national and regional large carnivore monitoring in Norway and Sweden. In the last decade, 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. 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 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 remain 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., 2019a, 2020b).

Rovquant first reported results based on the Rovbase data and OPSCR models for wolves in March 2019 (Bischof et al., 2019a), jointly for all three carnivore species in December 2019 (Bischof et al., 2019b, 2020b), and for wolves (Milleret et al., 2021, 2022d) and wolverines in 2021, 2022, and 2023 (Flagstad et al., 2021; Milleret et al., 2022b,c). In this report, we present an updated analysis of the Norwegian portion of the Scandinavian brown bear population, adding NGS and dead-recovery data from 2019, 2020, and 2021, for a total of ten consecutive monitoring seasons (2012 - 2021). Specifically, we provide:

- 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’s aim is to provide comprehensive analyses of large carnivore populations throughout their entire range in Norway and Sweden, we chose to analyze Norwegian and Swedish monitoring data separately this year. Preliminary analyses revealed inconsistent results across model permutations when the data were analyzed jointly for Norway and Sweden or for Sweden alone. This may be attributed to the patchy and staggered approach to monitoring in Sweden: 4 main regions monitored non-synchronously every 5 years. In addition, the reliability of the outcome of the genetic analysis of the Swedish samples has recently been drawn into question (Kindberg and Brøseth, 2021). Until the cause of inconsistencies associated with the analysis of the Swedish bear monitoring data have been identified and addressed, we believe it is prudent to conduct separate national estimation.

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.

MCMC: Markov chain Monte Carlo.

NGS: Non-invasive genetic sampling.

OPSCR: Open-population spatial. capture-recapture

p_0 : Baseline detection probability; probability of detecting an individual at a given detector, if the individual’s AC is located exactly at the detector location.

σ : Scale parameter of the detection function; related to the size of the circular home-range.

SCR: Spatial capture-recapture.

SNO: Statens naturoppsyn (Norwegian Nature Inspectorate) is the operative field branch of the Norwegian Environment Directorate (Miljødirektoratet).

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: 2022-06-15). 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 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 a marker 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).

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 reasons (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). Because bears detected in Norway can be recovered dead in Sweden, we incorporated all bears recovered dead within 50 km from the Norwegian border in the analysis.

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: 2022-06-09). Skandobs is a web application that allows anyone to register observations (e.g. visual, tracks, faeces, etc.) of bears, lynx (*Lynx lynx*), wolves, and wolverines in Scandinavia. This data currently consists of more than 20 000 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 2021 using a Bayesian open-population spatial capture-recapture (OPSCR) model (Bischof et al., 2019b, 2020b; Milleret et al., 2022b; Flagstad et al., 2021). OPSCR models allow 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, 2012).
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 2012-2021 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 2012-2021 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.

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 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). 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).

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

Model fitting We fitted sex-specific Bayesian OPSCR models using Markov chain Monte Carlo (MCMC) simulation with NIMBLE version 0.12.2 (Turek et al., 2021; de Valpine et al., 2017;

NIMBLE Development Team, 2019) and nimbleSCR (Bischof et al., 2021) in R version 4.1.0 (R Core Team, 2022). We ran 4 chains of 50 000 iterations each, 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 from which abundance estimates were derived. We considered models as converged when the Gelman-Rubin diagnostics (Rhat, Gelman and Rubin, 1992) was ≤ 1.1 for all parameters and by visually inspecting the trace plots.

Abundance estimates and density maps Here we report abundance based on AC locations (3.2). 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", 3.2); 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 limits 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 (3.2), 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 average proportion of individuals detected and the associated uncertainty were obtained by dividing the number of individuals detected through NGS sampling (Table A.1) by the abundance estimates and their associated credible intervals, respectively.

We derived the proportion of females in the population and the associated uncertainty by dividing the posterior distribution representing the number of females by the combined abundance estimate for males and females (Table A.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., 2022b).

3 Results

3.1 Non-invasive genetic samples and dead recoveries

A total of 5 518 (2 143 female; 3 375 male) genotyped bear genetic samples collected in Norway were included in the analysis. These samples were associated with 572 (201 female; 371 male) individuals. We also used 165 dead recoveries of bears in the OPSCR model, of which 154 (41 female; 113 male) were due to legal culling and 11 (5 female; 6 male) due to other causes of mortality. Annual tallies of NGS samples and associated individuals, as well as dead recoveries included in the analysis are provided in the Appendices (NGS samples and individuals: Table A.1, dead recoveries: Table A.2)

3.2 Density and abundance

The bear abundance for the entire study area in Norway (180 630 km², excluding the buffer area) was estimated (95% credible interval) between 98 and 121 individuals in 2021 based on the estimated locations of individual activity centers (Table 1). Estimates refer to the status of the population at the start of the annual sampling period (Apr. 1). The Norwegian bear population was estimated to be overall relatively stable with yearly population growth rates λ_{t} varying between 0.70-0.96 (95% credible interval) in 2014 and 1.01-1.37 in 2016 Table A.5. The proportion of females in the Norwegian bear population increased over the years (Figure 1) and was likely between 41% and 52% in 2021. See Table A.3 for annual abundance estimates for all of Norway and by large carnivore region between 2012 and 2021. The analysis also yielded annual density maps, which reveal changes in the distribution of bears over time (Figure 2, Figure A.5).

Table 1: Bear population size estimates in 2021 by sex and large carnivore management regions in Norway. 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 column "% Area". Readers should focus on the 95% credible interval provided in parentheses as these - unlike mean values - convey uncertainty inherent in abundance estimates. Numbers are based on estimated AC locations of 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)	0.2 (0-1)	0.2 (0-2)	7
Region 3	0.2 (0-1)	0.7 (0-3)	1 (0-3)	80
Region 4	0 (0-0)	0 (0-1)	0 (0-1)	23
Region 5	16.1 (12-20)	21.5 (17-27)	37.6 (32-44)	100
Region 6	9.9 (8-13)	13.7 (11-17)	23.6 (20-28)	82
Region 7	0 (0-0)	2.9 (2-5)	2.9 (2-6)	84
Region 8	24.4 (19-30)	19.5 (14-26)	43.9 (36-52)	69
TOTAL	50.7 (43-59)	58.6 (50-68)	109.3 (98-121)	56

