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RovQuant:

**Estimating density, abundance and
population dynamics of bears, wolverines
and wolves in Scandinavia**

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COVER PICTURE

Stylized ridgeline plots of densities of bears (left), wolverines (middle), and wolves (right) in Scandinavia. Source: RovQuant

NØKKELOORD

Ursus ursus, *Gulo gulo*, *Canis lupus*, rovdyrforvaltning, tetthet, deteksjonssannsynlighet, ikke-invaderende innsamling av genetisk materiale, åpen populasjon romlig fangst-gjenfangst, populasjonsdynamikk, bjørn, jerv, ulv

KEY WORDS

Ursus ursus, *Gulo gulo*, *Canis lupus*, carnivore management, population density, detection probability, non-invasive genetic sampling, open-population spatial capture-recapture, population dynamics, brown bear, wolverine, wolf

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Summary

Background Reliable estimates of population status are a pre-requisite for informed wildlife management. However, abundance estimates can be challenging to obtain, especially for species that are highly mobile, rare and elusive. For nearly two decades, management agencies in Norway and Sweden have been monitoring populations of three large carnivores – brown bear (*Ursus ursus*), wolf (*Canis lupus*), and wolverine (*Gulo gulo*) – using non-invasive genetic sampling (NGS). DNA extracted from faeces, urine, and hair can be used to identify the species, sex, and individual from which each sample originated. Samples thus become evidence of the presence of an individual carnivore in space and time. Project RovQuant was initiated in 2017 with the objective to develop statistical methods that allow a comprehensive assessment of population status and dynamics using NGS data and other sources of information collected by the national monitoring programs in Sweden and Norway.

Approach We developed a Bayesian open-population spatial capture-recapture (OPSCR) model that, using a combination of NGS and recoveries of dead carnivores, jointly estimates 1) the spatial variability in the probability of genetic detection, 2) the spatial distribution and inter-annual movements of individuals and 3) population size and dynamics. We fitted this model to the extensive individual-based monitoring data for bears, wolverines, and wolves, which had been compiled in the Scandinavian large carnivore database Rovbase 3.0 between 2012 and 2019.

Results The OPSCR model yielded annual density maps both total and jurisdiction-specific population sizes for each species. The estimated number of bears for April 1, 2018 was 2757 (95% credible interval, CrI: 2636 - 2877), of which 2615 (CrI: 2499-2732) were located in Sweden and 142 (CrI: 124-162) in Norway. The estimated number of wolverines for December 1, 2018 was 1035 (CrI: 985 - 1088), of which 660 (CrI: 619-703) were located in Sweden and 375 (CrI: 353-397) in Norway. The estimated number of wolves for October 1, 2018 was 375 wolves (CrI: 352 - 402), of which 297 (CrI: 274-322) were located in Sweden and 79 (CrI: 72-86) in Norway. In addition to density and abundance estimates, the OPSCR models also yielded estimates of survival, recruitment, and space use parameters for each species. Six additional tasks linked to the development of OPSCR model were implemented as either prerequisite technical developments or to address persistent challenges in monitoring and management of large carnivores in Scandinavia. Although this report focuses on the main results from the OPSCR model, findings related to these additional tasks are briefly described as well.

Conclusions The unique Scandinavian data set combined with a novel OPSCR model allowed RovQuant to quantify the population status of three large carnivore species at an unprecedented spatial scale (up to 593 000 km²). The approach used here has several advantages over proxy-based approaches for obtaining estimates of population size. The OPSCR model directly estimates annual abundance from NGS and dead recovery data while accounting for spatial and temporal variation in detection probability of individuals. The resulting estimates are spatially explicit, allowing extraction of abundance estimates and associated measures of uncertainty for any spatial extent desired by the user (e.g. management unit). Annual cause-specific mortality and recruitment are also estimated, which are both useful metrics of the population's status and trajectory. Importantly, this approach efficiently exploits the data (NGS and dead recoveries) currently collected annually by Swedish and Norwegian management authorities at the population level.

Although the OPSCR model has been extensively tested, it constitutes a novel approach and is still under development. The ability of the model to produce trustworthy estimates relies on several statistical assumptions and on the suitability of the input data. For example, although the model was able to produce annual density maps and abundance estimates for bears throughout Scandinavia, the current patchy sampling for this species in Sweden means that confidence in the reliability of the results for bear is substantially lower than for the other

two species. We discuss the strengths and limitations of our approach and suggest areas for further study and development in order to increase the reliability of the OPSCR model and the cost-efficiency of large carnivore monitoring in Scandinavia.

Sammendrag

Bakgrunn Gode estimater på populasjonsstatus er en forutsetning for en kunnskapsbasert viltforvaltning. Til tross for det, kan estimater på antall dyr være utfordrende å skaffe til veie, spesielt for arter som beveger seg over store avstander, er fåtallige og vanskelig å påvise. I nesten to tiår har forvaltningsmyndighetene i Norge og Sverige overvåket bestandene av tre store rovdyr arter – brun bjørn (*Ursus ursus*), ulv (*Canis lupus*) og jerv (*Gulo gulo*) – ved bruk av ikke-invasiv genetisk prøveinnsamling (NGS). DNA fra skit, urin og hår kan brukes til å identifisere art, kjønn og individ fra hver enkelt prøve. Prøvene blir således et bevis på tilstedeværelsen av et rovdyrindivid i tid og rom. Prosjektet RovQvant ble igangsatt i 2017, med et formål om å utvikle statistiske metoder som gjør det mulig å foreta en omfattende vurdering av bestandsstatus og -dynamikk ved bruk av NGS-data og andre informasjonskilder innsamlet gjennom de nasjonale overvåkingsprogrammene på store rovdyr i Sverige og Norge.

Tilnærming Vi utviklet en Bayesiansk åpen romlig fangst-gjenfangst populasjons modell (OP-SCR) som benytter en kombinasjon av NGS-data og gjenfunn av døde rovdyr. Modellen estimerer 1) den romlige fordelingen av den genetiske oppdagbarhetssannsynligheten, 2) den romlige fordelingen og mellomårs bevegelsene til individene, og 3) bestandsstørrelsen og -dynamikken. Vi tilpasset modellen til de omfattende individbaserte overvåkingsdatasettene på bjørn, ulv og jerv, som har vært innsamlet og ivaretatt i den skandinaviske databasen for store rovdyr (Rovbase 3.0) mellom 2012 og 2019.

Resultater OPSCR-modellen gav årlige kart med tetthet for den enkelte art hvor bestandsstørrelsen både totalt og innenfor ulike administrative enheter kunne avledes. Det estimerte antallet bjørner 1. april 2018 var 2 758 (CrI: 2 636 - 2 877), hvorav 2 615 (CrI: 2 499-2 732) var i Sverige og 142 (CrI: 124-162) i Norge. Det estimerte antallet jerver 1. desember 2018 var 1 035 (CrI: 985 - 1 088), hvorav 660 (CrI: 619-703) var i Sverige og 375 (CrI: 353-397) i Norge. Det estimerte antallet ulver 1. oktober 2018 var 375 (CrI: 352 - 402), hvorav 297 (CrI: 274-322) var i Sverige og 79 (CrI: 72-86) i Norge. I tillegg til estimater på tetthet og antall gav OPSCR-modellen også estimater på årlig overlevelse, rekruttering og arealbruk parametere. Seks tilleggsoppgaver, knyttet til utviklingen av OPSCR-modellen, ble iverksatt enten som nødvendig teknisk utvikling eller for å adressere eksisterende utfordringer i overvåkingen og forvaltningen av store rovdyr i Skandinavia. Selv om denne rapporten fokuserer på hovedresultatene fra OPSCR-modellen er også funnene knyttet til disse tilleggsoppgavene kort beskrevet.

Konklusjoner Det unike skandinaviske datasettet, kombinert med en helt ny OPSCR-modell, har gjort RovQvant i stand til å kvantifisere populasjonsstatusen til tre arter av store rovdyr på en romlig skala som savner sidestykke (opp til 593 000 km²). Tilnærmingen som er brukt har flere fordeler når man skal fremskaffe estimater på bestandsstørrelse, fremfor indirekte tilnærminger. OPSCR-modellen estimerer antall dyr direkte fra NGS-data og gjenfunn av døde rovdyr, samtidig som den tar hensyn til individenes sannsynlighet for å påvises i tid og rom. Estimaten fra modellen er romlig relatert, muliggjør ekstraksjon av bestandsestimater og tilhørende usikkerhet for en hvilken som helst geografisk enhet som brukeren ønsker (f. eks. nasjonalt nivå eller en forvaltningsenhet). Årlig årsaksspesifikk dødelighet og rekruttering blir også estimert, begge nyttig informasjon om bestandsstatus og -utvikling. Denne tilnærmingen utnytter effektivt data (NGS og gjenfangst av døde rovdyr) som i dag samles inn årlig både i Sverige og Norge på populasjonsnivå.

Selv om OPSCR-modellen har blitt omfattende testet så utgjør den en helt ny tilnærming som fortsatt er under utvikling. Evnen som modellen har til å produsere sikre estimater avhenger av flere statistiske antagelser og egnetheten til de data som puttes inn i den. For eksempel, selv

om OPSCR-modellen var i stand til å produsere årlige tetthetskart og bestandsestimater for bjørn i hele Skandinavia, så gjør dagens flekkvise overvåkingsdesign for bjørn i Sverige at tilliten til sikkerheten i resultatene for bjørn er vesentlig lavere enn for de to andre artene. Vi diskuterer styrkene og svakhetene ved vår tilnærming, og foreslår områder for videre utforsking og utvikling for å øke sikkerheten til OPSCR-modellen og få en kostnadseffektiv overvåking av store rovdyr i Skandinavia.

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1 Introduction

Non-invasive genetic sample collection, in combination with dead recoveries, have become a centerpiece of national and regional large carnivore monitoring in Norway and Sweden. Over almost two decades, both countries have accumulated extensive individual-based data sets for brown bear (*Ursus arctos*), wolverine (*Gulo gulo*) and wolf (*Canis lupus*), and plan to continue periodic monitoring in the future. Whereas the multi-national large carnivore database (Rovbase 3.0) is extensive and continues to grow rapidly, analytical treatment and the extraction of information needed by management authorities in both countries have lagged behind.

The vast information contained in Rovbase 3.0 offers tremendous opportunities to answer a wide range of applied questions related to carnivore ecology and management. At this time, regional and national management authorities in Norway and Sweden are primarily interested in models for estimating 1) annual carnivore abundance across space, 2) population dynamics over time and 3) population dynamic consequences of alternative management actions.

In this report, we summarize the results from project RovQuant, which began in March 2017 with the aim to build an analytical framework for effective utilization of large carnivore monitoring data compiled in Rovbase 3.0, thereby informing management of bear, wolverine and wolf in Scandinavia. At the core of the project lie spatially-explicit analytical models that can integrate multiple sources of information. The usefulness of such models for treating Scandinavian carnivore monitoring data has already been demonstrated (Bischof et al., 2016), at the same time highlighting the need to consider space explicitly when studying wildlife populations that transcend national and regional administrative boundaries. Today, these hierarchical spatially-explicit models offer the most promising framework for turning the multitude of available data into information at spatial and temporal scales relevant to management.

The project was motivated partially by the need to fill information gaps that were identified by the scientific board of the large carnivore monitoring program in 2015 (rovdata.no), the Swedish-Norwegian carnivore working groups and at meetings with Swedish and Norwegian management authorities. At the forefront was the need for abundance estimates that take into account imperfect detection and which could be obtained for different administrative units (countries and management regions) as well as the entire population. Another important aspect concerned monitoring efficiency, primarily non-invasive genetic sampling design. The work done as part of RovQuant follows the intent of the international agreement signed in 2015 by Miljødirektoratet and Naturvårdsverket (“Memorandum of Understanding Regarding the Establishment and Continuance of a Monitoring System for Large Carnivores in Sweden and Norway”). Among other items, the MoU 1) recognizes the trans-boundary nature of large carnivores in Scandinavia, 2) outlines the need to use standardized monitoring methods and 3) highlights the intent to implement actions that benefit both parties with respect to monitoring population status and addressing research needs. Coordinated and targeted analysis of data collected as part of national large carnivore monitoring schemes in Scandinavia falls clearly within the scope of this MoU. Throughout the project period, care was taken to invite input from managers in both Norway and Sweden and to use this feedback to adjust project goals and guide project implementation.

RovQuant was organized into seven tasks, that are methodologically and conceptually connected. The most important of these was to build and test robust spatially-explicit models that can produce estimates of annual population sizes, densities and population dynamic parameters of large carnivores in Scandinavia using primarily non-invasive genetic sampling data (but integrating additional data sources). The bulk of this report is dedicated to the implementation and findings of this task. The six remaining tasks were linked with this main task, either to yield prerequisite technical developments or to expand the framework and its application to address persistent challenges in monitoring and analysis. We touch on these tasks only briefly (section 3) in this report, but they constitute important developments that should be pursued further.

Box 1: Definitions and acronyms

AC: Activity center. Equivalent to 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.

CR: Capture-recapture.

CrI: 95% credible interval associated with a posterior sample distribution.

Detectors: Potential detection locations in the SCR framework. These can refer to fixed locations (e.g. camera-trap locations) or to areas searched (e.g. habitat grid cells where searches for genetic samples were conducted) as used in this project.

Fylkesmannen: Norwegian state's representative in the county, responsible for following up decisions, goals and guidelines from the legislature and the government.

Habitat buffer: buffer surrounding the searched area that is considered suitable habitat but was not searched.

Legal culling: Lethal removal of individuals by legal means including licensed recreational hunting, management removals, defense of life and property.

Länsstyrelserna: Swedish County Administrative Boards, in charge of the monitoring of large carnivores at the county level.

MCMC: Markov Chain Monte Carlo.

NGS: Non-invasive genetic sampling.

OPSCR: Open-population spatial capture-recapture.

p0: 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, the Norwegian Nature Inspectorate is the operative field branch of the Norwegian Environment Directorate (Miljødirektoratet).

WildMap: Research grant from the research council of Norway (NFR), project number: 286886 (see forskningsradet.no and researchgate.net for more details.)

2 Estimation of carnivore density, abundance, and vital rates

2.1 Data

RovQuant 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 for wolverines and wolves: 2019-10-08; for bears: 2019-09-20). 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, dead recoveries, GPS search tracks and carnivore observations. In the following sections, we describe the various types of data used in the analysis. We considered data collected between 2012 to 2019.

2.1.1 Non-invasive genetic sampling

Bear 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. In Sweden, bear scats are collected by volunteers, mainly hunters, between Aug 21 and Oct 31. The collection is coordinated at the county level by the County Administrative Boards (Länsstyrelserna) and at national level by the Swedish Museum of Natural History (NRM).

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 the individual had been detected more than twice previously, only two approved replicates of homozygous results were required. For further details on the DNA analysis procedure see Tobiassen et al. (2011); Andreassen et al. (2012); Gyllenstrand (2018); Fløystad et al. (2019).

Wolverine In Norway, the collection of DNA material is managed at the level of counties by SNO. Sample collection is conducted by SNO field officers, wardens at Statskog Fjelltjenesten (statskog.no), wardens at Fjellstyrene (fjellstyrene.no), local predator contacts, hunters and other members of the public. In Sweden, the DNA collection is managed by Länsstyrelserna at the regional level. Sample collections are carried out by field officers from Länsstyrelserna.

DNA was isolated using a manual method originally developed to isolate DNA from soil samples (PowerMax[®] Soil DNA Isolation Kit, MO BIO Laboratories, Carlsbad, California, USA). After DNA isolation and identification of genus-specific DNA in the sample, DNA profiles were generated from 12 microsatellite markers. Samples with identical DNA profiles were classified as the same individual. In addition to the 12 markers, all individuals (one sample per individual) were analyzed for an additional 7 markers. Genotyping across 19 markers ensures high precision in individual determination. For further details on the DNA analysis procedure (see Flagstad et al., 2004; Brøseth et al., 2010; Flagstad et al., 2018).

Wolf Swedish and Norwegian management authorities, SNO (Norway) and Länsstyrelserna (Sweden) conduct annual searches for sources of DNA (primarily scats and urine) throughout the Scandinavian wolf range. Although samples may be collected throughout the year, the official survey period starting with the 2014/15 season has been Oct 1 – Mar 31. About one third (30%) of DNA samples originate from opportunistic searches (without associated information on search effort) conducted by hunters or other members of the public (See Liberg et al. 2012

and Bischof et al. 2019 for further details about the data collection procedure). For individual identification, 17-21 microsatellite markers were used. All samples were amplified four times to account for the occurrence of allelic dropout and false alleles (Taberlet et al., 1996). Consensus genotypes were constructed from the replicated PCR runs using the threshold rule that the same alleles had to appear at least twice for a heterozygous genotype and three times for a homozygous genotype (Åkesson et al., 2016).

2.1.2 Dead recoveries

In Scandinavia, all large carnivores killed legally (e.g. legal hunting, management kills, defense of life and property) have to be reported to the management authorities (Fylkesmannen 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 carnivores for DNA extraction and analysis. DNA from dead carnivores, if genotyped, can be linked with NGS data via individual IDs and provide definite information about the fate of individuals. Dead recoveries associated with GPS-coordinates also provide additional information for the estimation of individual locations, especially valuable for individuals with few or no NGS detections.

2.1.3 GPS search tracks

The searchers involved in systematic searches for wolverine and wolf DNA (e.g. via snowmobiles, skis, snowshoes, etc.) documented their search efforts with GPS search track logs which were registered in Rovbase 3.0. Between 2012-2019, a combined search distance of GPS tracks for wolverines of >1 700 000 km and >1 000 000 km for wolves was registered (see Liberg et al. 2011; Bischof et al. 2019 for more information about tracking). GPS search tracks were included in the OPSCR model to account for spatial and temporal variation in the search effort (subsection 3.1) for wolverines and wolves, but not for bears, as NGS were collected by members of the public (predominantly hunters) with no record of effort.

2.2 OPSCR analysis

2.2.1 Model description

There are two primary challenges to estimating abundance and other population parameters from monitoring data. First, detection is typically imperfect, i.e. not all individuals present are detected. Capture-recapture (CR) models, a mainstay in wildlife research for half a century (Armstrup et al., 2005), account for imperfect detection, thus returning unbiased estimates of ecological parameters of interest, such as abundance (Williams et al., 2002). Second, once abundance estimates have been obtained with traditional CR analyses, it is not obvious which space the estimates are linked with if the survey area does not cover the entire habitat available to and used by individuals in the focal population. Spatial capture-recapture (SCR) models offer a powerful approach for establishing this link by estimating a latent variable – the location of an individual’s center of activity – from the spatial pattern of detections (Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008; Royle et al., 2014). The primary focus of project RovQuant has been the development and testing of open-population spatial capture-recapture models (OPSCR; Ergon and Gardner, 2014; Bischof et al., 2016; Gardner et al., 2018), as these formed the basis of all subsequent analyses for the three carnivore species.

The OPSCR model developed during RovQuant is composed of three sub-models:

1. A model for population dynamics and population size.
2. A model for individual carnivore activity center (AC) locations and movements of ACs between years.
3. A model for individual detections during DNA searches.

In the following sections, we describe each model component. Note that analytical methods and models are outlined in broad strokes only. We refer readers interested in methodological details and mathematical notation to Bischof et al. (2019) and other references provided in the following sections.