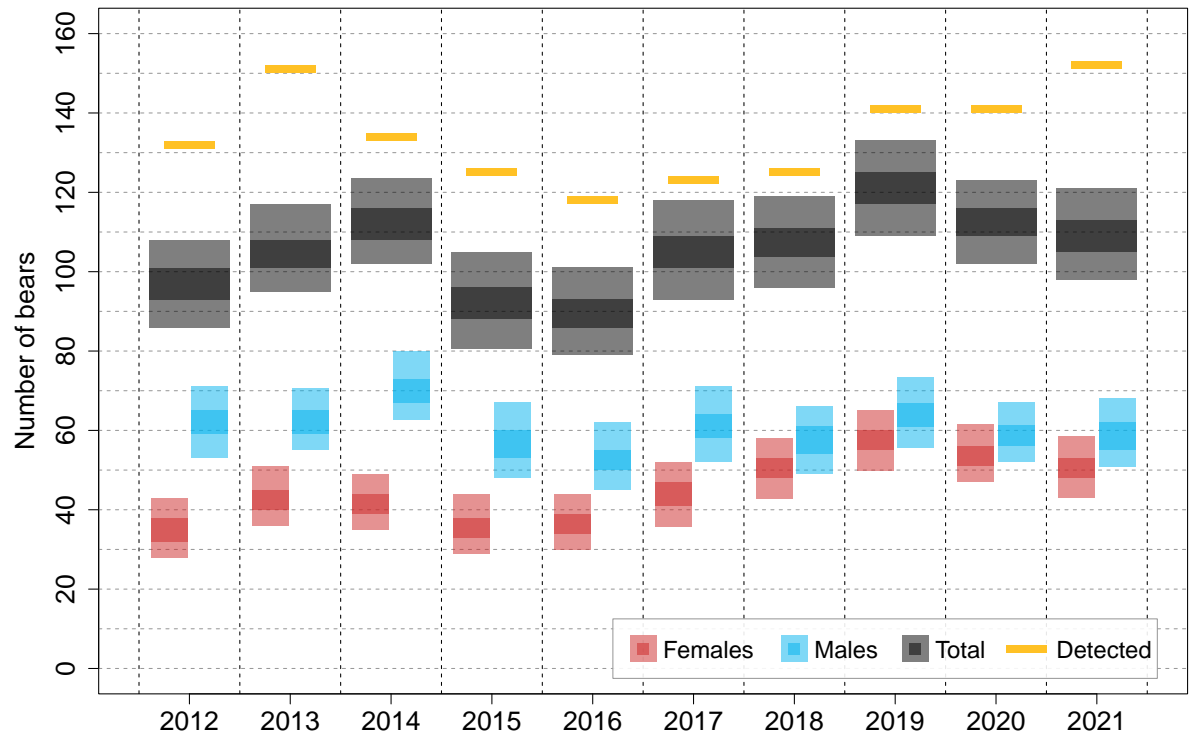


Figure 1: Total (black) and sex-specific (blue: males, red: females) annual bear population size estimates in Norway between 2012 and 2021 derived from the open-population spatial capture-recapture model. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Yellow bars show the number of individuals detected in Norway each year.

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 distribution 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 2021 based on individual activity center locations.

	Females	Males	Total
Region 2	0.1 (0-1)	0.2 (0-1)	0.2 (0-2)
Region 3	0.2 (0-1)	0.7 (0-3)	1 (0-3)
Region 4	0 (0-0)	0 (0-1)	0 (0-1)
Region 5	16.1 (12-20)	21.5 (17-27)	37.6 (32-44)
Region 6	9.9 (8-13)	13.7 (11-17)	23.6 (20-28)
Region 7	0 (0-0)	2.9 (2-5)	2.9 (2-6)
Region 8	24.4 (19-30)	19.5 (14-26)	43.9 (36-52)
TOTAL	50.7 (43-59)	58.6 (50-68)	109.3 (98-121)

Table 3: Brown bear population size estimates by sex in Norway in 2021 based on individual space use distributions.

	Females	Males	Total
Region 2	0.1 (0-1)	0.2 (0-1)	0.3 (0-1)
Region 3	0.4 (0-1)	1.1 (0-3)	1.4 (0-3)
Region 4	0 (0-0)	0.1 (0-1)	0.1 (0-1)
Region 5	17.6 (15-20)	23.5 (21-27)	41.2 (38-45)
Region 6	10.6 (9-13)	14.1 (12-17)	24.7 (22-28)
Region 7	0.1 (0-0)	3 (2-5)	3.1 (2-6)
Region 8	25.4 (22-29)	20.6 (17-25)	46 (41-52)
TOTAL	54.2 (48-60)	62.6 (57-70)	116.8 (108-126)

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 are overall higher than estimates based on activity center locations.

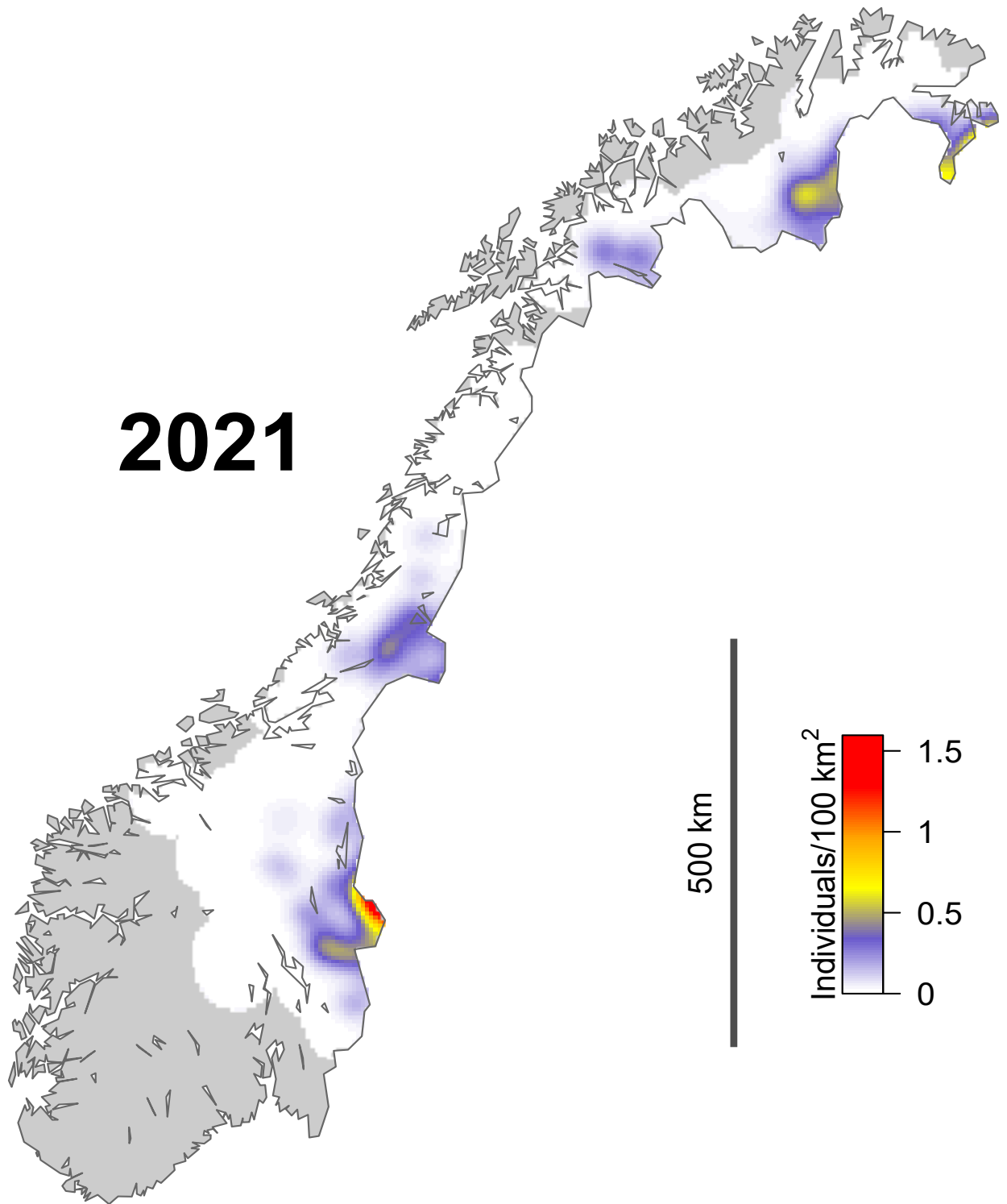


Figure 2: Brown bear density based on individual space use distributions throughout the study area (white background) in Norway in 2021. Density was estimated with an open-population spatial-capture recapture model fitted to NGS and dead recovery data collected between 2012 and 2021. See Methods section 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 3), as well as estimates of the average per capita recruitment rates over the 10-year period (Table A.4).

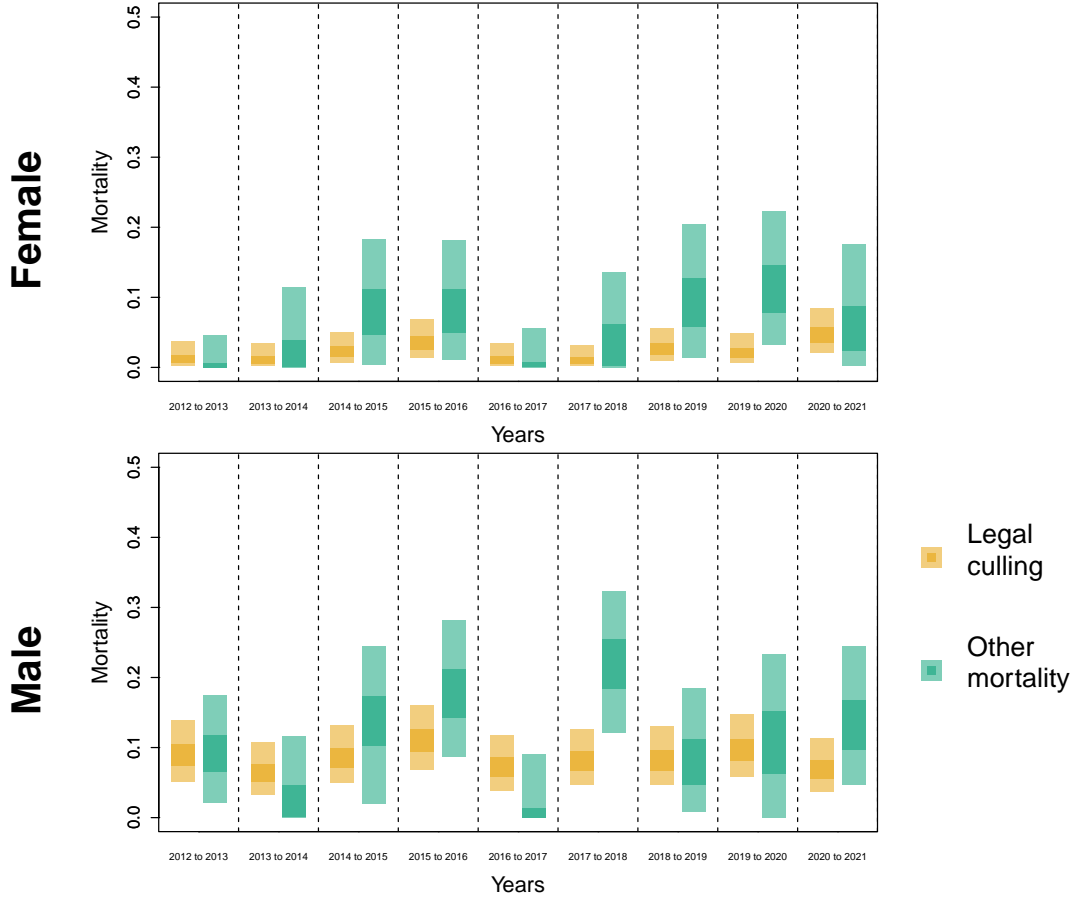


Figure 3: Mortality probabilities due to legal culling and all other causes for female and male brown bears. Shown are overall estimates throughout the study area in Norway, based on the sex-specific OPSCR models. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Estimates refer to deaths occurring between the start of one sampling season and the start of the next one. Consequently, estimates for mortality between 2021 and 2022 are not yet available for this analysis. Note that mortality due to other causes is the apparent mortality probability as it also incorporates emigration of bears outside of the 50 km buffer considered in the open-population spatial capture-recapture 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 Sweden. The average proportion of individuals detected is therefore over 100% and was likely between 126% to 155% in 2021 (Table A.7). In other words, the model estimated that between 31 and 54 individuals detected through NGS in Norway in 2021 had their activity center located in either Sweden, Finland or Russia, which corresponds to between 20% and 36% of the individuals detected in Norway that year

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

Box 3: Inconsistencies with previous estimates

Population size estimates in this report differ substantially from those previously published by RovQuant (Bischof et al., 2020b). The main reason for this lies in the exclusion of the Swedish bear data from the current analysis. A preliminary attempt to jointly analyse the latest Swedish and Norwegian bear NGS data produced unrealistic increases in population size. Further investigation revealed that estimates that made use of the Swedish bear monitoring data were strongly sensitive to the amount of data and to the type of model used (SCR or OPSCR or OPSCR with dead recoveries). The reasons for these inconsistencies are still to be determined. A potential reason is the spatio-temporal patchiness of sampling in Sweden, which required unrealistic assumptions (e.g., about spatially and temporally constant vital rates) and likely push the limits of OPSCR inferences in the presence of gaps in data collection (Milleret et al., 2020). Another important assumption of RovQuant models, like other capture-recapture models, is that individual identification is made without error. However, recently developed SCR models (Augustine et al., 2020) can incorporate partial identities and misidentification, which can cause substantial bias if not accounted for (Johansson et al., 2020).

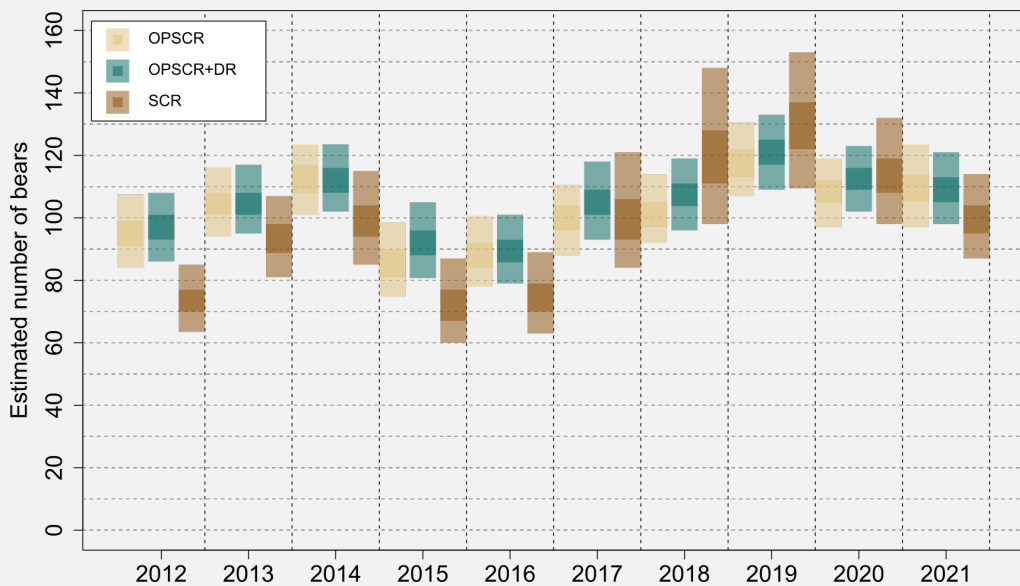


Figure 4: Bear population size estimates in Norway between 2012 and 2021 from different models. Presented are the results from single-season spatial capture-recapture models (SCR), open-population spatial capture-recapture models without dead recoveries (OPSCR) and open-population spatial capture-recapture models integrating dead recovery information (OPSCR + DR; this report). In the SCR models, survival and recruitment processes are not modelled. Data from each year is thus considered independently from that of other years. Darker and lighter bars show the 50% and 95% credible intervals, respectively.