Population dynamics and population size We modeled annual population dynamics as transitions between individual states (Bischof et al., 2009). Between two consecutive years, an individual can either remain in its current state or transition to another one, with transition probabilities corresponding to vital rates (e.g. recruitment and mortality). For the bear and wolverine models, we considered four different states (Figure 1):

1. “unborn” if the individual has not yet been recruited in the population
2. “alive” if it is alive
3. “dead legal” if it has died from legal culling between the start of the previous and current monitoring seasons.
4. “dead”: if it has a) died from any other cause of mortality between the start of the previous and current monitoring seasons or b) died earlier, regardless of the cause.

In the model, an individual is recruited by transitioning from state “unborn” to state “alive”. In subsequent years, it can remain alive or die from either legal culling (transition to state 3 “dead legal”) or from all other causes of mortality (transition directly to state 4 “dead”). Once in state 3, the individual must transition to state 4 in the next time step, which is the final, absorbent state (Figure 1). Total population size in each year is the sum of all individuals in the alive state (state 2). Note that for the wolf, we split the “alive” state into two different states depending on whether the individual had been identified as a scent-marking member of a pack or not (see Bischof et al. 2019 for more details).

We considered two competing sources of mortality: legal culling, which is always detected (e.g. legal hunting, management kills, defense of life and property), and all other mortalities, which may not always be detected (e.g. natural deaths, vehicle and train collisions, illegal hunting). By distinguishing between these two kinds of mortalities in the model and accounting for imperfect detection, the OPSCR model can produce estimates of total mortality, as well as separate estimates for each mortality type (Bischof et al., 2009). For wolf and wolverine, vital rates were allowed to vary between years, yielding annual estimates of recruitment and state and cause-specific mortality. For bears, the patchy configuration and large spatio-temporal gaps in sampling in Sweden (see subsection 3.4) did not allow us to estimate fully time-dependent vital rates; instead we split the total time into two periods (2012 – 2014 and 2015 – 2018) and allowed recruitment and "other" mortalities to differ between periods, while assuming that they were constant within each period. However, even for bears, mortality due to legal culling was allowed to vary annually, as dead recoveries were available every year in both Sweden and Norway. For all species, vital rates were estimated separately for males and females in sex-specific OPSCR models.

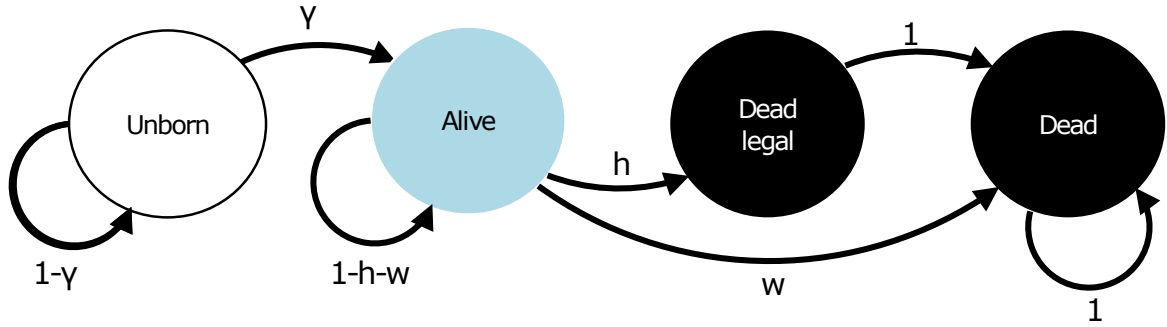


Figure 1: Diagram illustrating the transitions between states in the multi-state model of population dynamics for bears and wolverines (see Bischof et al. 2019 for a description of the state transitions in the wolf model). Circles depict the four possible states an individual can be in. Arrows represent transitions from one state to another and variables shown next to arrows represent the probabilities of these transitions: the probability of being recruited into the population from the unborn state (γ , from which the per-capita recruitment rate ρ can be derived), the probability of dying due to legal culling (h), and the probability of dying due to other causes of mortality (w).

Some individuals within the study area may not be detected. This is dealt with in the model by data augmentation (Royle and Young, 2008; Royle et al., 2009), whereby the model is provided with additional individuals that were not detected, but that may be part of the population (Bischof et al., 2019). The use of the “unborn” state allows for the inclusion of individuals that have remained undetected during monitoring (available “unborn” individuals that transition to “alive”).

Density, activity center location, and movement In OPSCR, the location of an individual is described by the location of its activity center (AC, Figure 2), which is equivalent to the center of a circular home range. The AC location of a detected individual in a given year is informed by the spatial configuration of detections of this individual. The AC location of individuals that were not detected are determined based on the spatial heterogeneity in detection probability and a spatial covariate (intensity surface) describing the distribution of activity centers (density) within the study area (Figure A.2). Undetected individuals are thus less likely to be placed where detection probability is high and density is low. We constructed spatial covariates for density by applying a smoothing kernel to locations of known packs for wolves (Figure A2.5. in Bischof et al., 2019), of known dens for wolverines (Figure A.2A) and all dead recovery locations for bears (Figure A.2B). Except for wolves, density covariates were multi-year aggregates of the aforementioned measures, with the purpose of providing coarse-scale information to the model.

Individual AC locations may shift over time (between years), due to dispersal and adjustments in landscape use or changes in territorial boundaries. The OPSCR model allows AC movements between years, ranging from no movement to long distance dispersal (Bischof et al., 2019). The distribution of AC movement distances is informed by the underlying intensity surface and the spatial distribution of detections of individuals detected in multiple years. ACs can be located and move to anywhere within the available continuous habitat and are not restricted to the detector grid.

Detections In SCR (Figure 2), detection is closely linked with the home range concept in that the probability of detecting an individual declines with increasing distance from its AC location. Most SCR models, including the ones used here, consider the half-normal model to represent this decline in detection probability (Figure 3; Royle et al. 2014). The detection function is a core element in SCR models and enables the estimation of latent (unobserved) AC locations, based on the spatial configuration of detectors and individual detections. Detectors are locations within the study area at which detection can occur, such as traps, bait stations, or observation

points along transect lines. Although individual detections can occur continuously in the landscape during searches, it is common to aggregate detections to the closest point (detector) in a grid (Milleret et al., 2018). Detectors in our study are represented by the center of cells in a spatial grid (10 x 10 km main detector cells divided into 100 1 x 1 km sub-detector cells, except for female bears : 8 x 8 km main detector cells divided into 64 1 x 1 km sub-detector cells, Milleret et al. 2018).

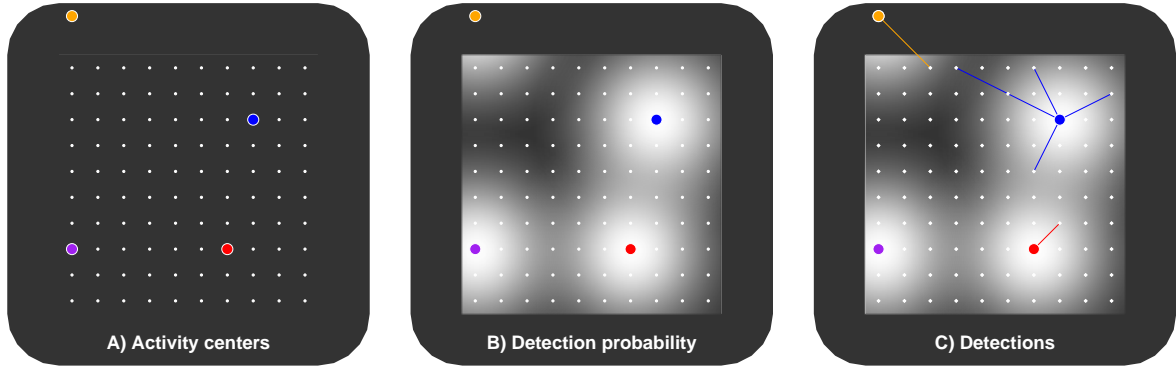


Figure 2: Schematic representation of the spatial capture-recapture process: A) Distribution of individual AC locations (colored dots) across the study region (black area: available habitat; small white dots: detectors). B) Heat map of a detection function describing the relationship between detection probability and distance to AC (lighter shading = higher detection probability). C) Realization of detections, shown as color-coded segments linking individual detections to their respective ACs. Note that individuals with ACs within the surveyed area may be missed completely (purple dot), and, conversely, individuals with ACs outside the surveyed area may be detected (yellow dot).

We considered a habitat buffer around the detector grid (bears and wolves: 40 km; wolverines: 60 km). The buffer area allows placement of individual ACs but does not contain any information about individual detections (Bischof et al., 2019). This is an important component of SCR models, as it allows the detection of individuals with ACs located outside the detector grid and movements of individual ACs in and out of the study area (Efford, 2011; Royle et al., 2014; Gardner et al., 2018).

Detection probability is informed by the detections and non-detections of individuals that were detected at least once. From this, the probability that an individual present in the population remains undetected at any detector is derived. The model can thus not only predict the likely location of detected individuals, but also the presence and distribution of undetected individuals.

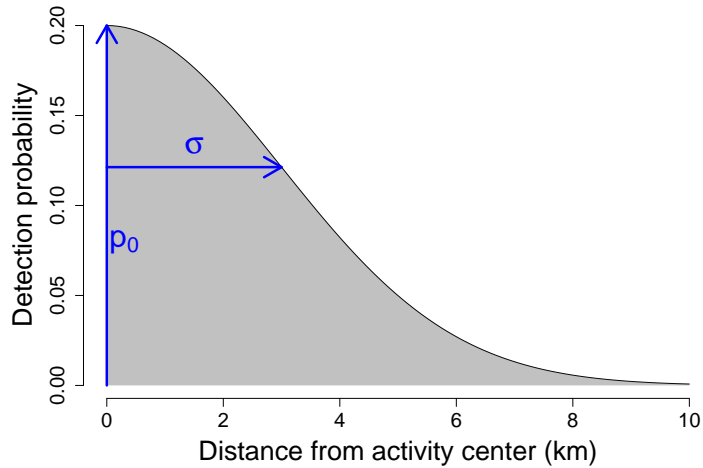


Figure 3: Half-normal detection function describing the decrease in detection probability with increasing distance from the activity center location. The detection function is directly related to the space use around an individual’s activity center. The baseline detection probability (p_0) is the intercept and is equal to 0.2 in this example. The scale parameter (σ) of the function dictates its shape and the speed of the decline in detection probability; it is equal to 3 km in this example.

Both the baseline probability (p_0) and scale parameter (σ) of the detection function (Figure 3) can be under the influence of individual and spatial, detector-specific factors. Depending on the species, we included the following effects on the baseline detection probability:

Detector-level covariates:

- Length of search tracks logged by searchers within each detector grid cell in each monitoring period (Bischof et al., 2019): this variable was included as a linear covariate on the baseline detection probability. Included for wolf and wolverine.
- Average distance from the nearest road (Bischof et al., 2019): the distance from each detector to the closest road (1:100 000, Lantmäteriet, Sweden; N50 kartdata, Statens kartverk, Norway). This variable represents accessibility, which we predict to facilitate detectability. Included for all three species.
- Average percentage of snow cover in each detector grid cell (MODIS at 0.1 degrees resolution, www.neo.sci.gsfc.nasa.gov, accessed 2019-10-11 ; Bischof et al. 2019) between October 1–March 31. As NGS during winter relies heavily on the presence of snow, we predicted that greater snow cover increases detectability. Included for wolf and wolverine.
- Jurisdiction: to control for differences in monitoring regimes between jurisdictions (counties), we estimated independent baseline detection probabilities for each county. Counties with only a few detections were merged with neighboring counties to yield sufficiently large sample sizes for reliable estimation of the baseline detection probability. Included for all three species.

Individual covariates:

- A prior detection could be expected to positively influence the probability of being detected at subsequent occasions. This is referred to as “trap-response” or “trap-happiness” in the capture-recapture literature (Williams et al., 2002). To account for this phenomenon, we used an indicator of whether an individual was detected or not during the previous monitoring season as a linear predictor of the baseline detection probability. Included for wolf and wolverine.

- Monitoring of wolves, especially in Sweden, is focused on scent-marking group members, as their presence defines the presence of pairs or packs. Being territorial, these individuals are actively scent-marking within their home range, thus facilitating the collection of urine or scats. Therefore, being designated as a scent-marking pair or pack member should increase the overall probability of detection of those individuals. For this reason, we modelled separate baseline detection probabilities for individuals in states “alive scent-marking adult” and “alive other” (Bischof et al., 2019). Included for wolf.

In addition to these covariates, we estimated different baseline detection probabilities for each annual monitoring period to control for temporal variation in search effort. Detection probability and the effect of the aforementioned individual and spatial factors were estimated separately for males and females in the sex-specific OPSCR models (Bischof et al., 2019).

2.2.2 Analysis

We fitted our Bayesian OPSCR models using Markov chain Monte Carlo (MCMC) simulation with NIMBLE (Turek et al., 2016; de Valpine et al., 2017; NIMBLE Development Team, 2019) in R version 3.3.3 (R Core Team, 2018). NIMBLE provides a new implementation of the BUGS model language coupled with the capability to add new functions, distributions, and MCMC samplers to improve computing performance. We ran four chains, each with 15000 iterations, including a 5000-iteration burn-in period. Due to the computing challenge associated with post-processing large amounts of data and because of differences in the number of individuals in the population, we thinned chains from which abundance estimates were derived by 5 samples for wolves and wolverines and by 10 samples for bears. A description of the MCMC process and its outcome is provided in Box 2 in Bischof et al. (2019). We used computing clusters (<https://cigene.no/tag/orion>; <https://www.sigma2.no/content/abel>) for running each MCMC chain on a separate core, ultimately enabling us to run many chains simultaneously thereby reducing the total time required to obtain results. 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.

OPSCR models represent a significant computational challenge due to the potentially millions of calculations involved. This challenge is amplified in our analysis because the model is unusually complex (multiple processes, many parameters estimated) and due to the size of the problem (number of individuals and spatial extent). For this reason, during project RovQuant we have developed approaches and implemented a number of features to substantially reduce computation time, thereby enabling us to run complex OPSCR models in a few days or weeks, instead of months or years (Turek et al. in prep.). These developments include:

1. Spatial aggregation: We developed a new observation model that allowed us to substantially reduce the number of detectors (and therefore runtime) without compromising precision and accuracy of model estimates (Milleret et al., 2018).
2. Local evaluation: We reduced the number of calculations to be performed by removing unnecessary evaluation of the likelihood whenever the distance between a detector and a predicted AC location was larger than a distance threshold (Milleret et al., 2019a).
3. NIMBLE: We moved model implementation from JAGS (Plummer, 2003) to NIMBLE (NIMBLE Development Team, 2019). NIMBLE compiles the model into machine code (C++) and thus allows for faster computation compared to software that requires the model definition to be parsed to an interpreter at run time. The flexibility of NIMBLE also allowed us to implement the aforementioned developments as time-saving NIMBLE functions (Turek et al. in prep.).

2.2.3 Parameter estimation

The OPSCR is a complex hierarchical model with many parameters estimated. Density and corresponding population size were the focus of the analysis, but we monitored additional parameters as they can be of interest from a management perspective or because they helped track model behavior and validate assumptions. These parameters included cause-specific mortality (legal culling and other causes), recruitment and home range size.

To obtain an estimate of abundance for any arbitrary area, we summed the number of OPSCR-predicted AC locations (live individuals) that fell within this region for each iteration of the MCMC chains, thus generating a posterior distribution of the abundance for this area. In this fashion, abundance estimates and the associated uncertainty can be extracted for any desired spatial unit, including country or county level estimates. For all parameters, except abundance, we reported the median and the 95% credible interval limits of the posterior distribution. To ensure that abundance estimates of spatial subunits add up to overall abundance estimates, we used the mean and the associated 95% credible interval limits to summarize posterior distributions of abundance. Combined (female/male) parameter estimates were obtained by merging the posterior samples obtained from the sex-specific models.

2.3 Results

2.3.1 Bear

Non-invasive genetic sampling and dead recoveries A total of 12 804 (6 476 female; 6 328 male) genotyped non-invasive genetic samples from brown bears were included in the analysis (Figure 4, Table B.1, Table B.4). The majority of samples (72%) originated from Sweden. Sweden sampled different regions in different years (and did not conduct NGS-based inventories at all in 2013 and 2018) between August and October. Norway sampled the same five regions every year between April and October. Non-invasive genetic samples were associated with 2 824 (1 527 female; 1 297 male) individuals (Table B.2). We also included 2 246 dead recoveries of bears, of which 2 132 (907 female; 1 225 male) were due to legal culling and 114 (57 female; 57 male) due to other causes of mortality (Figure 5, Table B.3). The majority of dead recoveries (97%) originated from Sweden.

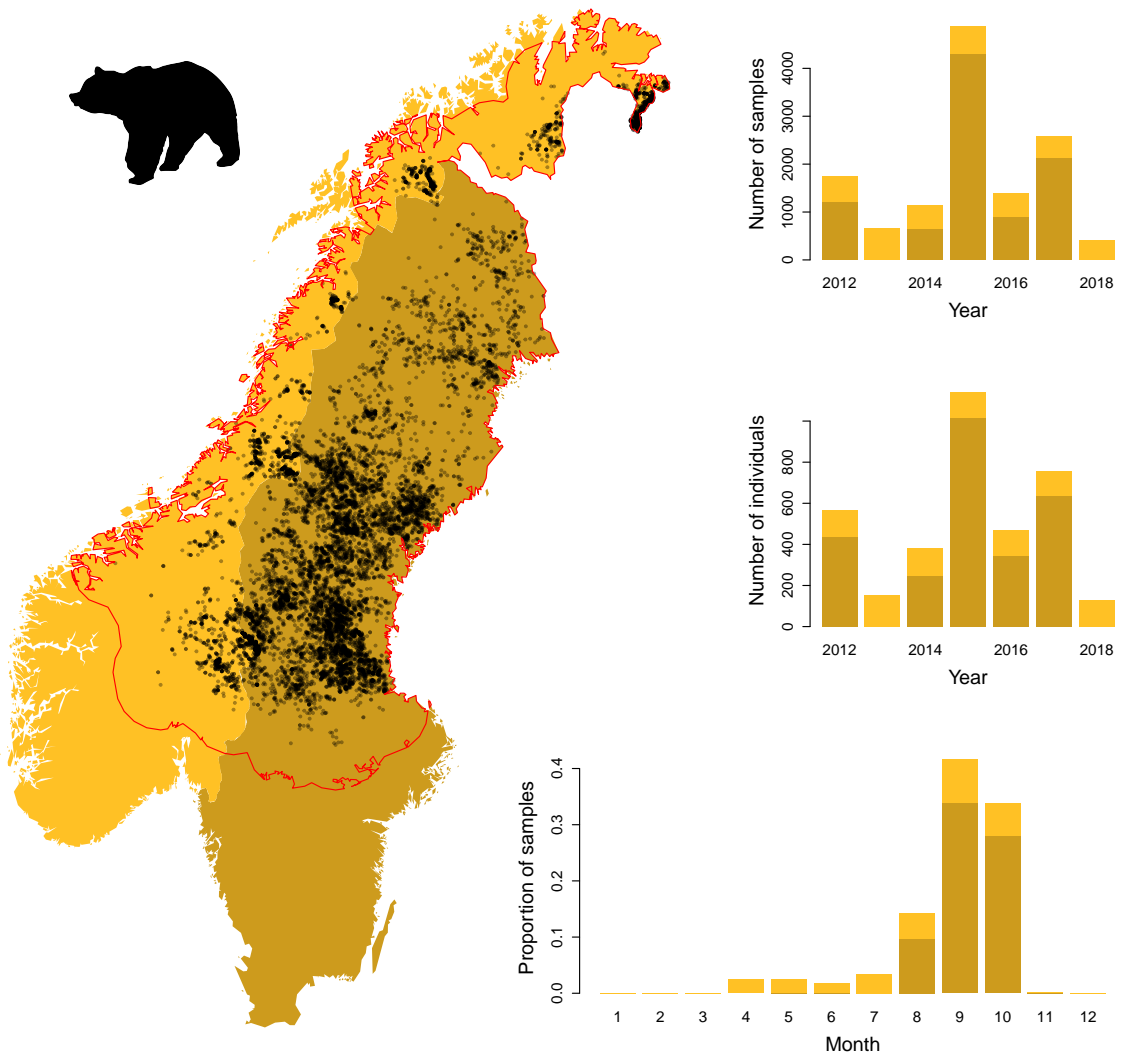


Figure 4: Spatio-temporal distribution of non-invasive genetic samples from bears collected between Apr 1 2012 and Oct 31 2018. The red polygon outlines the spatial extent included in the analysis. Only samples included in the OPSCR analysis are shown. Light and dark background colors represent Norway and Sweden, respectively.