A population-level (joint Norwegian-Swedish) treatment of monitoring data is desirable. However, due to inconsistencies in the results that incorporate the Swedish bear monitoring data, we focused this report on the brown bear NGS data collected in Norway only. Norway conducts searches for genetic samples each year throughout the bear range in the country, reducing the need for making severe assumption to fill monitoring holes in space and time. Furthermore, excluding Sweden from the analysis, reduces the potential for unaccounted variation in biological parameters (space use, vital rates, etc.). Estimates for Norway are also consistently lower when Swedish NGS data are ignored, and the precautionary principle in applied wildlife research favors conservative estimates. We note that SCR models are fully capable and were in fact developed to estimate density in geographically open populations and that we obtained consistent results from all analyses run only for Norway, regardless of model and data used (Figure 4). This was not the case once Swedish data were integrated in the analysis. Finally, female population size estimates from this analysis for the years 2012-2013 are consistent with estimates obtained during an earlier analysis that also excluded the Swedish data (Bischof et al. (2016); Table A.8)

4 Summary of changes made

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

1. Limited analysis to Norway.
2. Added data from the 2019, 2020, and 2021 monitoring seasons.
3. Only dead recoveries and live detections were used to reconstruct the state of individuals, age has been ignored to limit the risk of bias due to uncertain age.
4. Constrained per-capita recruitment to be constant among years.
5. Allowed for annual variation in both causes of mortality.
6. Used carnivore observation reports in Skandobs and ancillary carnivore samples recorded in Rovbase to generate new covariates that served as a proxy for sampling effort (spatially and temporally varying).
7. Used brown bear observation reports in Skandobs to generate a new covariate that serves as a proxy for bear density.

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 NGS data collected in Sweden to determine the reasons behind the observed differences in population size estimates when analyzing the Norwegian data jointly with the Swedish data compared with analyses that only use data from 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).
6. Account for spatial variation in survival (Milleret et al., 2022a).

6 Concluding remarks

The differences in the monitoring of the brown bear population between Sweden and Norway, and specifically the patchy and staggered nature of the monitoring in Sweden, makes it difficult to obtain reliable estimates at the population level. To facilitate a joint estimation and ultimately management of the brown bear in Scandinavia, we suggest the following:

1. Consider distributing the current effort over the entire Swedish range to obtain full spatial coverage of NGS in all regions for which estimates are desired each year.
2. Report information about how collected samples are selected/prioritized for DNA analysis.
3. Attempt to quantify and report spatio-temporal search effort. At a minimum, identify and delineate areas excluded from sampling and indicate the reason for exclusion (e.g., unable to search the area or low priority due to assumed lack of presence of the target species).
4. Explore the feasibility of using station-based detectors (e.g., rub trees, hair snares) for better control over and interpretation of the observation process.

7 Acknowledgements

This work was made possible by the large carnivore monitoring programs and the extensive monitoring data collected by Norwegian (SNO) and Swedish (Länstyrelsen) wildlife management authorities, as well as the public. Our analyses relied on genetic analyses conducted by the laboratory personnel at the DNA laboratories at NIBIO Svanhovd, the Swedish Museum of Natural History (NRM)s, and the Norwegian Institute for Nature Research. We also thank Swedish and Norwegian wildlife managers for feedback provided during project RovQuant and the Research Council of Norway for partial funding (NFR 286886; project WildMap). The computations/simulations were performed on resources provided by NMBU’s computing cluster “Orion”, administered by the Centre for Integrative Genetics and by UNINETT Sigma2 - the National Infrastructure for High Performance Computing and Data Storage in Norway. We are grateful to the NIMBLE team (P. de Valpine and D. Turek) for help with the formulation of the OPSCR model. J. Vermaat provided helpful comments on drafts of this report.