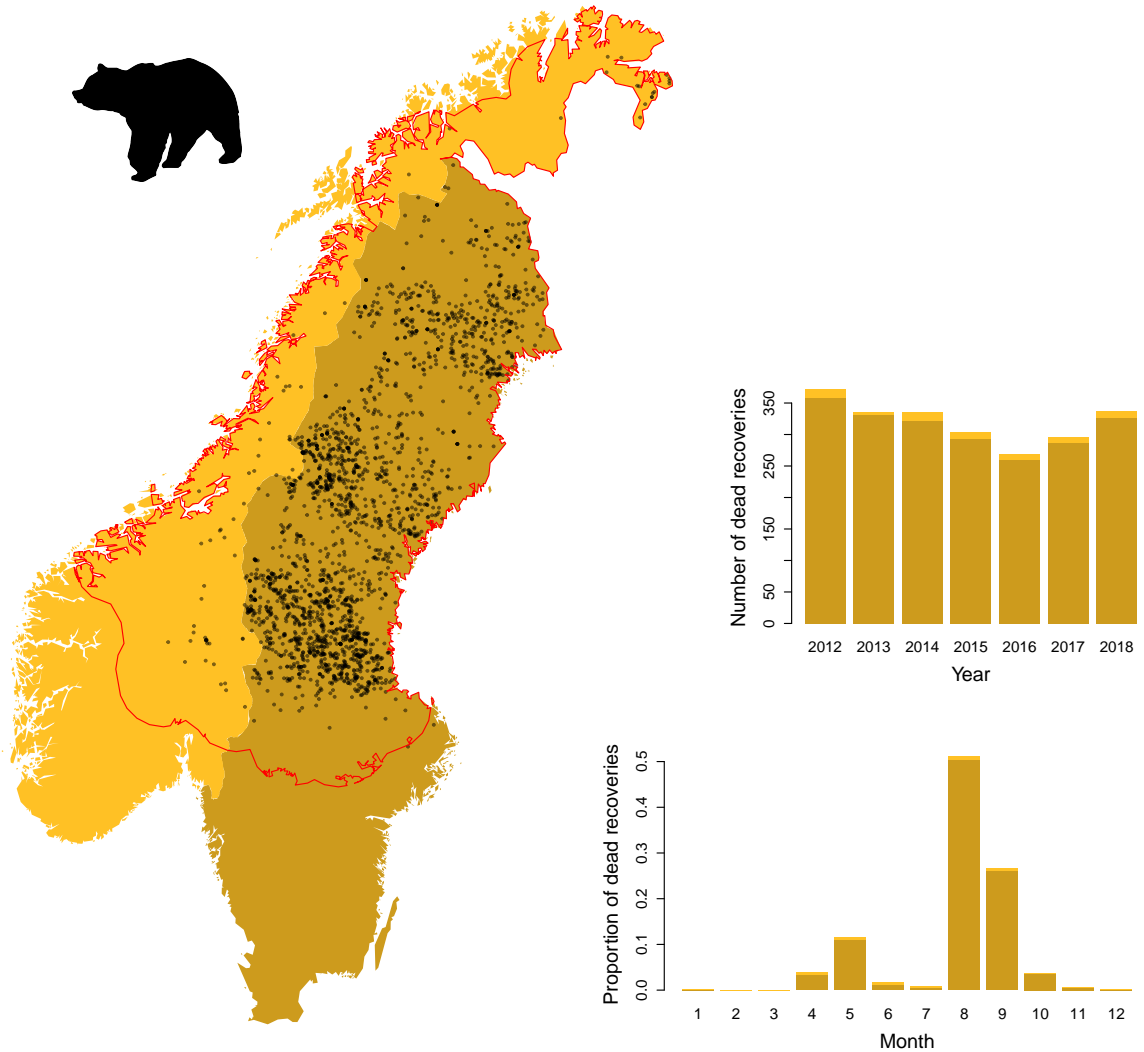


Figure 5: Spatio-temporal distribution of dead recoveries of bears between 2012 and 2018. The red polygon outlines the spatial extent of the analysis. Only dead recoveries included in the analysis are shown. Light and dark background colors represent Norway and Sweden, respectively.

Density and abundance The model-estimated population size for the entire study area (526 000 km², excluding the 40 km buffer area) ranged from 2 757 bears (CrI: 2 636-2 877) in 2018 to 3 205 bears (CrI: 3 136-3 281) in 2015 (Figure 6). Estimates refer to the status of the population at the start of the annual sampling period (April 1). Overall, the Scandinavian bear population was estimated to be female-biased, with 59% (56%-61%) of individuals being female. Based on the predicted location of ACs, we estimated that in 2018, 2 615 bears (CrI: 2 499-2 732) could be attributed to Sweden and 142 (CrI: 124-162) to Norway (Table 1). Estimated bear population size in Scandinavia increased from 2012 to 2015 and subsequently declined until 2018. However, this coarse pattern may 1) be an artifact of the patchy configuration of bear NGS in Sweden (subsection 3.4) and 2) may mask greater interannual variation in abundance because some vital rates (recruitment and mortality due to causes other than legal hunting) were only allowed to differ between these two periods but not annually as for wolves and wolverines. Estimation of reliable annual abundance and vital rates will likely only be possible if a more evenly spread monitoring configuration (in space and time) is adopted for bears in Sweden. A further breakdown into annual region-specific estimates is provided in Table 1 and Table B.5. **Note:** In regions with small abundance estimates the uncertainty is very large relative to the

mean abundance. For example in carnivore management region 7 in Norway, the mean estimate of female brown bears was 4.4, but an abundance estimate as low as 1 individual is within the 95% CrI. Inferences about local population status should be made cautiously with this in mind.

In some cases the number of individuals detected in a region exceeds the mean estimated population size for that region. This is for example the case for bears in Västernorrland in 2015 (293 individuals detected, estimated number of bears attributed: 261.4; CrI: 251-273) and in Gävleborg in 2017 (383 individuals detected, estimated number of bears attributed: 374.4, CrI: 359-390; Table B.5). This is not unexpected: when detectability is very high, as it is during sampling years in Sweden, not only are most individuals within a region detected, but numerous additional individuals may be detected that have their ACs located outside the boundaries of that region. The ability to detect “outside” individuals was one of the main motivations behind the development of SCR models, which, by accounting for “outside” individuals, yields estimates of spatially-explicit abundance (Efford, 2004; Royle et al., 2014). This phenomenon has already been documented for bears in Norway previously (Bischof et al., 2016).

Table 1: Population size estimates by sex and jurisdiction based on OPSCR-estimated activity center locations of bears in Scandinavia in 2018. Dark bold font indicates estimates for regions in years with systematic sampling. All Swedish regions remained unsampled in 2018 (lighter font), making associated estimates less reliable as they are based primarily on information indirectly propagated in the model (from neighboring regions and years with sampling) rather than being directly informed by contemporary local data. Combined female-male estimates are obtained by joining the sex-specific posterior distributions. Rounding may result in small deviations between total estimates shown here and the sum of the estimates from constituent regions. **Note:** Until periodic and range-wide NGS is implemented in Sweden, we recommend that only estimates for regions in years with sampling are used for inferences. By contrast, estimates throughout the Norwegian bear range are supported by data for every year of the time series.

	Females	Males	TOTAL
TOTAL	1619.5 (1521-1717)	1138 (1063-1217)	2757.5 (2636-2877)
NORWAY	69 (57-82)	73.1 (60-88)	142.1 (124-162)
Region 1	0 (0-0)	0 (0-1)	0 (0-1)
Region 2	0 (0-0)	0.3 (0-2)	0.3 (0-2)
Region 3	0.6 (0-2)	1.5 (0-5)	2.1 (0-6)
Region 4	0.2 (0-1)	0.2 (0-1)	0.4 (0-2)
Region 5	19.9 (14-27)	17.2 (13-23)	37.1 (29-46)
Region 6	20.6 (15-27)	23.6 (18-31)	44.2 (36-54)
Region 7	4.4 (1-9)	5.1 (1-10)	9.5 (4-16)
Region 8	23.2 (18-29)	25 (18-33)	48.2 (39-58)
SWEDEN	1550.5 (1455-1644)	1064.9 (992-1140)	2615.4 (2499-2732)
Dalarna	266.2 (239-295)	160.8 (138-184)	427 (391-464)
Gävleborg	272.8 (248-300)	183 (160-207)	455.8 (421-491)
Jämtland	487.1 (446-530)	299.7 (265-334)	786.8 (732-840)
Norrbotten	257.2 (235-280)	175.6 (155-198)	432.8 (401-466)
Örebro	0.8 (0-3)	2.6 (0-6)	3.4 (0-7)
Södermanland	0 (0-0)	0.1 (0-1)	0.1 (0-1)
Uppsala	1.4 (0-4)	2.4 (0-6)	3.8 (1-8)
Värmland	5.6 (2-10)	8.2 (3-14)	13.8 (7-21)
Västerbotten	138 (119-157)	126.1 (105-148)	264.1 (236-292)
Västernorrland	120.2 (104-137)	103.4 (85-123)	223.6 (198-248)
Västmanland	1.4 (0-4)	3.2 (0-7)	4.6 (1-9)

The national abundance estimates provided here are comparable to the latest population size estimates available for the Norwegian (between 125 and 148 individuals during 2012-2018; Fløystad et al. 2019) and Swedish populations (2782 bears in 2013; Kindberg and Swenson 2014 and 2877 in 2017; Kindberg and Swenson 2018).

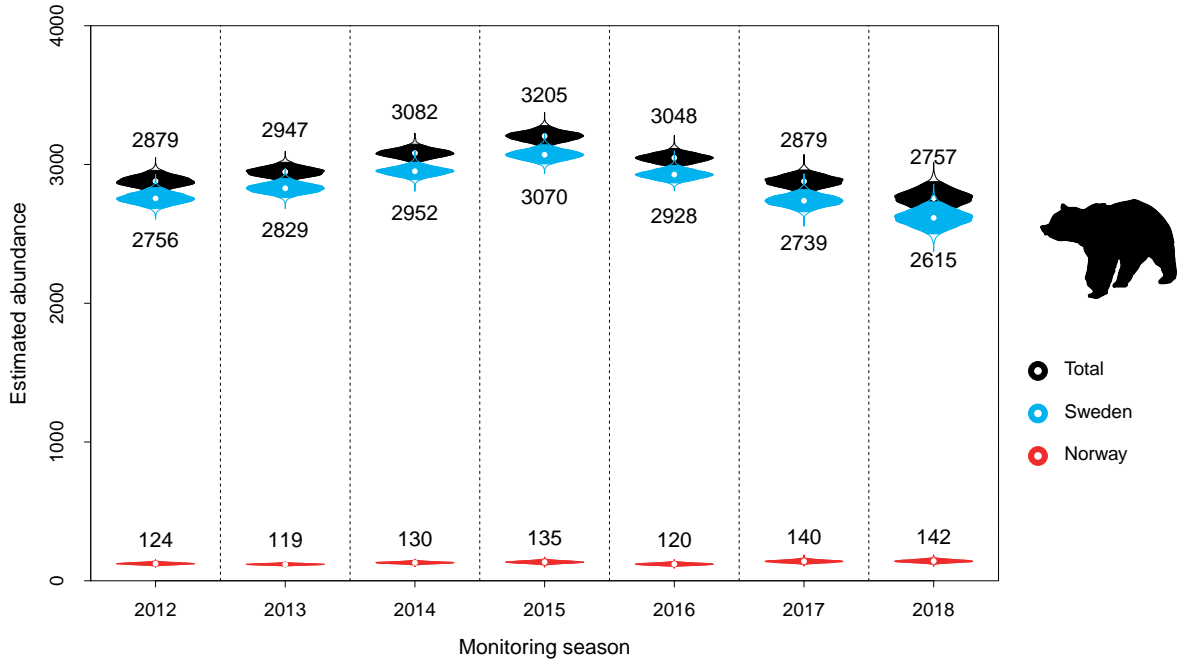


Figure 6: Total and country-specific annual bear population size estimates from the OPSCR model. Violins show the posterior distribution of the annual population size estimates (points and values: mean estimates; solid colors: 95% credible interval).

The OPSCR model yielded annual density maps (Figure 7, Figure B.1), which illustrate the spatial distribution of individuals and changes therein over time. Average density in 2018 was estimated at 0.154 bears per 100 km² (CrI: 0.151 – 0.159) throughout the 526 000 km² study area. As shown previously (Kindberg et al., 2011), the population is organized into three pronounced core areas, with the highest densities associated with the southernmost and central core areas (Figure 7). Greater detail can be discerned on the density maps in regions and years with genetic sampling, because individual AC locations are estimated with higher precision when individuals are detected, leading to discernible spatial variation in density. This is particularly apparent when contrasting brown bear densities in years with and without sampling in Sweden (Figure B.1). Here too, those parts of the density surface that are associated with unsampled combinations of years and regions in Sweden should be interpreted with caution.

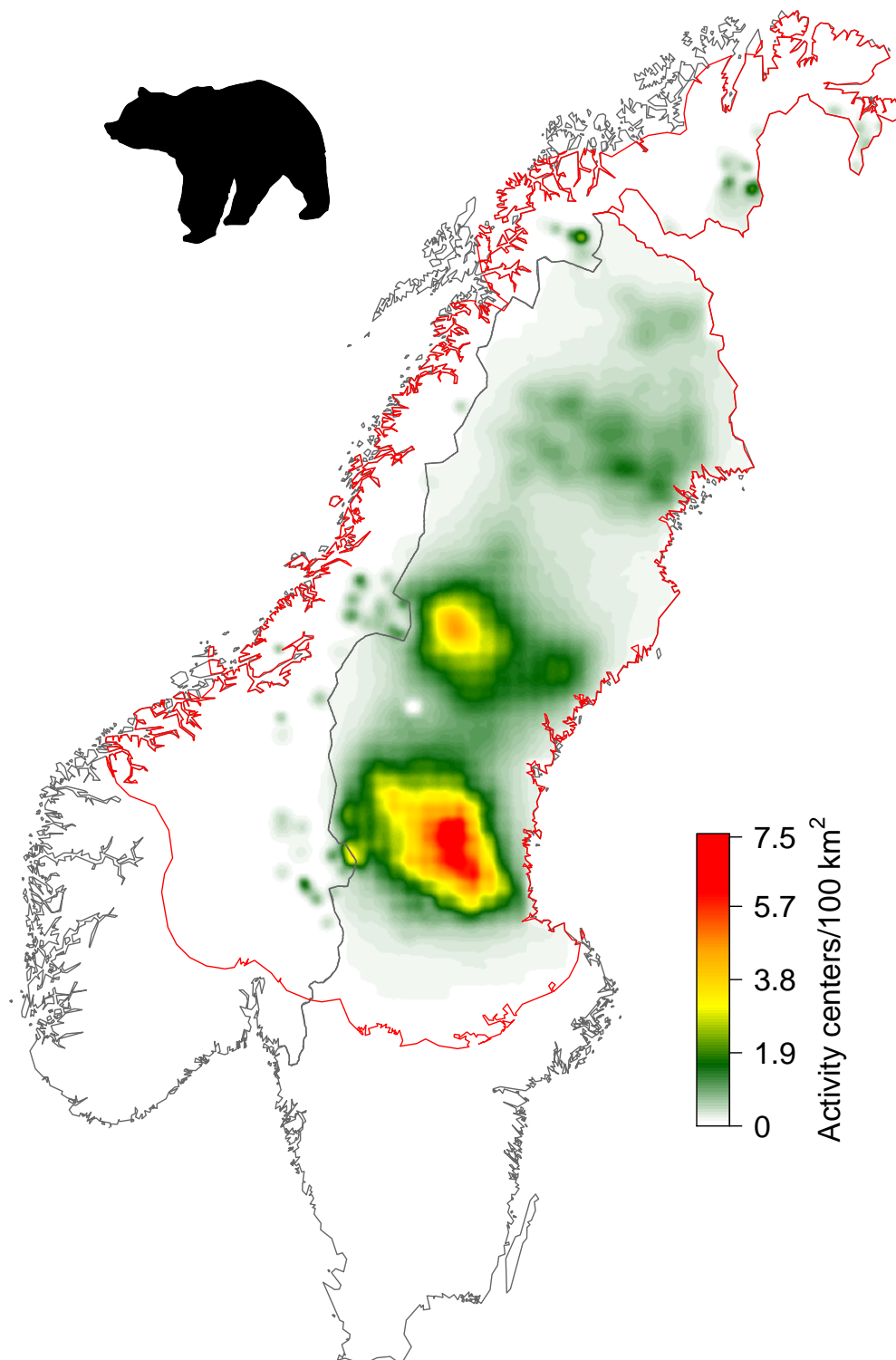


Figure 7: Brown bear density throughout Scandinavia in 2018, derived from the OPSCR model. The area for which estimates were generated is outlined in red. Note that no non-invasive genetic monitoring was conducted in Sweden in 2018.

Vital rates The model produced annual estimates of legal mortality. Mortality associated with other causes and per capita recruitment rate were estimated separately for the two periods considered in the analysis (Figure 8; Table B.6). Male bears experienced significantly higher (approx. 1.5 fold) legal mortality than female bears (Figure 8). No significant differences in mortality due to other causes was detected between the sexes. Whereas annual legal culling mortality appeared to have declined over the study period (with a slight increase again in the last time step), estimated mortality due to other sources increased for both males and females from the first time period (before 2015) to the second (after 2015). Overall mortality, and therefore survival, has remained relatively stable during the study period (Figure 8; Table B.6). We also detected a significant decline in per-capita recruitment (number of new recruits per animals in the population at the start of the previous season) from the first to the second time period (Table B.6). Here too, the abrupt pattern may be an artifact of the patchy configuration of sampling in Sweden and/or may mask a more gradual decline in recruitment over the study period because vital rates were not fully time-dependent. Note that vital rates reported here, are overall rates for the population and not age-specific. Of the three species, the OPSCR fitted to the bear data can be expected to produce the least reliable inferences, because the spatio-temporally patchy data in Sweden do not lend themselves to range-wide estimation (subsection 3.4). However, the magnitude and general patterns (lower survival of males compared with females; legal culling as the main source of mortality) are consistent with what has been reported for this population previously (Bischof et al., 2009).

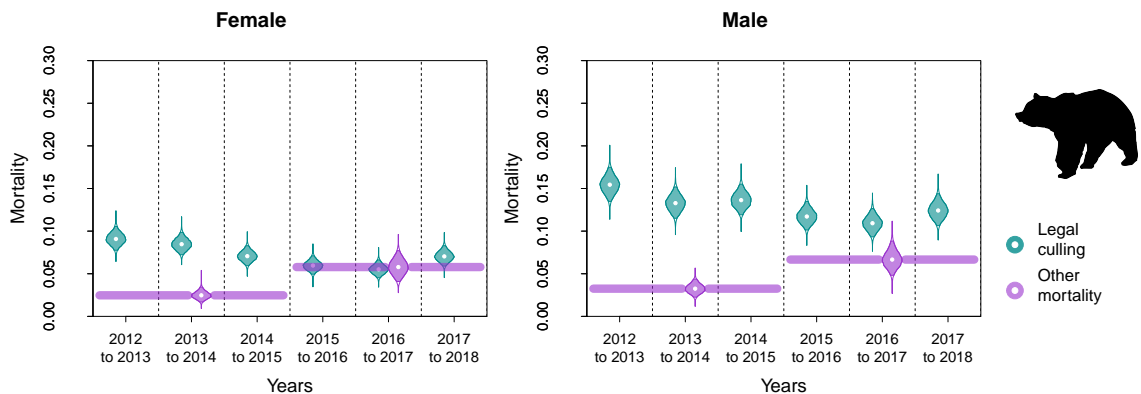


Figure 8: Mortality probability due to legal culling and all other causes for female and male bears. Shown are overall estimates throughout Scandinavia. Violins show the posterior distribution of mortality estimates (points: median estimates; solid colors: 95% credible interval). Horizontal bars indicate the time period to which “other” mortality estimates apply to, as these were not fully time-dependent in the model.

Home range size We estimated the scale parameter of the detection function (σ) as 6 km (CrI: 5.91-6.11 km) for female bears and 8.9 km (CrI: 8.8-9.1 km) for males. The estimated median home range size for bears, derived from σ (Royle et al., 2014), was 679 km² (CrI: 657 km² - 702 km²) for females and 1 495 km² (CrI: 1 445 km² - 1 546 km²) for males. As we do not currently model the age structure in the population, space use parameters are average over all age classes and include dispersing individuals. The home range sizes are comparable to those reported by Swenson et al. (2001) and Bischof et al. (2016) for the same population. Although both our estimates and those by Swenson et al. (2001) are larger than home range sizes reported by Dahle and Swenson (2003), those authors conceded that their estimates were likely biased low by a factor of 1.5 – 2. A recent analysis based on 186 GPS-equipped bears in Sweden found comparable home range sizes for male bears (1 622 km²; Mattisson et al. 2019). However, they reported smaller home-range sizes for females (between 256-360 km² depending on age class). This difference might be explained in part by the fact that the estimates by Mattisson et al. 2019

are based on a 4-month period, whereas the values reported here apply to the 7-month period between April 1 and October 31. Indeed, Mattisson et al. (2019) showed that the home-range size estimates steadily increased with the length of the sampling period (especially for females with cubs).”

Detection probability The baseline detection probability varied between counties and over time, and was generally higher for females than males (Figure B.2). This does not necessarily imply lower overall detection of males, as males compensate for a lower baseline detection probability with a larger corresponding home range size (and corresponding scale parameter). Detection probability decreased in areas further away from roads for both males ($\beta = -0.95$, CrI: -1.05 to -0.84; predictor variable was standardized) and females ($\beta = -1.24$, CrI: -1.39 to -1.10). Patterns in detection probability are dominated by the patchy monitoring design in Sweden (Figure B.2; subsection 3.4).

2.3.2 Wolverine

Non-invasive genetic sampling and dead recoveries A total of 13 184 (6 031 female; 7 153 male) genotyped non-invasive genetic samples from wolverine were included in the analysis (Figure 9, Table C.1), with 60% of samples originating from Norway. These samples were associated with 2 118 (1 137 female; 981 male) individuals (Table C.2). We also included 596 dead recoveries of wolverines, of which 578 (286 female; 292 male) were due to legal culling and 18 (5 female; 13 male) due to other causes of mortality (Figure 10, Table C.3). The majority of dead recoveries (82%) originated from Norway.

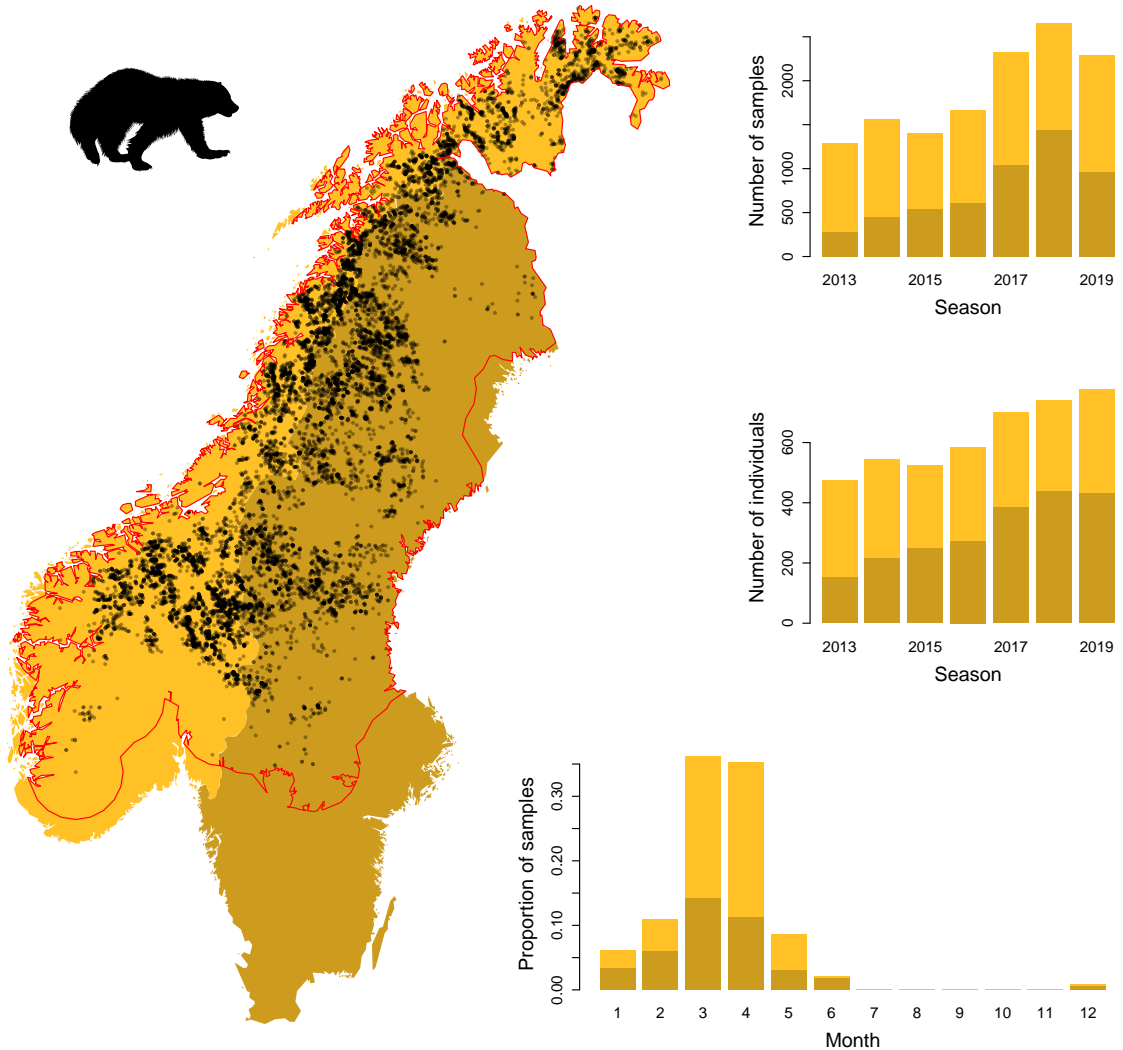


Figure 9: Spatio-temporal distribution of non-invasive genetic samples from wolverines between Dec 1, 2012 and June 31, 2019. The red polygon defines the spatial extent included in the analysis; only samples included in the OPSCR analysis are shown. Light and dark background colors represent Norway and Sweden, respectively.

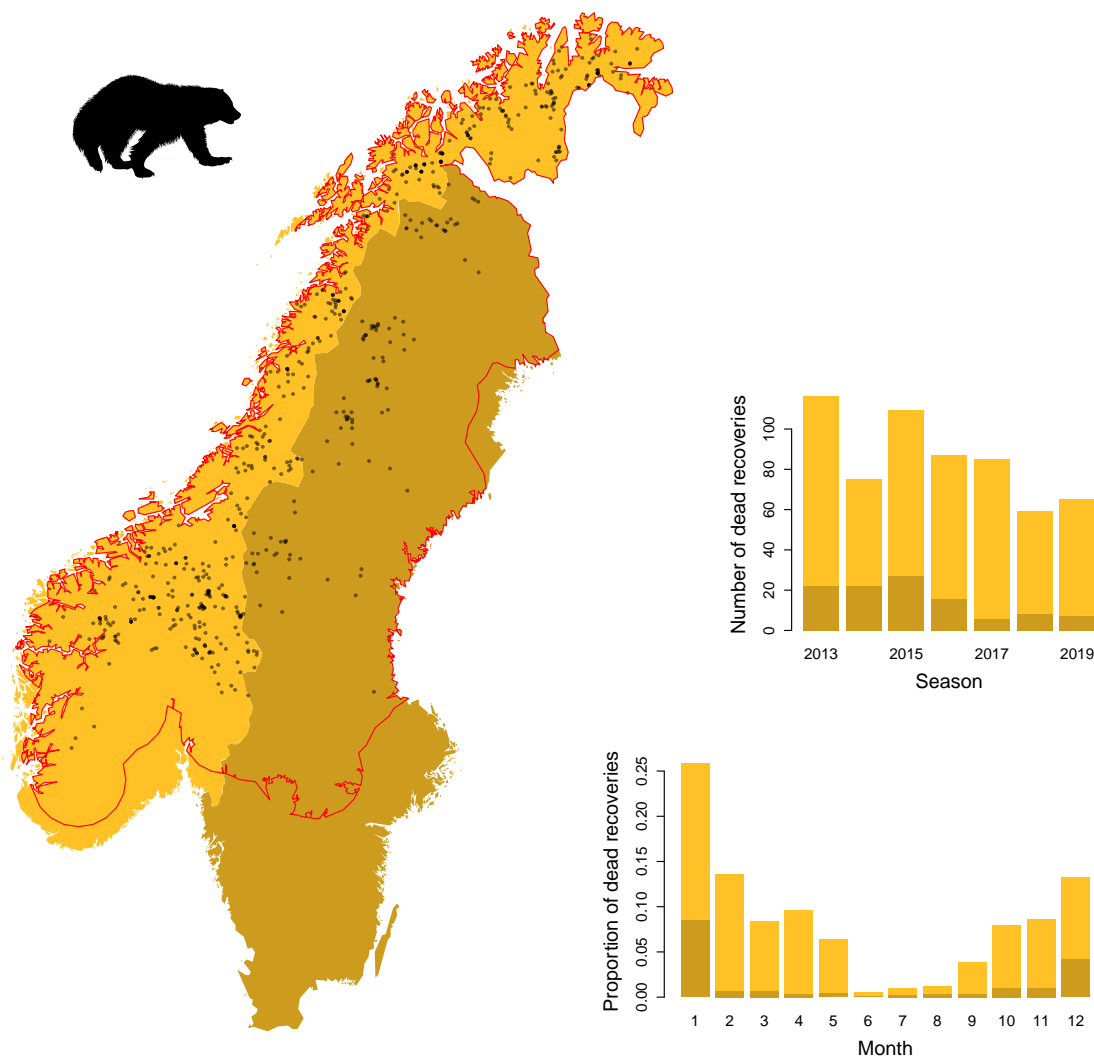


Figure 10: Spatio-temporal distribution of dead recoveries of wolverines between 2012 and 2019. The red polygon defines the spatial extent included in the analysis; only dead recoveries included in the OPSCR analysis are shown. Light and dark background colors represent Norway and Sweden, respectively.

Density and abundance The model-estimated population size for the entire study area (593 000 km², excluding the buffer area) ranged from 885 wolverines (CrI: 843-931) in the winter 2014/15 to 1 035 wolverines (CrI: 985-1 088) during winter 2018/19 (Figure 11). These estimates are consistent with numbers reported elsewhere for the same population, which varied between 846 (90%CI: 733-1 023) and 1 069 (90%CI: 936-1 270) during the study period (Höglund et al., 2019). Our estimates refer to the state of the population at the start of the annual sampling period (December 1), but note that most DNA searches began in January. Overall, the Scandinavian wolverine population was estimated to be female-biased, with 60% (57%-62%) females.

Based on the predicted location of ACs, we estimated that in 2019, 660 wolverines (CrI: 619-703) could be attributed to Sweden and 375 (CrI: 353-397) to Norway (Figure 11, Table 2). For comparison, the 2019 annual wolverine inventory report (Höglund et al., 2019) estimated that there were 679 (90%CI: 584-832) and 332 (90%CI: 283-405) wolverines in Sweden and Norway respectively for the same period. Estimated wolverine population size in Sweden increased during the study period, whereas a slight decrease was detectable in the Norwegian part of the population. A further breakdown into annual region-specific estimates is provided in Table 2 and Table C.4.

Table 2: Wolverine abundance estimates by sex and jurisdiction in 2019 based on OPSCR-estimated AC locations in Scandinavia. Combined female-male estimates are obtained by joining the sex-specific posterior distributions. Rounding may result in small deviations between total estimates and the sum of the estimates from constituent regions.

	Females	Males	TOTAL
TOTAL	616.7 (573-664)	418.1 (395-444)	1034.8 (985-1088)
NORWAY	224.5 (207-244)	150.2 (139-162)	374.7 (353-397)
Region 1	3.8 (1-7)	2.2 (0-6)	6 (2-11)
Region 2	1.2 (0-4)	1.5 (0-4)	2.8 (0-6)
Region 3	16.7 (13-21)	10.6 (7-14)	27.3 (22-33)
Region 4	0.5 (0-2)	0.4 (0-2)	0.9 (0-3)
Region 5	47 (41-54)	40.3 (35-46)	87.3 (79-96)
Region 6	56.1 (48-65)	41.5 (36-47)	97.6 (87-109)
Region 7	37.5 (31-45)	24.9 (20-30)	62.4 (54-71)
Region 8	61.7 (53-72)	28.7 (23-35)	90.4 (80-102)
SWEDEN	392.1 (358-429)	268 (247-292)	660.1 (619-703)
Östergötland	0 (0-0)	0 (0-0)	0 (0-0)
Dalarna	21 (15-28)	20.6 (16-26)	41.6 (34-50)
Gävleborg	14.6 (10-19)	18.4 (14-23)	33 (27-40)
Jämtland	127.7 (112-144)	83.5 (74-95)	211.3 (192-231)
Norrbotten	126.2 (111-143)	68.3 (57-81)	194.4 (175-215)
Örebro	0.7 (0-3)	0.8 (0-3)	1.5 (0-4)
Södermanland	0 (0-0)	0 (0-1)	0 (0-1)
Uppsala	0 (0-0)	0 (0-0)	0 (0-0)
Värmland	4 (1-7)	4.4 (2-7)	8.4 (4-13)
Västerbotten	81.3 (69-95)	52.2 (43-63)	133.5 (117-151)
Västernorrland	16.2 (11-22)	19.3 (14-25)	35.5 (28-43)
Västmanland	0.2 (0-1)	0.3 (0-2)	0.6 (0-2)
Västra Götaland	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)

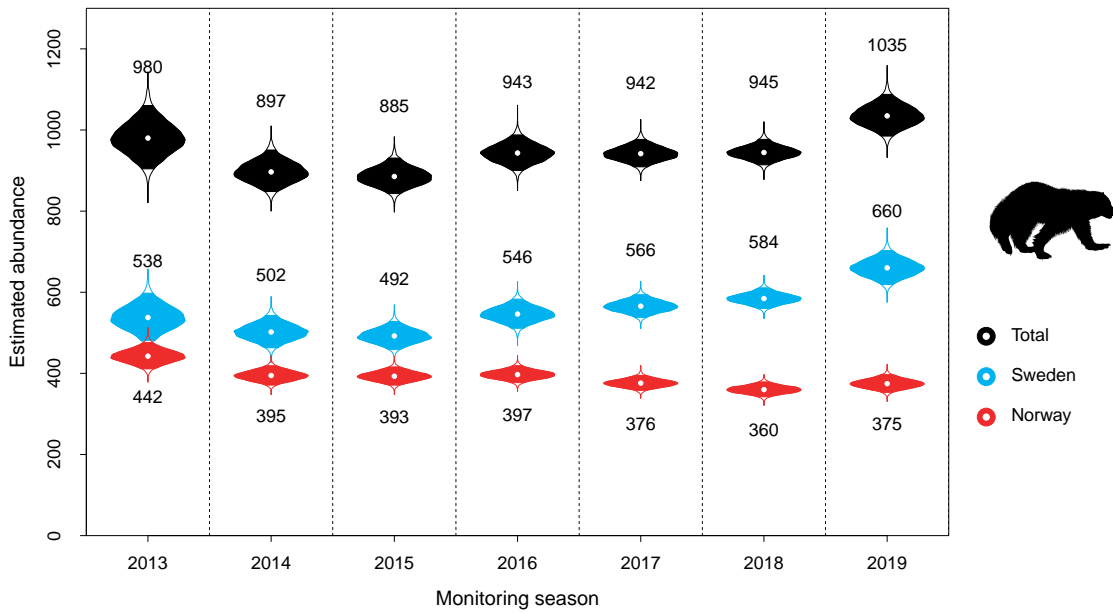


Figure 11: Total and country-specific annual wolverine population size estimates from the OPSCR model within the study area. Violins show the posterior distribution of the annual population size estimates (points: mean estimates; solid colors: 95% credible interval). Values indicate rounded mean estimates.