8 Data availability

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

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Appendices

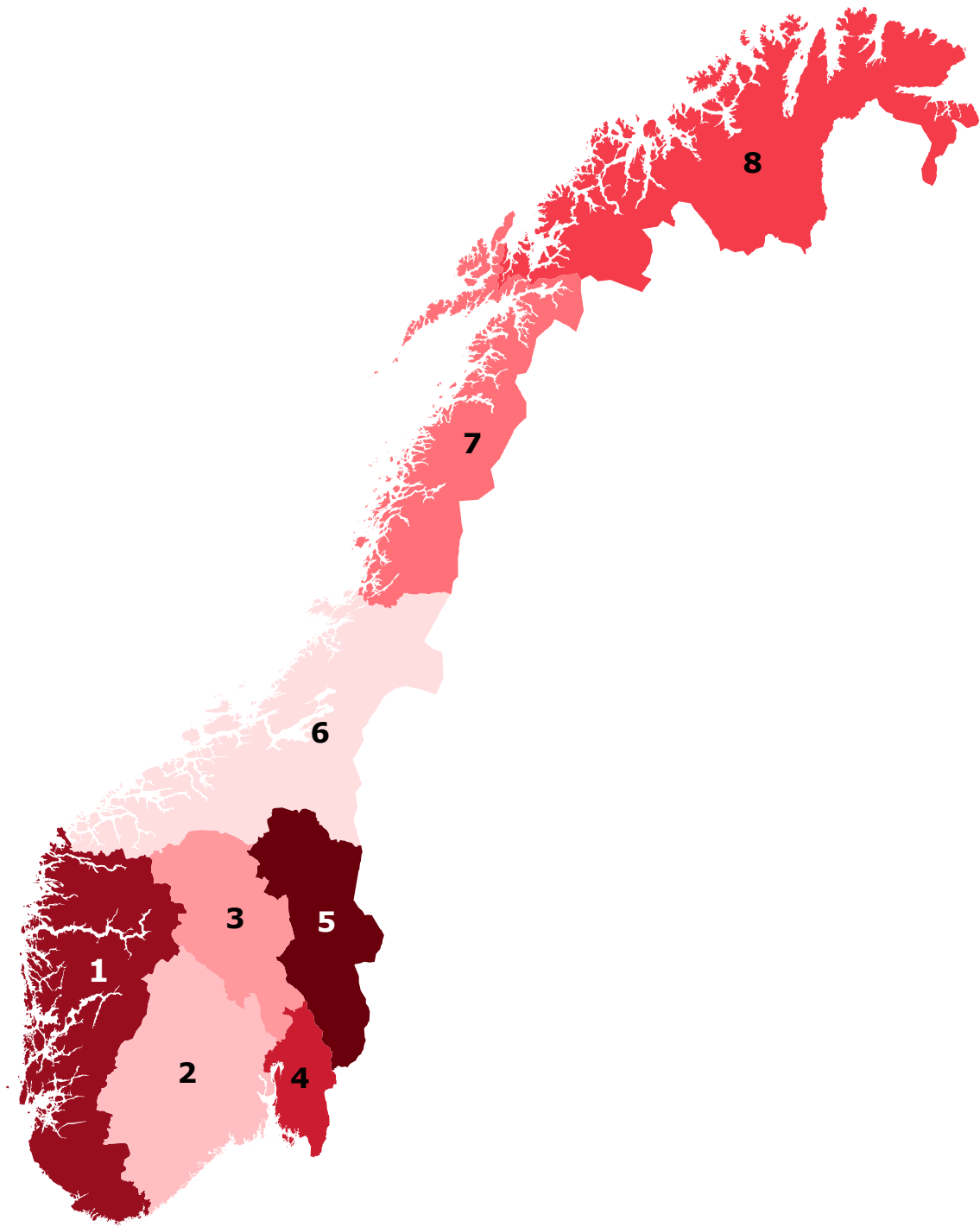


Figure A.1: Management units in Norway (carnivore management regions).

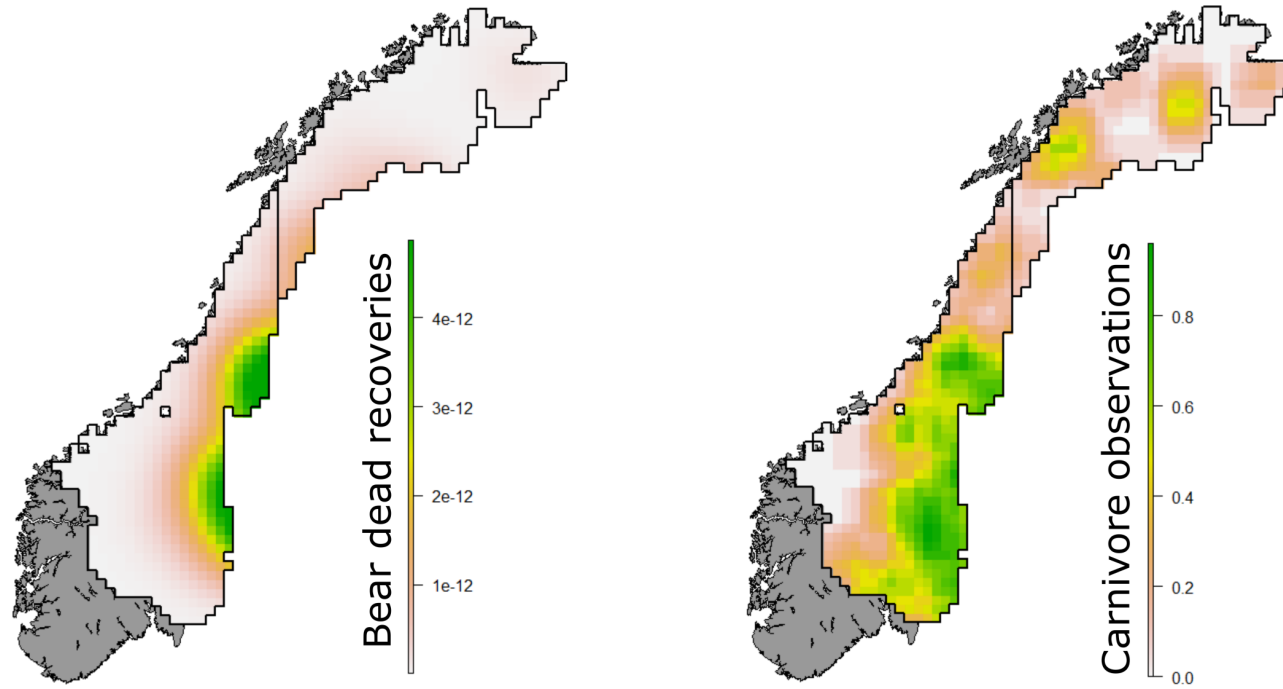


Figure A.2: Spatial covariates denoting the scaled density of dead recoveries (left) and carnivore observations (right) per 400km^2 in Norway as used in the density and movement sub-models of the open-population spatial capture-recapture model.

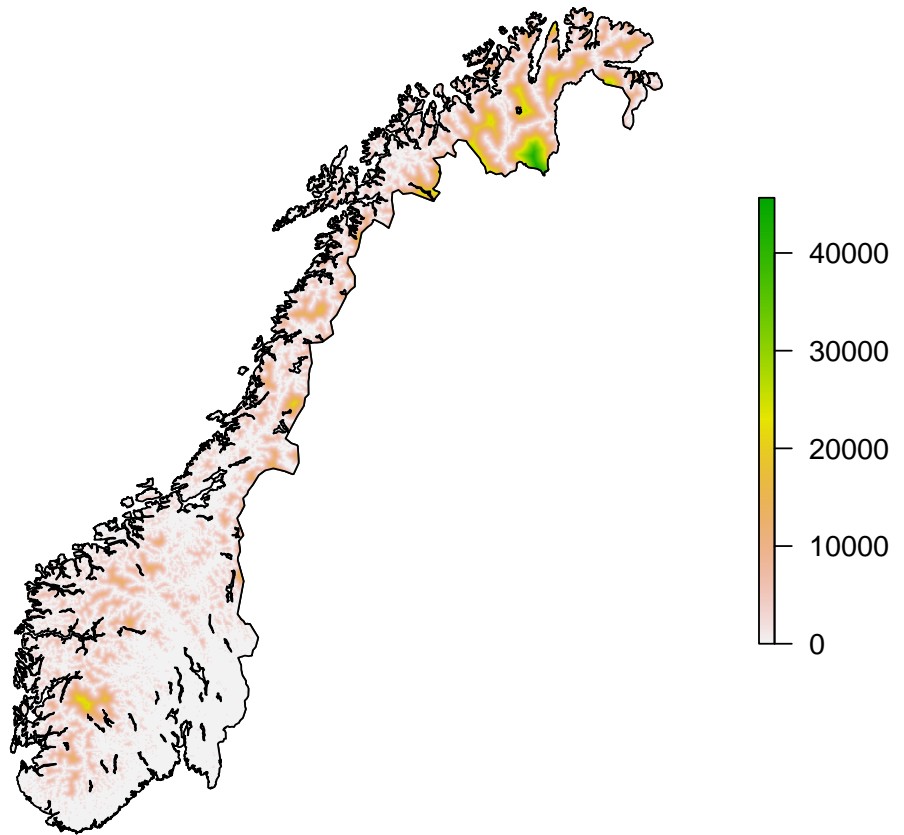


Figure A.3: Spatial covariate denoting the distance to roads (in meters) in Norway as used in the detection sub-model of the open-population spatial capture-recapture model.