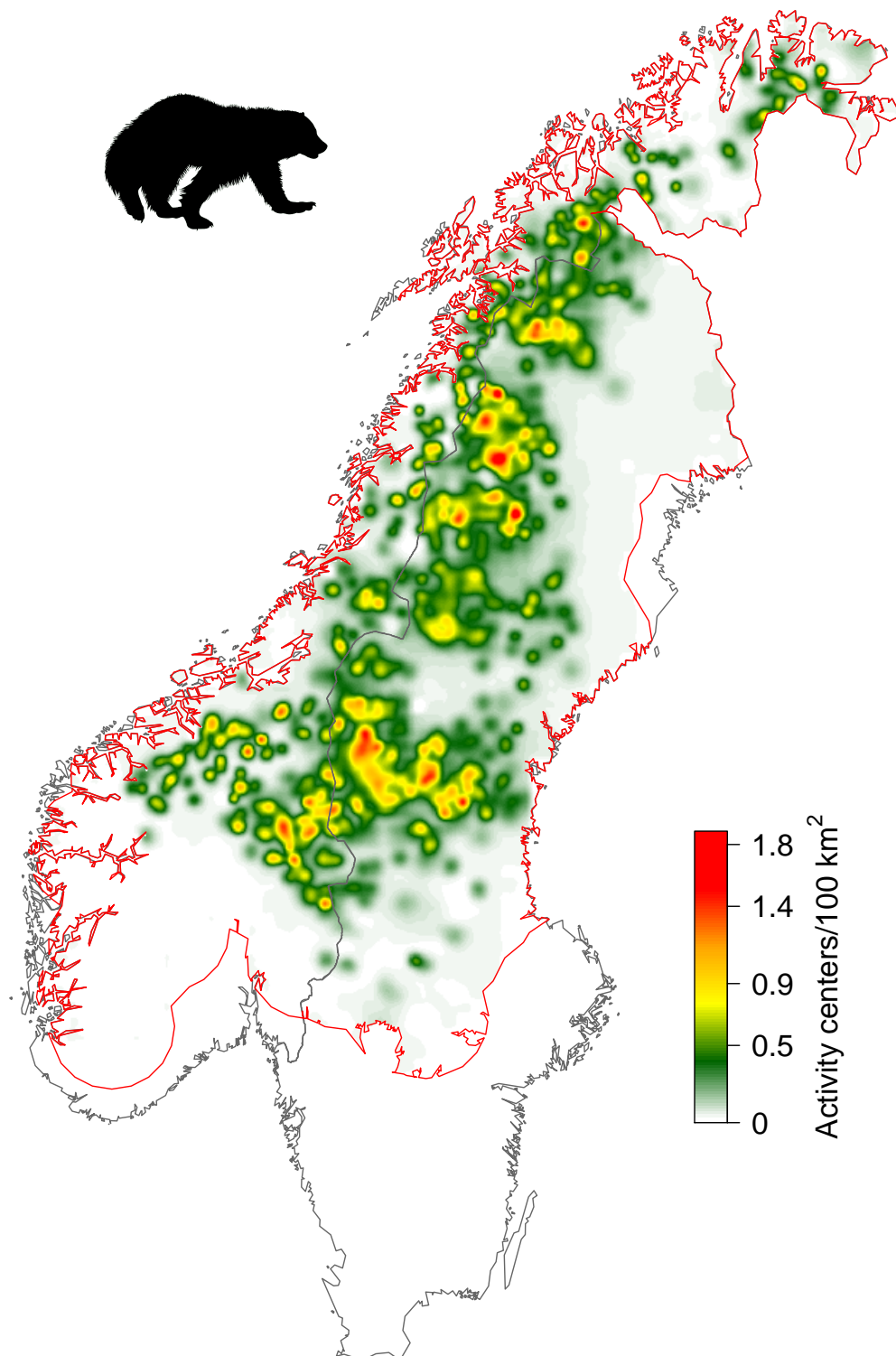


Figure 12: Wolverine density throughout the study area in Scandinavia in winter 2018/19, derived from the OPSCR model. The area for which estimates were generated is outlined in red.

Average wolverine density in 2019 was estimated at 0.174 individuals (activity centers) per 100 km² (CrI: 0.166 – 0.183) throughout the 593 000 km² study area (Figure 12). Changes in wolverine density over time are shown in Figure C.1.

Vital rates The model produced annual estimates of legal hunting mortality, mortality associated with other causes and per capita recruitment rates (Figure 13; Table C.5). Overall, male wolverines were more vulnerable than female wolverines to both legal culling and mortality due to other causes (Figure 13). Legal culling mortality was consistently lower than mortality due to other causes (Figure 13). No significant difference in mortality due to other causes was detected between the sexes. Note that vital rates reported here are overall rates for the population, not age-specific rates. However, the magnitude and general patterns of lower survival of males compared with females are consistent with what has been reported previously for a subset of this population (Brøseth et al., 2010) and in North America (Squires et al., 2007). The levels of legal culling mortality and other mortality were also consistent with the values reported in (Squires et al., 2007), where harvesting decreased the overall survival in the population from 0.80 to 0.57.

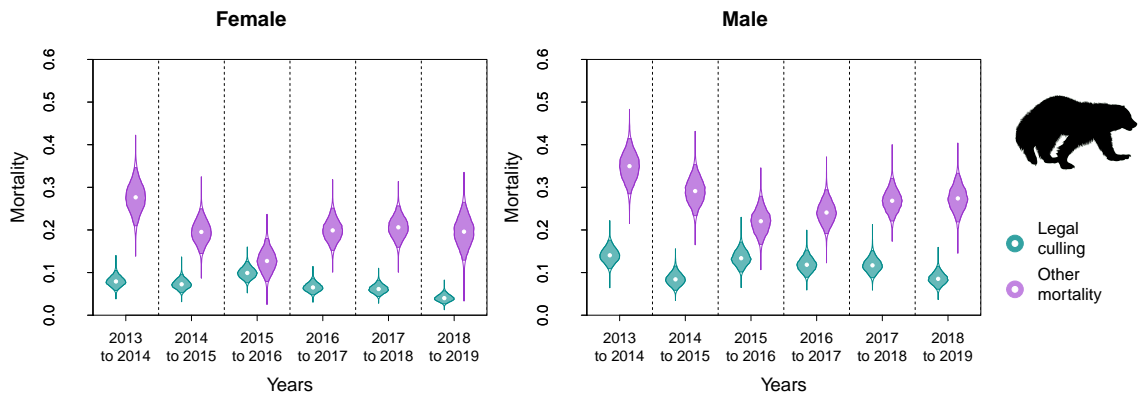


Figure 13: Mortality probability due to legal culling and other causes for female and male wolverines. Shown are overall estimates throughout Scandinavia. Violins show the posterior distribution of mortality estimates (points: median estimates; solid colors: 95% credible interval).

Home range size We estimated the scale parameter of the detection function (σ) as 7.4 km (CrI: 7.2-7.5 km) for female wolverines and 10.3 km (CrI: 10.1-10.5 km) for males. The estimated median home range size for wolverines, derived from (σ), was 1 017 km² (CrI: 976 km² - 1 059 km²) for females and 1 996 km² (CrI: 1 933 km² - 2 061 km²) for males. These values are larger than previously reported for the Scandinavian population (e.g. Persson et al. 2009; Mattisson et al. 2011; but see Dawson et al. 2010 for similar values in a Canadian population). There are several potential explanations for this. 1) The aggregation of detections to a coarse detector grid (a necessary step to deal with the computational challenge associated with the large spatial extent of the analysis) is known to produce larger home range estimates, but without a pronounced impact on density estimates (Milleret et al., 2018). 2) Our estimates represent overall values for the population and do not account for individual variation, that would for example be associated with different age classes or habitats occupied. In this regard, note also that credible intervals around the estimates are expressions of uncertainty around the model-estimated median, not variation of home range size in the population. 3) Home-range sizes reported here rely on the assumption of a normally distributed circular home range, and it has been shown that SCR-based home range size estimates are sensitive to misspecification of the shape of the detection function (Royle et al., 2014).

Detection probability The baseline detection probability (p_0 , Figure C.2) varied between counties, generally increased with time and was higher for females than males (Figure C.2). This does not imply higher overall detectability, as males compensate for lower baseline detectability with higher σ values due to their larger home ranges. Overall, baseline detection probability was higher in Norway than in Sweden (Figure C.2). Detection probability increased with the length of recorded search trails (males: $\beta = 0.44$, CrI: 0.41 - 0.46; females: $\beta = 0.41$, CrI: 0.38 - 0.44) and showed a trend of a decline with increasing distance from roads (males: $\beta = -0.04$, CrI: -0.07 - 0.00; females: $\beta = -0.03$, CrI: -0.07 - -0.01). The average proportion of snow cover during the sampling period had a positive effect on the baseline detection probability in both sexes (males: $\beta = 0.10$, CrI: 0.05 - 0.16; females: $\beta = 0.10$, CrI: 0.03 - 0.16). Detection probability was also generally higher for individuals if they had already been detected during the previous period (males: $\beta = 0.64$, CrI: 0.57 - 0.71; females: $\beta = 0.24$, CrI: 0.17 - 0.32).

2.3.3 Wolf

Non-invasive genetic sampling and dead recoveries A total of 9 590 (4 156 female; 5 434 male) genotyped wolf genetic samples were included in the analysis (Figure 14, Table D.1), of which 74% originated from Sweden. These samples were associated with 1 092 (489 female; 603 male) individuals (Table D.2). We also included 457 dead recoveries of wolves, of which 366 (154 female; 212 male) were due to legal culling and 91 (43 female; 48 male) due to other causes of mortality (Figure 15; Table D.3). The majority of dead recoveries (71%) originated from Sweden.

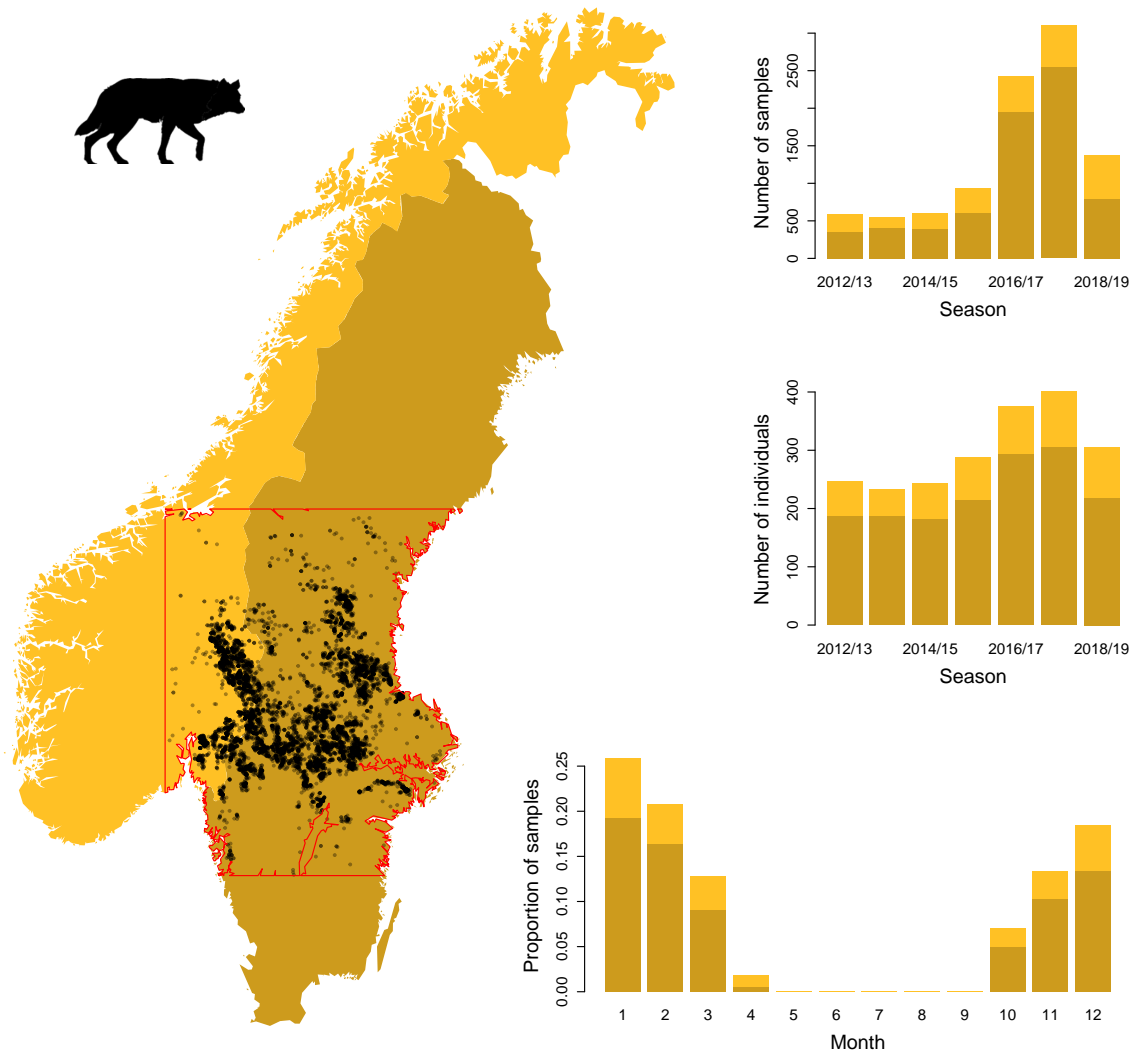


Figure 14: Spatio-temporal distribution of non-invasive genetic samples from wolves between Oct 1, 2012 and Apr 30, 2019. The red polygon defines the spatial extent included in the analysis; only samples included in the OPSCR analysis are shown. Light and dark background colors represent Norway and Sweden, respectively.

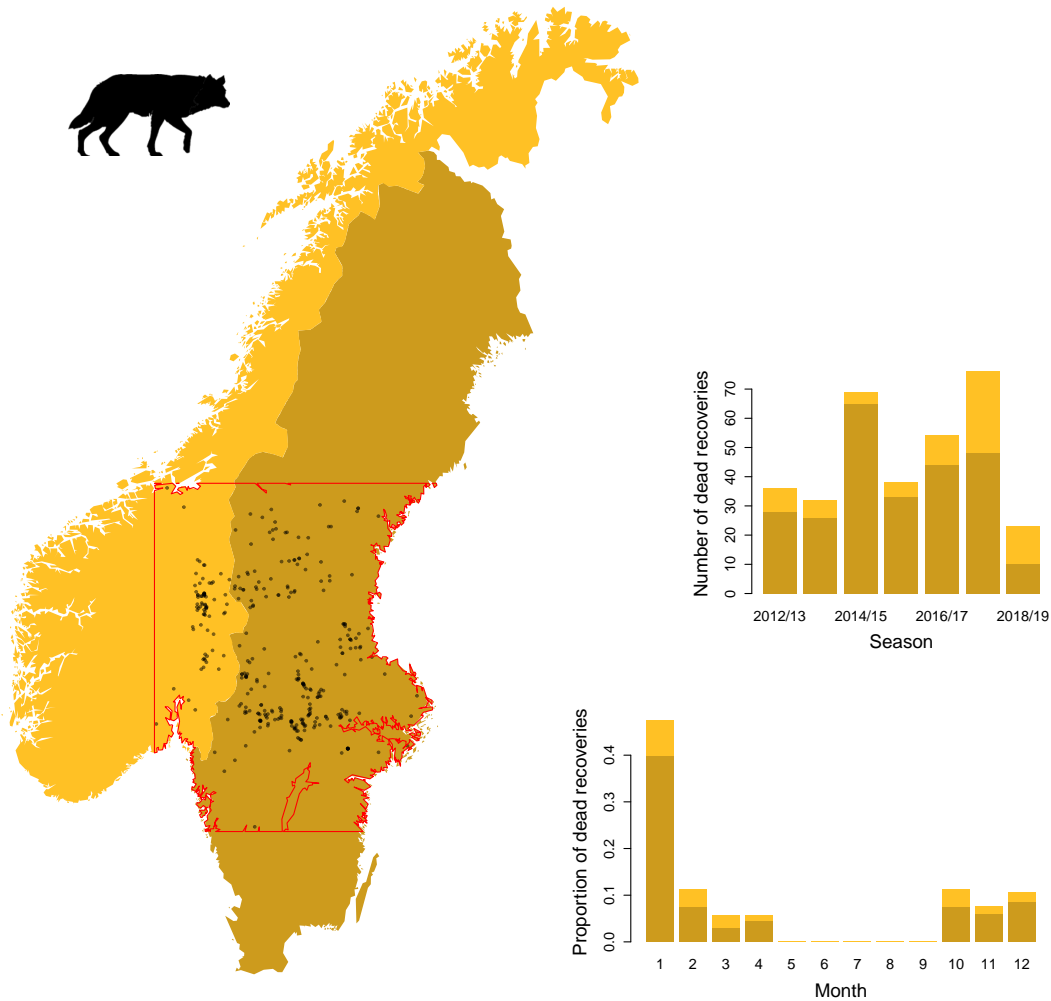


Figure 15: Spatio-temporal distribution of dead recoveries of wolves 2012/13 - 2018/19 within the spatial extent considered in this analysis (red polygon). Light and dark colors represent Norway and Sweden, respectively.

Density and abundance The model-estimated wolf abundance for the entire study area (254 000 km², excluding the buffer area) ranged between 357 (CrI: 337-381) in 2013/14 and 424 (CrI: 400-450) in 2014/15 (Figure 16). Estimates refer to the status of the population at the start of the annual sampling period (Oct. 1). In contrast to wolverines and bears, the Scandinavian wolf population exhibits an even sex ratio (49% females; CrI: 45-52; Table 3). Based on the model-predicted location of ACs, we estimated that in 2018/19, 297 wolves (CrI: 274-322) could be attributed to Sweden and 79 (CrI: 72-86) to Norway. This is compatible with what was reported for the same monitoring season by Svensson et al. (2019), i.e. 380 wolves in Scandinavia of which 300 were estimated to reside in Sweden. Whereas the OPSCR-estimated number of wolves in Sweden fluctuated without a clear upward or downward trend, we detected an increase in the Norwegian part of the wolf population during the study period (Figure 16). A further breakdown into annual county-specific estimates is provided in Appendix D (Table D.4). The greater number of detections associated with the increased survey effort in Sweden during the 2016/17 and 2017/18 seasons led to higher precision in estimates of population size (Figure 16). Note that estimates provided here differ slightly from those provided in Bischof et al. (2019). This is explained by the inclusion of 2 additional monitoring seasons, 2012/13 and 2018/19, which led to changes in the amount of information available for estimation in the remaining years, as information is propagated between years in the Bayesian OPSCR model.

Table 3: Population size estimates by sex and jurisdiction during the 2018/19 season based on OPSCR-estimated activity center locations of wolves in the study area. Combined female-male estimates are obtained by joining the sex-specific posterior distributions. Rounding may result in small deviations between total estimates shown here and the sum of the estimates from constituent regions.