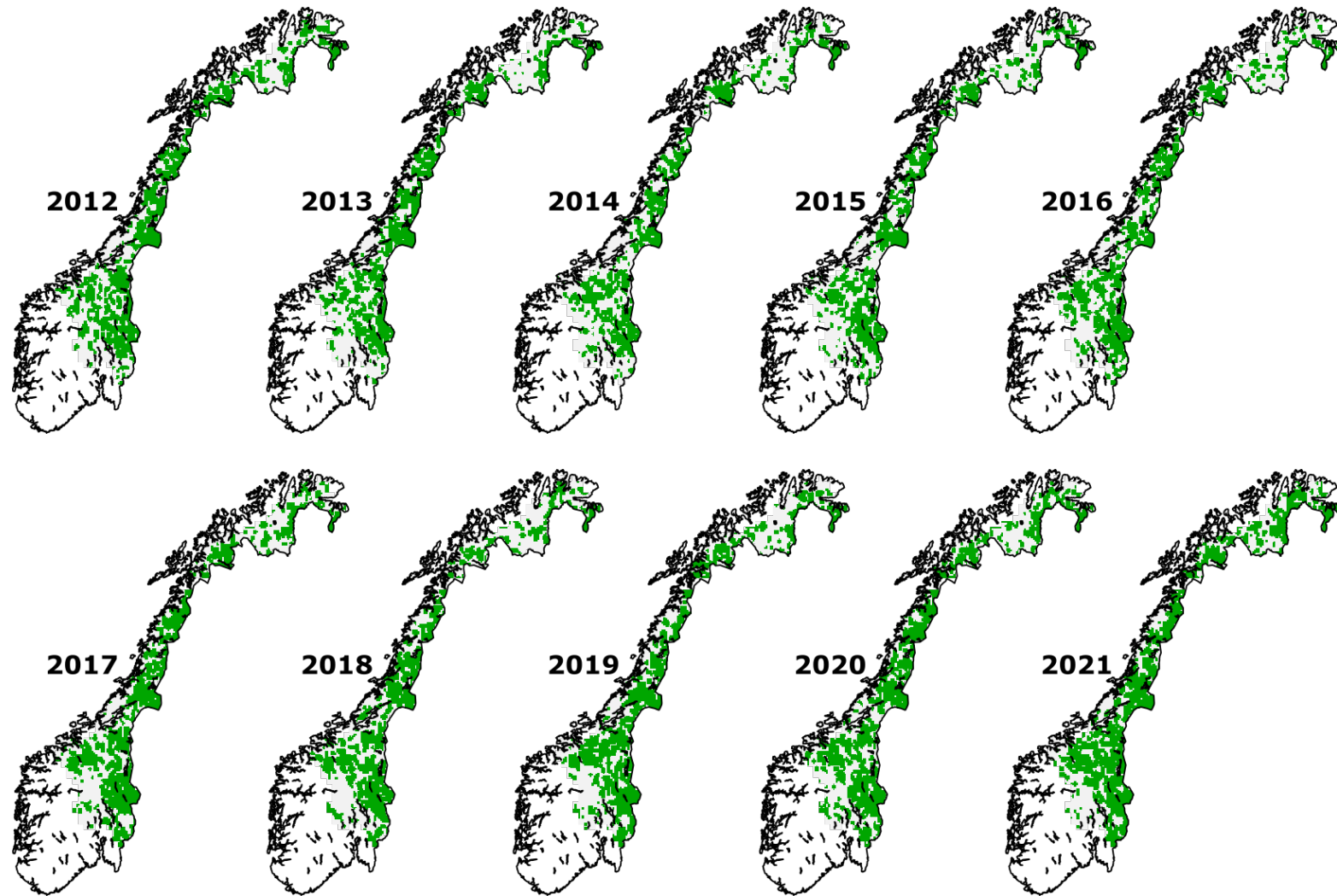


Figure A.4: Spatial covariate denoting the presence (green cells) of carnivore observations between 2012 and 2021 per 5 km detector grid cell, as used in the detection sub-model of the open-population spatial capture-recapture model.

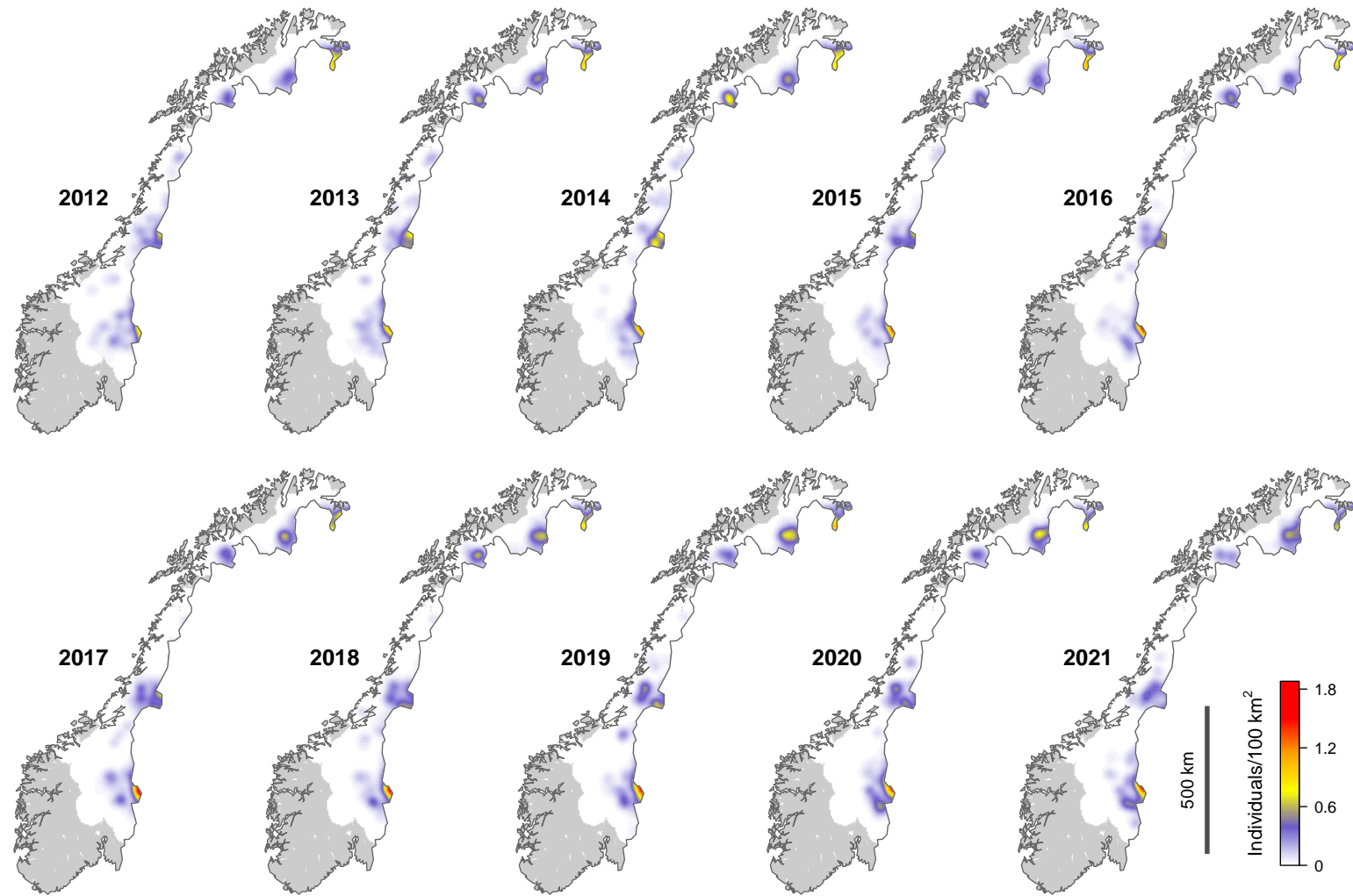


Figure A.5: Annual brown bear density based on individual space-use throughout Norway between 2012 and 2021. Density was estimated using the open-population spatial capture-recapture model.