	Females	Males	TOTAL
TOTAL	182.4 (166-202)	193 (178-211)	375.4 (352-402)
NORWAY	36.2 (31-43)	42.5 (39-47)	78.6 (72-86)
Region 2	0.4 (0-1)	0.1 (0-1)	0.5 (0-2)
Region 3	0.8 (0-3)	0.3 (0-2)	1.1 (0-4)
Region 4	7.7 (5-12)	12.6 (10-15)	20.3 (16-25)
Region 5	25.9 (21-31)	27.6 (24-31)	53.5 (47-60)
Region 6	1.2 (0-4)	1.7 (1-4)	2.8 (1-6)
SWEDEN	146.2 (130-165)	150.5 (136-168)	296.7 (274-322)
Östergötland	2.5 (1-5)	2.2 (1-5)	4.7 (2-8)
Dalarna	25.4 (19-32)	27.7 (21-35)	53.1 (44-63)
Gävleborg	24 (19-30)	26.4 (21-33)	50.4 (43-59)
Jämtland	6.9 (3-12)	10.6 (6-16)	17.5 (11-25)
Jönköping	0.2 (0-1)	0.2 (0-1)	0.4 (0-2)
Kalmar	0.2 (0-1)	0.2 (0-1)	0.4 (0-2)
Örebro	14.2 (9-21)	20 (16-25)	34.1 (27-42)
Södermanland	2.5 (1-5)	2.6 (1-5)	5.1 (2-9)
Stockholm	1.6 (0-4)	0.8 (0-3)	2.4 (0-5)
Uppsala	2.7 (1-6)	2.5 (1-5)	5.2 (2-9)
Värmland	46.5 (40-54)	38.4 (32-46)	84.9 (76-95)
Västerbotten	0 (0-0)	0 (0-0)	0 (0-0)
Västernorrland	2.3 (0-6)	3.2 (0-7)	5.5 (2-11)
Västmanland	10.6 (7-15)	8.2 (5-12)	18.8 (14-25)
Västra Götaland	6.7 (3-11)	7.8 (4-12)	14.5 (9-21)

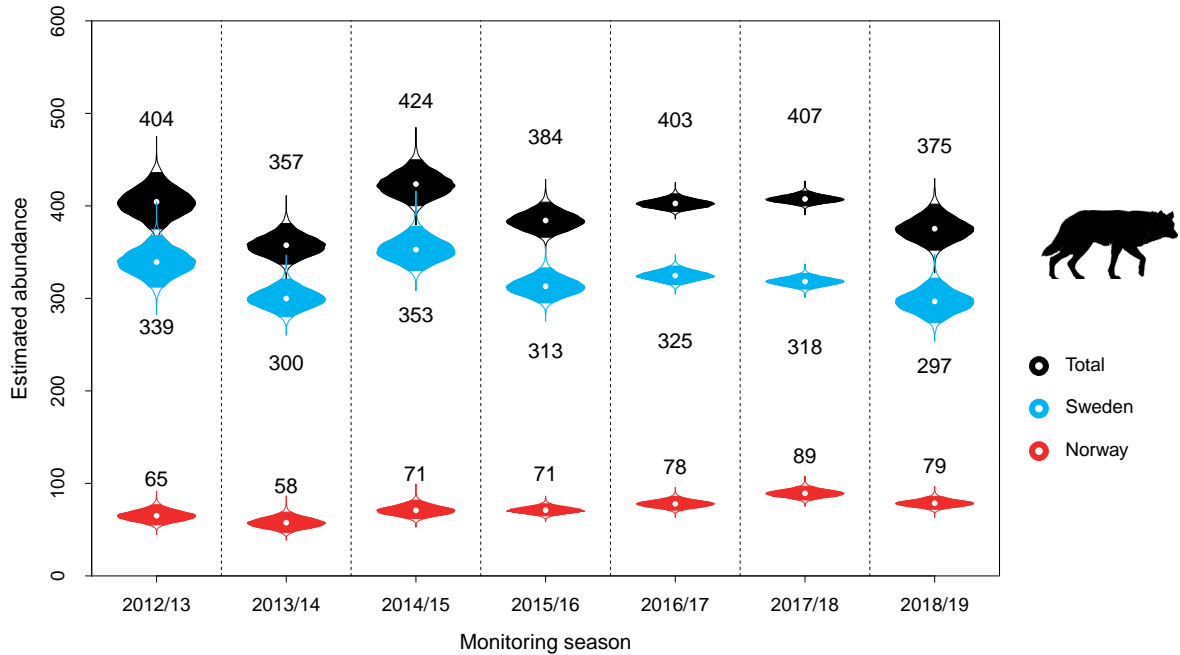


Figure 16: Total and country-specific annual wolf population size estimates from the OPSCR model within the study area. Violins show the posterior distribution of the annual population size estimates (points: mean estimates; solid colors: 95% credible interval). Values indicate rounded mean estimates.

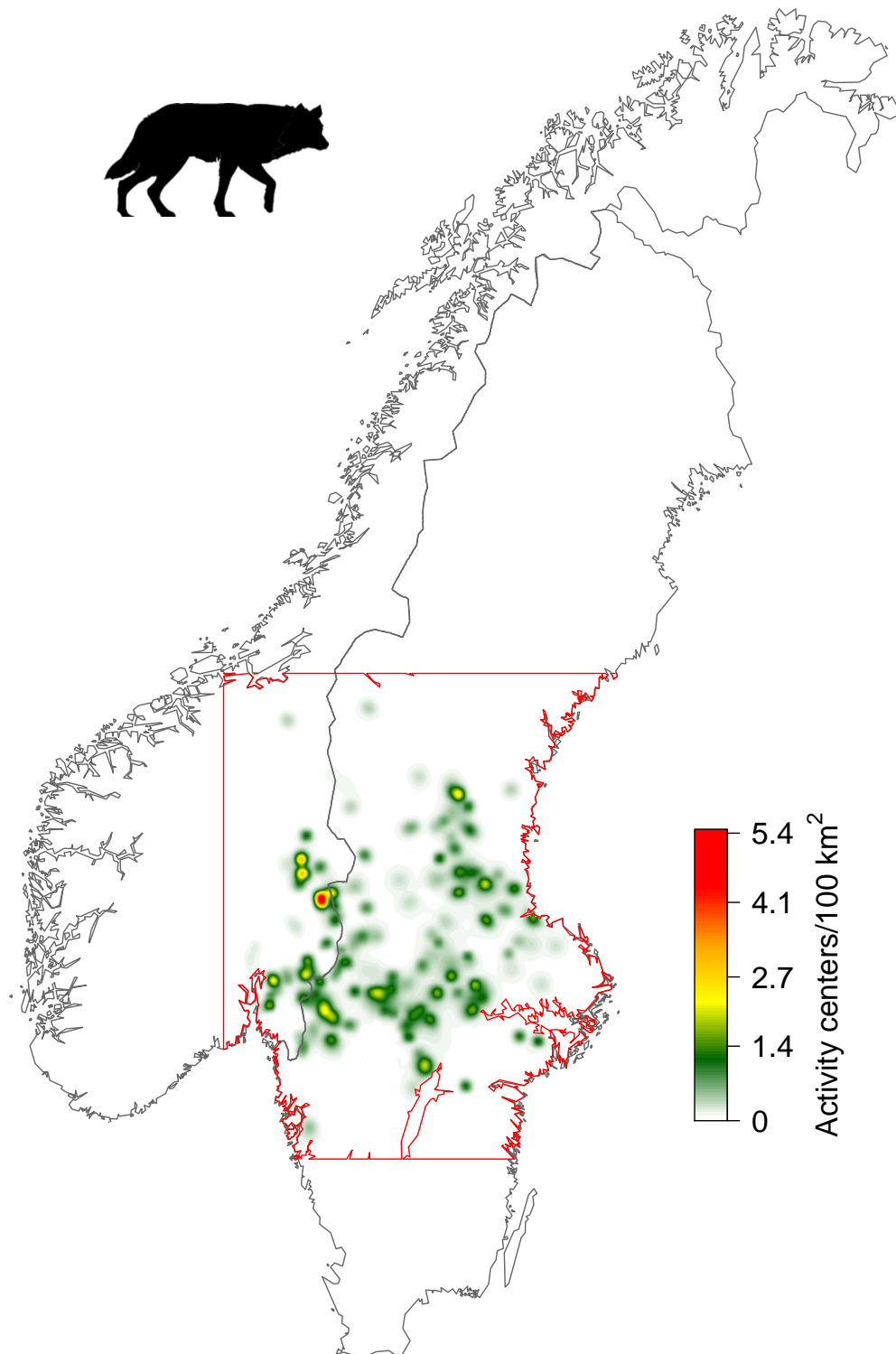


Figure 17: Wolf density throughout the study area in Scandinavia in 2018/19 derived from the OPSCR model. The area for which estimates were generated is outlined in red.

The OPSCR model yielded annual density maps, which illustrate changes in the distribution of wolves over time (Figure D.1). Average density in 2018/19 was estimated at 0.146 wolves per 100 km² (CrI: 0.137 – 0.156) throughout the 254 000 km² study area (Figure 17).

Vital rates The model produced annual estimates of legal hunting mortality, mortality associated with other causes and per capita recruitment rates (Figure 18; Table D.5). We detected no pronounced systematic differences in survival of female vs. male wolves. Overall, wolves identified as scent-marking adults were less vulnerable than other individuals to both legal culling and mortality due to other causes (Figure 18). With the exception of the 2018/19 season, legal culling mortality was consistently lower than mortality due to other causes (Figure 18). Note that vital rates reported here are not age-specific, but survival estimates are comparable to estimates reported for this population previously (population average: 0.7, Liberg et al. 2011; class specific: 0.42 - 0.79, Chapron et al. 2016).

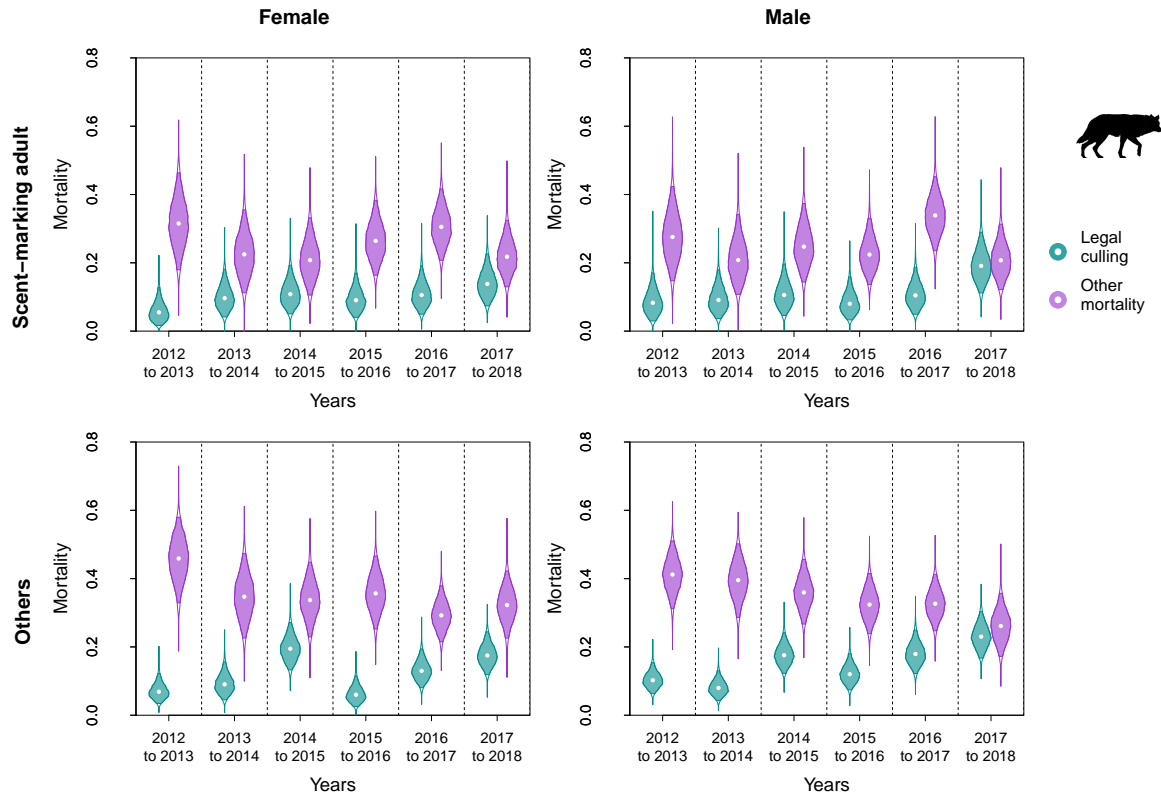


Figure 18: Mortality probabilities due to legal culling and other causes for female and male wolves. Shown are overall estimates throughout the study area. Violins show the posterior distribution of mortality estimates (points: median estimates; solid colors: 95% credible interval). Estimates reflect mortalities occurring between the start of one sampling season and the start of the next (hence mortality estimates between 2018/19 and 2019/20 are not yet available).

Home range size We estimated the scale parameter of the detection function (σ) as 7.7 km (CrI: 7.5-7.9 km) for female wolves and 8 km (CrI: 7.9-8.2 km) for males. The estimated median home range size for wolves, derived from σ , was 1 120 km² (CrI: 1 072 km² - 1 181 km²) for females and 1 216 km² (CrI: 1 173 km² - 1 259 km²) for males. As we do not currently model the age structure in the population, these values are averages over all age classes and include dispersing individuals. The similarity in home range sizes between males and females is not surprising, given that wolves move in packs. Our estimates are comparable to home ranges sizes reported previously for this population based on telemetry of scent-marking adults (\approx 1 000 km²; Mattisson et al. 2013)

Detection probability The baseline detection probability varied between counties, generally increased with time and was higher for individuals that had been identified as scent-marking members of pair or pack vs. those that had not (Figure D.2; more info in Bischof et al. 2019). Detection probability increased with the length of recorded search trails (males: $\beta = 0.29$, CrI: 0.26 - 0.32; females: $\beta = 0.29$, CrI: 0.26 - 0.32) and decreased in areas further away from roads for both males ($\beta = -0.41$, CrI: -0.57 - -0.26) and females ($\beta = -0.70$, CrI: -0.94 - -0.48). The average proportion of snow cover had no significant effect on the baseline detection probability for either sex (males: $\beta = -0.00$, CrI: -0.08 - 0.08; females: $\beta = 0.05$, CrI: -0.04 - 0.14). Detection probability increased significantly in Sweden during the two seasons with intensified NGS (Appendix 7). Detection probability was also generally higher for individuals if they had already been detected during a previous sampling season (males: $\beta = 0.11$, CrI: 0.02 - 0.21; females: $\beta = 0.38$, CrI: 0.28 - 0.48).

3 Other analyses

3.1 Mapping non-invasive genetic sampling effort

Genetic data collected as part of large carnivore monitoring in Scandinavia is the result of both systematic sampling by the authorities and opportunistic sampling by members of the public. As a consequence, not all areas within Scandinavia are sampled with equal intensity, and some areas may be subjected to no or insufficient sampling effort. To avoid biased abundance estimates, variation in search effort over time and across space should be accounted for. The OPSCR models can account for and quantify the effect of different covariates on detection probability; this includes temporal, individual and spatial covariates (Bischof et al., 2019). Any relevant spatial data can be used to model the variability in sampling effort and detection probability in general, including information about snow cover, distance to roads, and the intensity of searches (e.g. length of GPS search tracks within an area). In addition, the model can account for differences in overall detection effort between regions (e.g. counties or management regions). As a result, it is possible to map heterogeneity in detection probability using the predicted baseline detection probability (p_0). This provides a more general assessment of spatial variation in detectability and helps identify under-sampled regions (Figure 19).

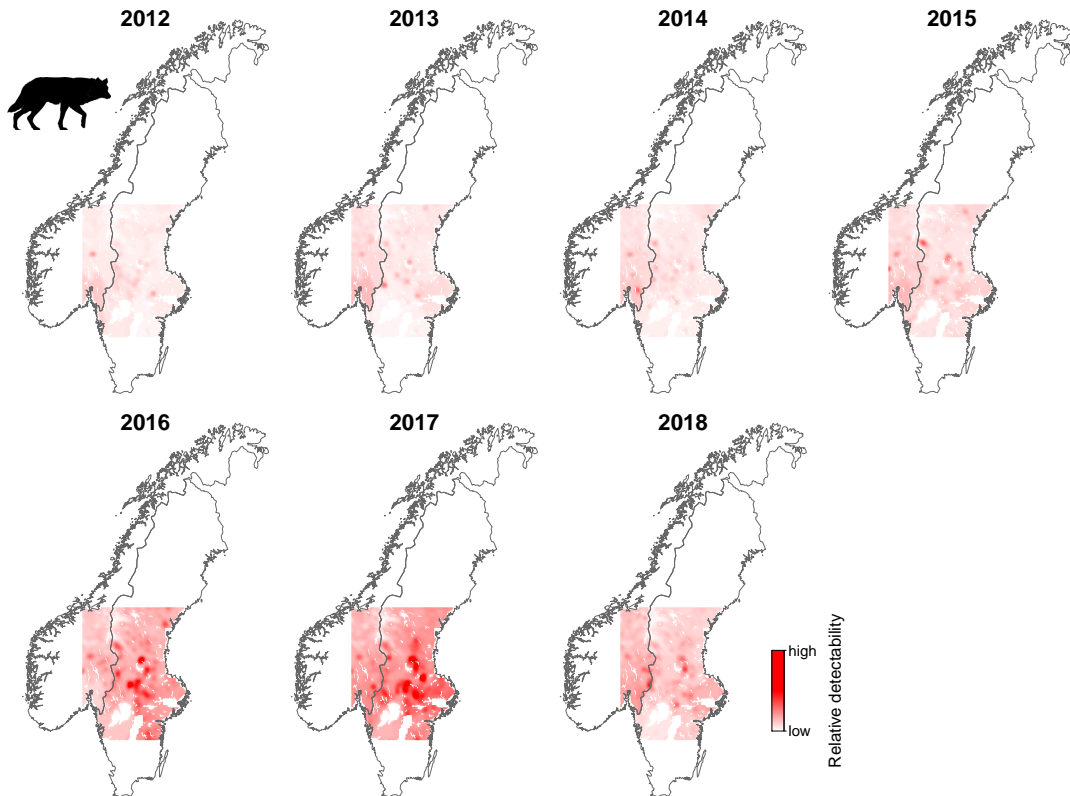


Figure 19: Annual maps of OPSCR-estimated relative baseline NGS detection probability for wolves during the study period.

3.2 Incorporating age into DNA-based estimation models

Important population parameters, such as survival and fecundity, are age-specific. However, individual age is not available directly from non-invasive genetic data. The ability to incorporate age information into models based on genetic sampling data would greatly expand their utility for studying and projecting population dynamics, as well as facilitate the estimation of age structure and effective population size (Luikart et al., 2010). We explored two ways in which age can be

incorporated into the OPSCR model. First, we reconstructed life histories for individuals with known age, using data from dead recovered and aged individuals. This reduces uncertainty about the demographic process - as some state transitions no longer need to be estimated - and the detection process - as some states are known even if the individual was not detected. Further testing is now needed to explore the conditions under which life history reconstruction can be done safely without biasing parameter estimates. Second, we have built a version of the OPSCR model that treats age as a latent variable which can be estimated by the model. While functional when age is known for a high proportion of detected individuals, the model so far fails to estimate age when the proportion of individuals with known age drops to levels encountered in empirical data or when detection probability is low. We will continue exploring latent age models during project WildMap (researchgate.net).

3.3 Assessing the consequences of reduced genetic sampling intensity

NGS of large carnivores in Scandinavia is costly. To date, neither the spatio-temporal configuration of the field collection effort, nor the subsequent selection of samples to be analyzed, have received a rigorous evaluation. Optimization of the monitoring design and sampling process can help balance the inherent tradeoff between the need for reliable and precise estimates and cost efficiency. To mimic a reduction in search effort, we artificially reduced the number of genetic samples in the Scandinavian wolverine NGS dataset by a) randomly removing a fixed proportion of samples and b) randomly removing a fixed proportion of search tracks and their associated samples. We then fit single-season SCR models to the subsampled data in order to quantify the impact of effort reduction on the precision and accuracy of abundance estimates. Relative bias was mild for low to moderate subsampling (25-50%) at the sample level, but was pronounced once 75% of samples were removed or 50% to 75% of tracks (Figure 20). The precision of the estimates decreased with the proportion of samples/tracks removed. These results suggest that a moderate reduction of sampling effort might be possible without significantly reducing the precision of the wolverine abundance estimates. Additional sampling reduction scenarios will be explored during 2020, including also NGS of wolf and bear.