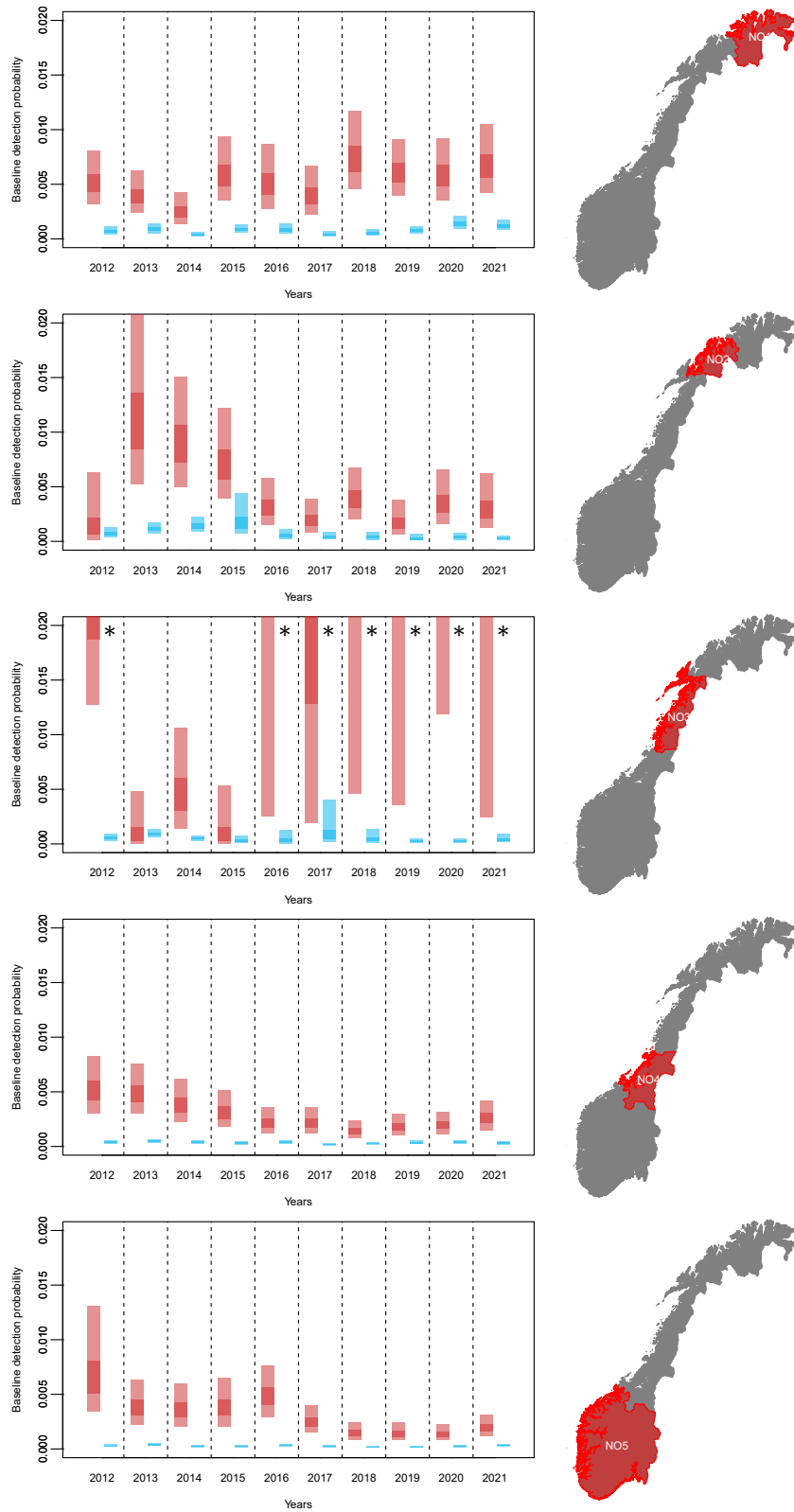


Figure A.6: Sex-specific baseline detection probability (p_0) estimated by the open-population spatial capture recapture models (females in red and males in blue). Results are separated into panels based on regions. Estimates are shown for the mean values of the detection covariates. Darker and lighter bars show the 50% and 95% credible intervals, respectively. Stars in the middle plot indicate years with very low number of female detections in the region and consequently high uncertainty in estimates of baseline detection probabilities. 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). We included only samples collected within the study area during the primary monitoring period (Apr 1 - Nov 30) between 2012 and 2021.

	2012		2013		2014		2015		2016		2017		2018		2019		2020		2021	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
number of NGS samples	230	336	216	420	163	301	246	334	198	265	180	279	185	206	244	348	216	423	265	463
number of NGS individuals	52	81	56	95	53	81	55	71	48	70	57	73	58	68	58	86	62	79	64	88

Table A.2: Number of cause-specific dead recoveries of bears included in the OPSCR analysis between 2012 and 2021. 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 (2021) were not used in this analysis because survival is modeled as part of the transition from one season to the next.

	Country	2012		2013		2014		2015		2016		2017		2018		2019		2020		2021	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	0	0	0	0	0	0	1	0	0	0	0	0	1	1	2	0	1	3	0	0
	Sweden	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Legal culling	Norway	0	11	0	4	1	9	1	6	0	7	0	7	2	4	2	8	1	4	1	9
	Sweden	1	1	5	4	3	2	4	6	2	2	5	9	4	3	2	6	7	5	0	6
TOTAL	Total	1	12	5	8	4	11	6	12	2	9	5	18	7	8	6	14	9	12	1	15

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.

	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Region 2	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0 (0-1)	0.1 (0-1)	0.1 (0-1)	0.2 (0-2)
Region 3	5.5 (4-8)	2.8 (1-5)	1.4 (0-4)	2.3 (0-5)	3.3 (1-6)	1.7 (0-4)	1 (0-3)	1.7 (0-4)	0.9 (0-3)	1 (0-3)
Region 4	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0 (0-1)	0 (0-1)	0.1 (0-1)	0.1 (0-1)	0 (0-1)	0 (0-1)
Region 5	22 (18-27)	24.9 (21-29)	27.4 (22-33)	23 (17-29)	23.4 (18-29)	31.4 (25-39)	28.3 (23-34)	33.3 (26-40)	39 (33-45)	37.6 (32-44)
Region 6	25.6 (21-31)	27.1 (22-31)	25.3 (20-31)	21.8 (17-27)	24.9 (20-30)	30.2 (25-36)	31.1 (26-37)	29.5 (26-34)	26.8 (23-31)	23.6 (20-28)
Region 7	6.1 (4-9)	7.6 (6-10)	9.3 (7-12)	5 (2-8)	2.3 (1-5)	1.1 (0-3)	2 (0-4)	4.3 (3-6)	3.5 (3-5)	2.9 (2-6)
Region 8	37.2 (29-46)	41.8 (34-51)	48.5 (40-57)	40 (32-48)	35.1 (27-43)	40.4 (32-50)	45 (37-53)	52.1 (44-61)	42.1 (35-50)	43.9 (36-52)
TOTAL	96.9 (86-108)	104.5 (94-117)	112.2 (102-124)	92.3 (80-105)	89.2 (78-101)	105 (93-118)	107.5 (95-119)	121.1 (109-133)	112.3 (101-123)	109.3 (98-121)

Table A.4: Estimates of the demographic parameters obtained from the bear OPSCR model and data collected in Norway between 2012-2021. 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).