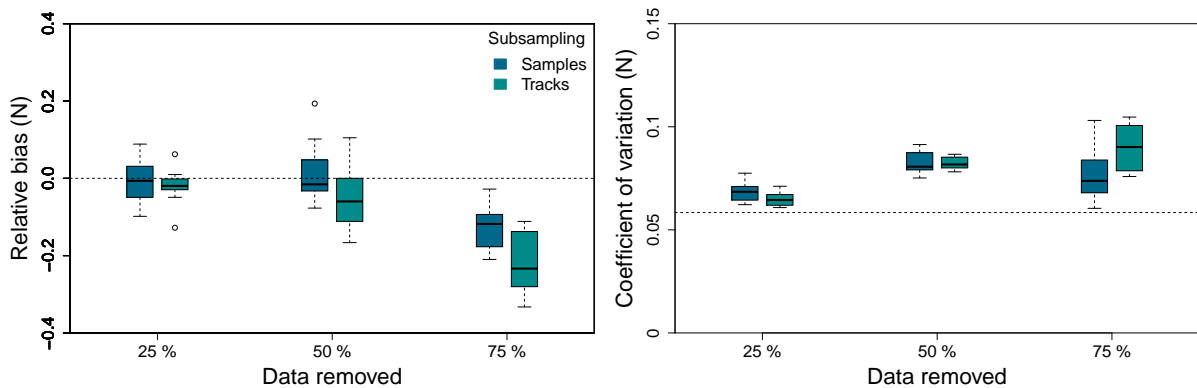


Figure 20: Relative bias and coefficient of variation in abundance (N), resulting from random removal of samples (blue boxes) and search tracks (blue-green boxes). Boxplots visualize the distribution of relative bias and coefficient of variation associated with 10 repetitions of a given random removal scenario. The higher the coefficient of variation, the lower the precision. Dashed horizontal lines indicate the relative bias and coefficient of variation associated with the model using 100% of the data (male and female wolverines in Norway; 2014/15 season).

3.4 Coping with patchy sampling data for brown bears in Sweden

The Norwegian brown bear monitoring program conducts annual sample collections throughout the bear range in the country. By contrast, the Swedish monitoring scheme consists of shifting regions (based on counties), with multi-year gaps between consecutive sampling in any given region, and some years without any sampling at all (Figure 21).

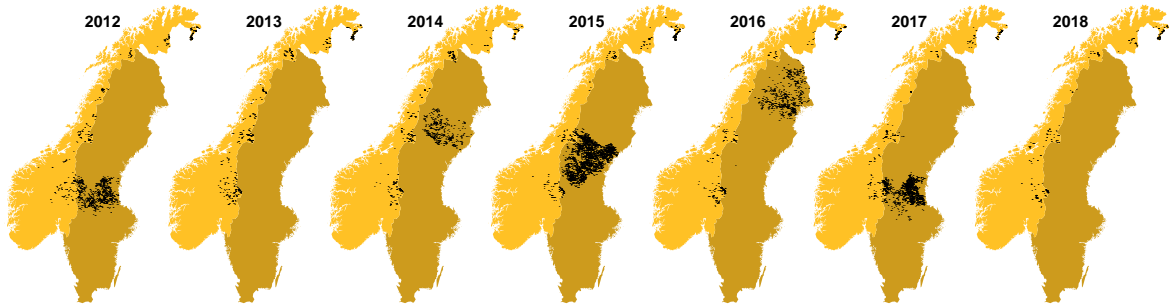


Figure 21: Annual distribution of brown bear non-invasive genetic samples collected in Norway and Sweden during the study period.

Although population size can be estimated with SCR methods for a given region at the time of sampling, the resulting discontinuous time series poses a challenge for modeling population dynamics and estimating annual population sizes. In theory, population-level OPSCR models may be able to accommodate spatial and temporal gaps in the data, as information about individual life histories is propagated across years and regions (Milleret et al., 2019b). This is in part due to bears being long-lived species with large home ranges: the same individuals may be available for detection in multiple regions and multiple monitoring seasons, even if the latter are separated by several years.

We first assessed whether estimates from OPSCR models are reliable in the presence of gaps in the sampling time series (i.e. discontinuous sampling). We used a simulation study in which we introduced temporal gaps during sampling of a hypothetical population and then fitted the OPSCR model to these data. We found that the model was able to reliably estimate abundance even when there are gaps in the time series, although the precision decreased with the proportion of interruptions in the time series (Figure 22, Milleret et al., 2019b).

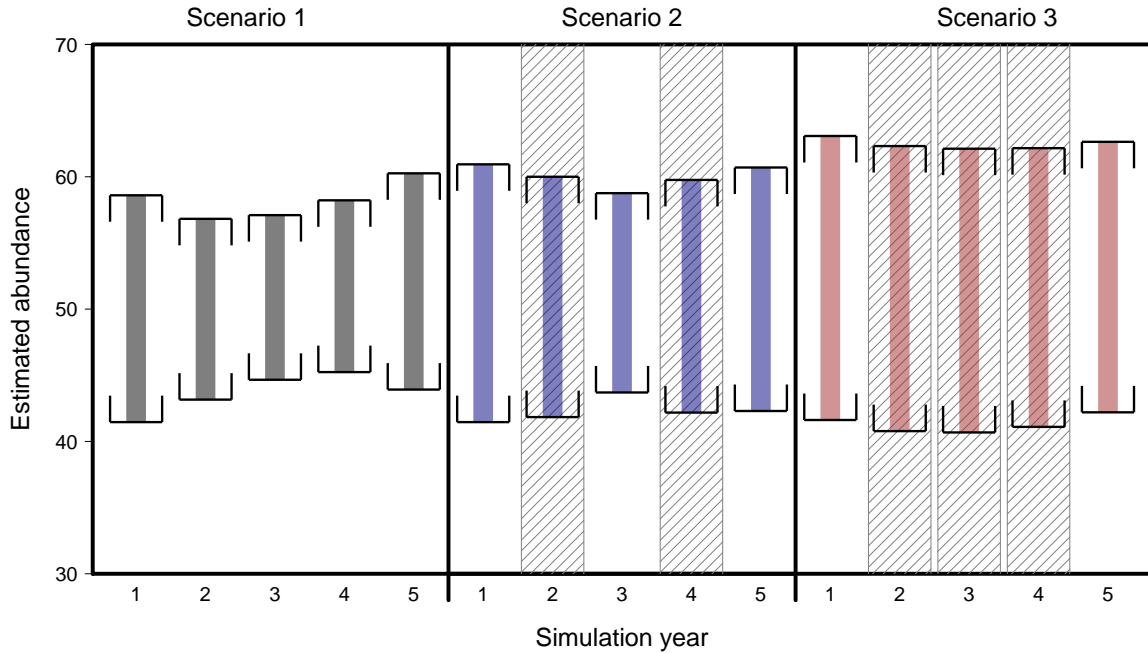


Figure 22: Bars indicating the width of the 95% credible interval associated with posterior estimates of annual population size for three different sampling scenarios. Wider credible intervals indicate greater uncertainty. Estimates obtained using an OPSCR model fitted to simulated populations of approximately 50 individuals each year, monitored over five consecutive years. Shown are aggregated results from 50 repeated simulations for each sampling scenario. Grey backgrounds indicate years without sampling.

Second, we quantified the gains in precision of the abundance estimates that arise from integrating dead recovery data (which are available every year for the bear population, including years without non-invasive genetic sampling) into the OPSCR model. Dead recovery data inform the analysis by allowing reconstruction of movement trajectories and life histories of some individuals (known fates; often known birth years). In cases where NGS detection probability is low, the precision gains from integrating dead recoveries can be substantial and, in some particularly data-sparse situations, this allowed fitting the model in the first place (RovQuant, unpublished). The ability of OPSCR to deal with gaps in NGS data collection, and to exploit information from annual dead recoveries enabled us to estimate annual density maps for brown bears (see subsection 2.3.1 and Figure B.1) despite the current patchy configuration of non-invasive genetic monitoring. However, for bears, we believe that we pushed the boundaries of what OPSCR model can accomplish with a highly irregular sampling design; results for this species should therefore be interpreted cautiously. Beyond estimates for the Norwegian extent (which was sampled regularly) and Swedish regions in years in which they were sampled, model estimates are of questionable reliability. It is possible that even a single year of range-wide NGS data added to the information analyzed with the OPSCR model may substantially change entire abundance and density time series, whereas current results from wolverines and wolves are less likely to be impacted by future data. More regular and range-wide monitoring of bears in Sweden, would greatly enhance the reliability of OPSCR-derived inferences about the bear population in Scandinavia.

3.5 Mapping vital rates

The OPSCR model yields population-level vital rates (survival, recruitment), which are not readily attainable with VHF/GPS-tagging studies (the usual source for vital rates in large carnivores), as these typically only target a small and non-random fraction of the population

and are limited in their spatial extent. The individual-based and spatially-explicit nature of the OPSCR model allows us to map mortality or per capita recruitment (see an example of mortality map, Figure 23). During project WildMap, we will expand the OPSCR model to include relevant spatial covariates and other sources of heterogeneity in vital rates, which will, among other things, allow identification of areas with low survival (e.g. due to unidentified sources of mortality; Bischof 2015) that may function as population sinks.

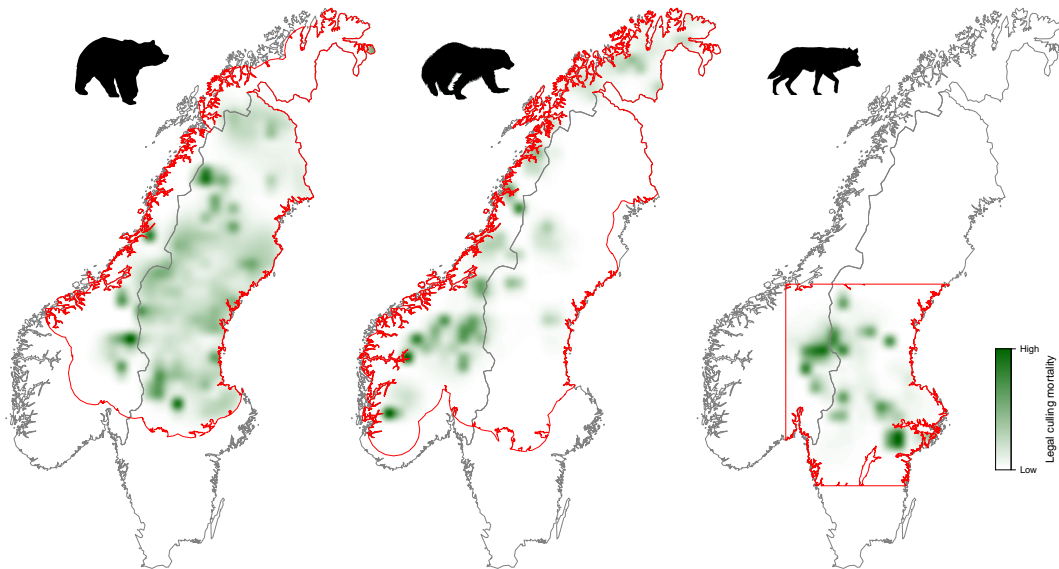


Figure 23: Smoothed OPSCR-derived maps of relative mortality due to legal culling for bears, wolverines and wolves in Scandinavia between the start of the two most recent monitoring seasons. Intensity of shading indicates the relative probability (light: low; dark: high) that an individual with an AC in that location will die due to legal culling. Note that in regions with low density (e.g. near the periphery of the range), mortality estimates are based on only few individuals. As a consequence, highly influential data points may be evident as point-like patterns (e.g. if only one individual is located in a given area and died due to culling, the probability of dying from culling in that area is equal to one).

3.6 Population projection

The main motivation for population monitoring of large carnivores in Scandinavia is to inform adaptive management, i.e. to assess current state, evaluate the outcome of past decisions, and to guide future ones. Trial and error is not a viable option for large-scale management of wildlife, and there is a long history of using predictive population models to evaluate the outcome of different management scenarios (Peterson et al., 2003; Jepsen et al., 2005; McRae et al., 2008). Because the Bayesian OPSCR model developed during project RovQuant explicitly models population dynamics, it can be used not only to estimate past and current abundance, but also to forecast future population abundance under different management scenarios (e.g. various harvest rates; Figure 24). In addition, the model captures the increase in uncertainty that arises as predictions are made further into the future (see violins in Figure 24). This application of the OPSCR model presents opportunities to evaluate the potential merits and risks of proposed management actions for the population. The next step in this development is an assessment of the reliability of forecasts made by the model by comparing predictions with estimates for years with known data. Conditional on the outcome of this assessment, the OPSCR models will be ready to use for making projections for alternative scenarios, at least for wolves and wolverines.

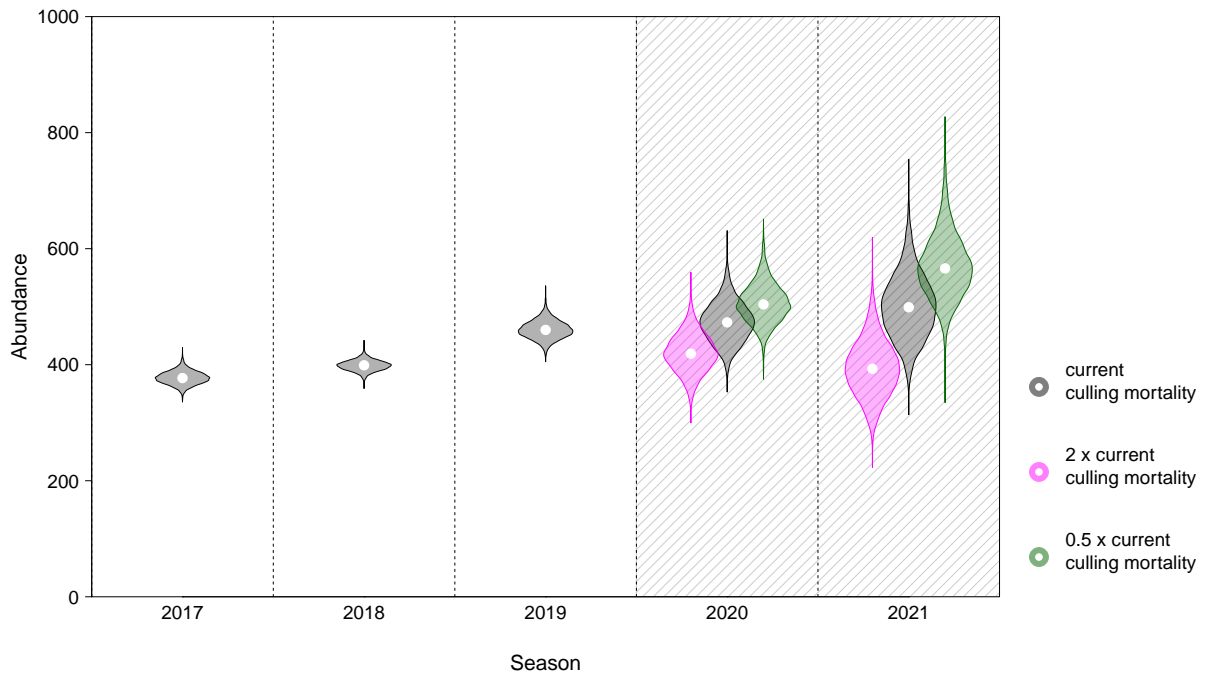


Figure 24: Estimates and forecast of abundance for a subset of the Swedish wolverine population (male only). Violins in the clear area show abundance estimates based on 3 years of non-invasive genetic sampling. Violins in the hashed area show abundance forecasts for two years for which non-invasive genetic sampling are not yet available. Forecasts are shown for three alternative levels of culling; “current” refers to the average annual hunting mortality estimated for the period with data (2017-2019).

4 General discussion

During project RovQuant we developed an OPSCR model that can be applied to monitoring data collected at an unprecedented scale. The model enabled us to exploit the extensive data collected by the Scandinavian monitoring programs and derive estimates of density, abundance and vital rates throughout the Scandinavian range of three large carnivore species: brown bears, wolverines, and wolves. We expect these results to become a valuable resource for large carnivore management, research, and public education in Scandinavia. Annual OPSCR-derived density maps for wolves have already been incorporated into the Scandinavian large carnivore database Rovbase 3.0 as an information source for managers and the public. Maps for bears and wolverines will soon be added.

RovQuant’s OPSCR model can now be applied to new monitoring data collected each year. This will result in up-to-date abundance and density estimates, as well as a growing time series of these parameters. Because information is propagated through time in the model, annual estimates are expected to become more precise as the time series of available data lengthens. Note that, as more information is incorporated, new estimates for earlier years may deviate from previously reported ones, especially for the bear, where the spatio-temporal configuration of sampling is not suited for range-wide estimation (subsection 3.4). In addition, continuation of the long-term monitoring and annual estimation will provide opportunities for testing and further development of the model. We strongly encourage an adaptive approach, whereby model predictions are validated against new information as it becomes available each year and necessary adjustments are made to the model to guarantee an evolution in both performance and reliability.

An essential step in the scientific process, is the rigorous vetting and review of ideas, methods, and results by the scientific community. Some of the work conducted as part of RovQuant has already been published in the peer-reviewed scientific literature, including versions of the OPSCR model (Bischof et al., 2016, 2017; Milleret et al., 2019b), specialized methods developed as part of the model (Milleret et al., 2018, 2019a), and tests of deviations from model assumptions (Dupont et al. et al., 2019, Bischof et al. in press). More of the work remains to be developed into scientific articles and subjected to peer review; this will be a focus for our research group during the coming two years.

With the ability to turn monitoring data compiled by the national monitoring programs in Sweden and Norway into annual estimates of spatially-explicit abundance using RovQuant’s OPSCR model, management is now nearing a crossroads with new options to monitor large carnivore populations, assess their status, and express population goals. In the current Norwegian management system, population goals are expressed as number of reproductions, i.e. the number of females (or, in the case of wolves, breeding packs) that have produced offspring. In Sweden, the population goals are expressed as number of individuals for all species, but even here, wolf abundance estimates are derived from the number of breeding packs using a conversion factor, Chapron et al. (2016); Bischof et al. (2019). The use of conversion factors or proxies for population size is in part a result of the elusiveness of direct estimates of abundance (Chapron et al., 2016). With both annual total and jurisdiction-specific population size estimates from the OPSCR model, management agencies in Scandinavia can now consider other options relying on direct carnivore abundance estimates in their management system, although this transition will be easier to implement in Sweden, where population goals are already expressed as abundance values. For brown bears in Sweden, we recommend a change to regular and range-wide sampling before relying on OPSCR-derived assessments of status in counties and years without sampling. Finally, in regions with very low abundance estimates (< 10 individuals), we advise against focusing on mean estimates, as the relative width of the credible interval is large and often includes or approaches zero.