	2012 to 2013		2013 to 2014		2014 to 2015		2015 to 2016		2016 to 2017	
	F	M	F	M	F	M	F	M	F	M
ρ	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)
ϕ	0.98 (0.94-1.00)	0.82 (0.73-0.90)	0.98 (0.87-1.00)	0.92 (0.81-0.96)	0.90 (0.79-0.98)	0.78 (0.67-0.89)	0.88 (0.78-0.96)	0.71 (0.61-0.81)	0.99 (0.93-1.00)	0.92 (0.83-0.96)
h	0.01 (0.00-0.04)	0.09 (0.05-0.14)	0.01 (0.00-0.03)	0.06 (0.03-0.11)	0.02 (0.01-0.05)	0.08 (0.05-0.13)	0.03 (0.01-0.07)	0.11 (0.07-0.16)	0.01 (0.00-0.03)	0.07 (0.04-0.12)
w	0.00 (0.00-0.05)	0.09 (0.02-0.17)	0.01 (0.00-0.11)	0.01 (0.00-0.12)	0.08 (0.00-0.18)	0.14 (0.02-0.24)	0.08 (0.01-0.18)	0.18 (0.08-0.28)	0.00 (0.00-0.06)	0.00 (0.00-0.09)
	2017 to 2018		2018 to 2019		2019 to 2020		2020 to 2021			
	F	M	F	M	F	M	F	M	F	M
ρ	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)	0.09 (0.07-0.12)	0.20 (0.17-0.23)
ϕ	0.96 (0.85-1.00)	0.70 (0.59-0.80)	0.88 (0.77-0.96)	0.84 (0.73-0.92)	0.87 (0.75-0.95)	0.79 (0.67-0.91)	0.90 (0.78-0.96)	0.80 (0.68-0.89)		
h	0.01 (0.00-0.03)	0.08 (0.05-0.13)	0.03 (0.01-0.06)	0.08 (0.05-0.13)	0.02 (0.01-0.05)	0.10 (0.06-0.15)	0.04 (0.02-0.08)	0.07 (0.04-0.11)		
w	0.03 (0.00-0.14)	0.22 (0.12-0.32)	0.09 (0.01-0.21)	0.08 (0.01-0.18)	0.11 (0.03-0.22)	0.11 (0.00-0.23)	0.05 (0.00-0.18)	0.13 (0.05-0.24)		

Table A.5: 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.

	2012 to 2013	2013 to 2014	2014 to 2015	2015 to 2016	2016 to 2017	2017 to 2018	2018 to 2019	2019 to 2020	2020 to 2021
λ	1.08 (0.94-1.25)	1.08 (0.94-1.22)	0.82 (0.70-0.96)	0.97 (0.83-1.13)	1.18 (1.01-1.37)	1.03 (0.88-1.19)	1.13 (0.99-1.29)	0.93 (0.82-1.05)	0.97 (0.85-1.10)

Table A.6: 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_{dead} corresponds to the effect of the locations of all bears recovered dead throughout the 2012-2021 period and β_{obs} corresponds to the effect of the presence of bear observations registered in SkandObs on AC locations (Bischof et al., 2020b). β_{roads} corresponds to the effect of the average distance to the nearest road and β_{obs2} corresponds to the effect of the presence of any other 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	M	F
	τ	35.14 (33.21-37.15)	9.72 (8.72-10.65)
Density process	β_{dead}	0.34 (0.29-0.40)	0.39 (0.26-0.49)
	β_{obs}	0.22 (0.12-0.32)	0.11 (-0.03-0.25)
	σ	12.78 (12.40-13.18)	7.86 (7.56-8.19)
Detection process	β_{roads}	-0.79 (-0.89-(-)0.70)	-0.81 (-0.93-(-)0.70)
	β_{obs2}	2.34 (2.08-2.61)	0.93 (0.59-1.27)

Table A.7: Average proportion of individuals detected via non-invasive genetic sampling (NGS) in Scandinavia. Values were calculated as the number of individuals detected with NGS (Table A.1) divided by the total and sex-specific abundance estimates obtained from the OPSCR models (Table A.3). Credible intervals (95%) are shown in parentheses.

	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
F	1.51 (1.21-1.86)	1.33 (1.10-1.56)	1.27 (1.08-1.51)	1.53 (1.23-1.86)	1.33 (1.09-1.60)	1.27 (1.06-1.57)	1.14 (0.98-1.36)	1.00 (0.88-1.16)	1.17 (1.01-1.33)	1.27 (1.09-1.49)
M	1.30 (1.13-1.51)	1.54 (1.35-1.74)	1.16 (1.01-1.31)	1.26 (1.06-1.48)	1.34 (1.13-1.57)	1.12 (0.96-1.31)	1.20 (1.03-1.39)	1.32 (1.14-1.53)	1.35 (1.18-1.52)	1.51 (1.29-1.76)
Total	1.37 (1.22-1.53)	1.45 (1.29-1.60)	1.20 (1.08-1.31)	1.36 (1.19-1.56)	1.33 (1.17-1.50)	1.18 (1.04-1.32)	1.17 (1.05-1.31)	1.17 (1.06-1.29)	1.26 (1.15-1.39)	1.39 (1.26-1.55)

Table A.8: Comparison of brown bear population size estimates in Norway with previously published studies. Credible intervals (95%) are shown in parentheses.

Model	2012			2013			2014			2015		
	F	M	Total	F	M	Total	F	M	Total	F	M	Total
Bischof et al. 2016	34 (25-45)			35 (25-47)								
Bischof et al. 2020	44.3 (36-53)	79.4 (69-91)	123.7 (110-138)	49.3 (42-57)	69.3 (63-77)	118.6 (109-129)	54 (45-64)	76.2 (67-86)	130.3 (117-144)	59.4 (49-71)	75.1 (62-88)	134.6 (118-152)
this report	34.9 (28-43)	61.9 (53-71)	96.9 (86-108)	42.4 (36-51)	62.1 (54-71)	104.5 (94-117)	41.9 (35-49)	70.3 (62-80)	112.2 (102-124)	35.6 (29-44)	56.6 (48-67)	92.3 (80-105)
	2016			2017			2018					
Model	F	M	Total	F	M	Total	F	M	Total	F	M	Total
Bischof et al. 2016												
Bischof et al. 2020	55.1 (46-65)	65 (55-77)	120.1 (107-135)	65.1 (53-78)	74.9 (63-89)	140 (123-159)	69 (57-82)	73.1 (60-88)	142.1 (124-162)			
this report	36.5 (30-44)	52.7 (44-62)	89.2 (78-101)	43.8 (35-52)	61.2 (52-71)	105 (93-118)	50.3 (42-58)	57.2 (49-66)	107.5 (95-119)			