RovQuant was made possible by the extensive long-term monitoring data compiled by the national monitoring programs in Sweden and Norway. At the same time, the project faced a se-

ries of significant challenges, due to the novelty of the methods employed and the unprecedented spatial scale at which RovQuant was working. Spatial capture-recapture models are a relatively recent development (Efford, 2004; Royle et al., 2014) and a series of conceptual and technical innovations were necessary to transition from the basic SCR model to an OPSCR model that included population dynamics, interannual movements, and multiple sources of information. All developments were accompanied by extensive tests, including simulation studies, in order to ensure that the resulting models produced reliable estimates. Perhaps the most significant challenge was computational. SCR studies are typically conducted in study areas of small to moderate size, ranging from a few hectares to a few thousand square kilometers (e.g. Goldberg et al. 2015; Humm et al. 2017; Efford and Schofield 2019; Goswami et al. 2019; Nelson et al. 2019; Petersen et al. 2019). By far, the largest study area used in SCR analysis outside of Scandinavia was a wolverine study in Canada (Mowat et al., 2019), with a total area of $>50\,000\text{ km}^2$ and 126 detected individuals, analyzed with a single-season SCR model. The authors still had to take a number of shortcuts to reduce the size of the computational problem. By comparison, the sizes of the study areas involved in RovQuant were $526\,000\text{ km}^2$ (bear), $593\,000\text{ km}^2$ (wolverine), and $254\,000\text{ km}^2$ (wolf), analyzed in a 7-year OPSCR model that included a total of 2 824 (bear), 2 118 (wolverine), and 1 092 (wolf) detected individuals. We were able to perform the millions of calculations required as part of these analyses (and the many tests and simulations conducted to test model performance) through methodological innovations that improved model efficiency (Milleret et al., 2018, 2019a), by implementing our modeling framework in NIMBLE with the assistance of the Nimble development team (NIMBLE Development Team, 2019; Turek et al., 2016; de Valpine et al., 2017), and by making use of computer clusters that allowed extensive parallelization. As a consequence, we are now able to fit OPSCR models to Scandinavian large carnivore monitoring data within a few days, whereas running earlier versions of our model would have not been feasible (e.g. using a rough extrapolation for a 2017-version of the model to this scale, we estimated a computation time of more than 3 years).

Aside from continuing the implementation and adaptation of the OPSCR model for analyzing the annual large carnivore monitoring data, RovQuant’s work will be expanded on by WildMap, a research project funded by the Research Council of Norway (NFR 286886; 2019-2022; researchgate.net). WildMap focuses on further development of the computation methods for processing large scale monitoring data and on exploring the spatial patterns and drivers of wildlife population dynamics. Among other things, these developments should allow us to further improve the OPSCR models by incorporating more species-specific details in the population dynamics and observation process aspects of the model.

If population-level abundance estimation is a goal, we recommend that brown bear monitoring in Sweden transitions from the current configuration with shifting survey areas and multi-year gaps between consecutive sampling in any given region, to regular and range-wide monitoring. Although the cost-precision tradeoff of alternative sampling designs still needs to be assessed, it may be possible to maintain the current overall sampling intensity, but spread sampling to cover all or most of the brown bear range in Sweden and perhaps conduct sampling biennially or every third year. While range wide estimates would clearly be beneficial for a comprehensive assessment of population status, this tradeoff also includes the costs of reduced precision of estimates at the county level and the logistic challenges associated with mobilizing volunteers for sample collection throughout a much larger spatial extent. Furthermore, we recommend avoiding non-random subsampling and prioritization of DNA samples subjected to genotyping, as this can invalidate the observation process model (function) and lead to biased estimates. This is especially a concern for wolves, where in most years resource and time constraints lead to non-random selection of samples for analysis. Most importantly, we recommend continued open communications between management, monitoring, and research, to ensure cost efficient collection of data that is suitable for large scale analysis and yields reliable parameter estimates useful to managers and policy makers.

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Appendices

A-D

Appendix A
Additional information

A Additional information

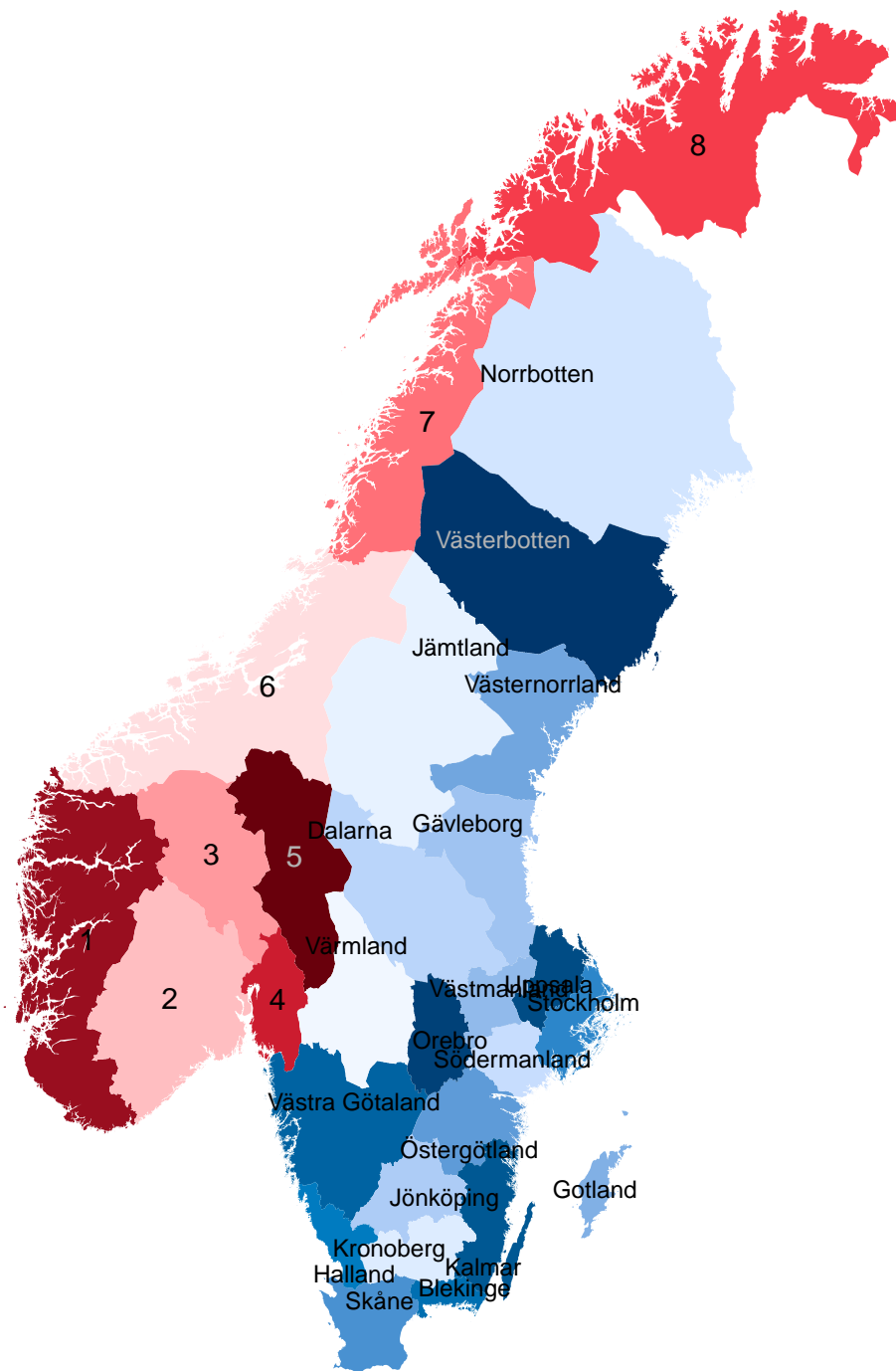


Figure A.1: Management units in Norway (carnivore management regions) and Sweden (counties).

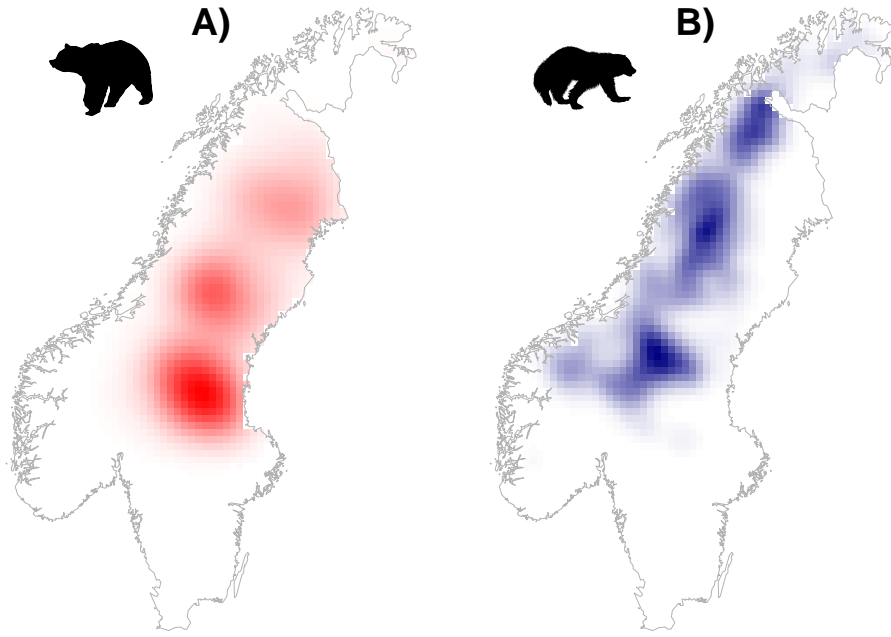


Figure A.2: Density covariate used in the OPSCR model for bear (A) and wolverine (B). Maps were obtained by applying smoothing kernel to location of known dens for wolverines and to all dead recovery locations for bears. See Bischof et al. (2019) for information about the density covariate used for wolf

Appendix B

Additional results for bear

B Bear

Table B.1: Annual number of brown bear non-invasive genetic samples included in the OPSCR analysis by country, for females (F) and males (M). We included only samples collected within the study area and during the primary monitoring period (Apr 1 – Nov 30) between 2012 and 2018.

	2012		2013		2014		2015		2016		2017		2018	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	213	324	227	421	185	305	236	339	183	281	187	268	190	213
Sweden	635	581	5	1	339	307	2250	2055	571	366	1253	867	2	0
Total	848	905	232	422	524	612	2486	2394	754	647	1440	1135	192	213

Table B.2: Annual number of individual brown bears detected via non-invasive genetic sampling that were included in the OPSCR analysis. Numbers are reported by country, for males (M) and for females (F). We included only individuals associated with samples collected within the study area and during the primary monitoring period (Apr 1 – Nov 30) between 2012 and 2018. Some individuals were detected in both countries during the same year, hence the sum of the national counts exceeds the total number of unique individuals detected in Scandinavia.

	2012		2013		2014		2015		2016		2017		2018	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	50	80	56	95	52	81	53	70	50	74	54	66	60	69
Sweden	239	196	2	1	131	116	584	436	212	136	375	261	2	0
Total	281	268	56	95	183	194	631	503	256	207	422	315	62	69

Table B.3: Number of cause-specific dead recoveries of brown bears in Scandinavia between 2012 and 2018 that were included in the OPSCR analysis. Numbers are reported by country, for males (M) and for females (F).

	Country	2012		2013		2014		2015		2016		2017		2018	
		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	1	1	0
	Sweden	9	4	5	6	9	7	10	7	7	11	5	6	10	15
Legal culling	Norway	0	13	0	4	2	11	2	7	0	8	0	8	2	8
	Sweden	155	190	148	173	127	179	113	163	101	141	125	151	132	169
Total	Total	164	207	153	183	138	197	126	177	108	160	130	166	145	192

Table B.4: Annual number of brown bear non-invasive genetic samples included in the OPSCR analysis, by country and management unit. The latter refers to counties (“Län”) in Sweden and large carnivore management regions in Norway (Figure A.1). We included only samples collected within the study area and during the primary monitoring period (Apr 1 – Nov 30) between 2012 and 2018.

	2012	2013	2014	2015	2016	2017	2018
TOTAL	1753	654	1136	4880	1401	2575	405
NORWAY	537	648	490	575	464	455	403
Region 1	0	0	0	0	0	0	0
Region 2	0	0	0	0	0	0	0
Region 3	17	7	2	8	5	0	2
Region 4	0	0	0	0	0	0	0
Region 5	136	165	151	138	166	181	124
Region 6	122	173	99	77	105	100	74
Region 7	65	69	55	6	5	33	6
Region 8	197	234	183	346	183	141	197
SWEDEN	1216	6	646	4305	937	2120	2
Dalarna	713	5	0	11	41	741	1
Gävleborg	471	0	0	3	0	1307	0
Jämtland	12	0	7	2978	1	26	0
Norrbotten	2	1	1	0	895	0	1
Örebro	0	0	0	0	0	2	0
Södermanland	0	0	0	0	0	0	0
Uppsala	0	0	0	0	0	0	0
Värmland	18	0	0	0	0	35	0
Västerbotten	0	0	638	18	0	0	0
Västernorrland	0	0	0	1295	0	7	0
Västmanland	0	0	0	0	0	2	0

Table B.5: Annual abundance estimates for brown bears at three spatial scales: the entire study area, by country, and by management unit. The latter refers to counties (“Län”) in Sweden and large carnivore management regions in Norway (Figure A.1). Estimates are the posterior distribution means of abundance based on OPSCR-estimated activity center locations. Credible intervals (95%) are shown in parentheses. Dark bold font indicates estimates for regions in years with systematic sampling. Swedish regions remain unsampled in most years (lighter font), making associated estimates less reliable as they are based primarily on information indirectly propagated in the model (from neighboring regions and years with sampling) rather than being directly informed by contemporary local data. Small deviations between the total estimate and the sum of abundance estimates from the constituent subregions may arise due to rounding.

	2012	2013	2014	2015	2016	2017	2018
TOTAL	2879.5 (2805-2958)	2947.2 (2880-3016)	3081.8 (3020-3147)	3205 (3136-3281)	3047.8 (2985-3116)	2878.9 (2797-2961)	2757.5 (2636-2877)
NORWAY	123.7 (110-138)	118.6 (109-129)	130.3 (117-144)	134.6 (118-152)	120.1 (107-135)	140 (123-159)	142.1 (124-162)
Region 1	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Region 2	0.1 (0-1)	0 (0-1)	0.1 (0-1)	0.2 (0-1)	0 (0-1)	0.2 (0-1)	0.3 (0-2)
Region 3	5.5 (4-8)	1.8 (1-4)	2 (0-4)	1.6 (0-4)	2 (1-4)	1.2 (0-4)	2.1 (0-6)
Region 4	0.2 (0-2)	0 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.1 (0-1)	0.4 (0-2)
Region 5	31.8 (26-39)	30 (25-36)	36.1 (29-43)	36 (28-44)	32.4 (26-39)	37.4 (31-44)	37.1 (29-46)
Region 6	34.1 (27-41)	35.8 (31-41)	32.4 (27-38)	41.5 (32-52)	37.7 (30-46)	43.8 (35-53)	44.2 (36-54)
Region 7	9.7 (6-14)	9.7 (8-12)	11.2 (8-15)	11.7 (6-18)	7.3 (3-13)	10.6 (5-17)	9.5 (4-16)
Region 8	42 (34-51)	41 (35-48)	48.2 (41-57)	43.2 (36-51)	40.5 (32-49)	46.5 (37-58)	48.2 (39-58)
SWEDEN	2755.8 (2682-2834)	2828.6 (2763-2898)	2951.5 (2890-3016)	3070.4 (3003-3142)	2927.7 (2867-2993)	2738.9 (2659-2819)	2615.4 (2499-2732)
Dalarna	285.2 (265-306)	397.3 (369-427)	441.5 (411-474)	506.9 (471-543)	452 (420-485)	322.8 (302-344)	427 (391-464)
Gävleborg	366.1 (340-393)	413.1 (384-443)	441.9 (410-473)	501.4 (466-535)	457.8 (426-489)	374.4 (359-390)	455.8 (421-491)
Jämtland	899 (855-943)	864.6 (826-905)	924.2 (887-962)	833.8 (814-854)	931.4 (892-971)	923.1 (874-974)	786.8 (732-840)
Norrbotten	579.2 (552-607)	525 (500-551)	514.4 (491-540)	533 (506-561)	437.5 (423-453)	499.5 (470-529)	432.8 (401-466)
Örebro	3.6 (0-8)	3.2 (0-7)	3.2 (0-7)	3.7 (0-8)	3.5 (0-8)	4 (1-8)	3.4 (0-7)
Södermanland	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)	0.1 (0-1)
Uppsala	5.9 (2-11)	5.7 (2-11)	5.5 (2-10)	6.2 (2-11)	4.7 (1-9)	4.4 (1-9)	3.8 (1-8)
Värmland	14.7 (9-22)	14.2 (8-21)	12.3 (6-19)	15.3 (9-23)	12.7 (6-20)	14.8 (10-21)	13.8 (7-21)
Västerbotten	343.3 (317-371)	335.3 (311-359)	311.2 (294-330)	402.2 (379-426)	333.6 (310-358)	316.7 (289-345)	264.1 (236-292)
Västernorrland	253.6 (229-278)	264.4 (240-289)	291.4 (270-314)	261.4 (251-273)	289.4 (266-312)	274.7 (250-300)	223.6 (198-248)
Västmanland	5.4 (1-10)	5.8 (2-11)	6 (2-11)	6.8 (2-12)	5.2 (1-10)	4.6 (1-9)	4.6 (1-9)

Table B.6: Estimates of the demographic parameters obtained for brown bear from the OPSCR model. Parameters represent transition rates from April 1 to March 31 in the following year. Median estimates and 95% credible intervals (in parentheses) for recruitment rate (ρ), survival (ϕ), mortality due legal culling (h), and mortality due to other causes (w) are presented for males (M) and females (F). Due to the spatio-temporally patchy genetic sampling in Sweden, recruitment rate (ρ) and "other" mortality (w) were assumed to be constant within a given time period (¹ 2012-2015; ²2015-2018). See Bischof et al. (2019) for a full description of the model parameters.

	2012-2013		2013-2014		2014-2015		2015-2016		2016-2017		2017-2018	
	M	F	M	F	M	F	M	F	M	F	M	F
ρ	0.21 (0.19-0.23) ¹	0.15 (0.13-0.17) ¹	0.21 (0.19-0.23) ¹	0.15 (0.13-0.17) ¹	0.21 (0.19-0.23) ¹	0.15 (0.13-0.17) ¹	0.13 (0.10-0.15) ²	0.08 (0.06-0.10) ²	0.13 (0.10-0.15) ²	0.08 (0.06-0.10) ²	0.13 (0.10-0.15) ²	0.08 (0.06-0.10) ²
ϕ	0.81 (0.79-0.83)	0.88 (0.87-0.90)	0.83 (0.81-0.85)	0.89 (0.87-0.91)	0.83 (0.81-0.85)	0.90 (0.89-0.92)	0.82 (0.79-0.84)	0.88 (0.86-0.90)	0.82 (0.80-0.85)	0.89 (0.86-0.91)	0.81 (0.78-0.84)	0.87 (0.85-0.89)
h	0.15 (0.13-0.17)	0.09 (0.08-0.11)	0.13 (0.12-0.15)	0.08 (0.07-0.10)	0.14 (0.12-0.16)	0.07 (0.06-0.08)	0.12 (0.10-0.13)	0.06 (0.05-0.07)	0.11 (0.09-0.13)	0.06 (0.05-0.07)	0.12 (0.11-0.14)	0.07 (0.06-0.08)
w	0.03 (0.02-0.04) ¹	0.02 (0.02-0.03) ¹	0.03 (0.02-0.04) ¹	0.02 (0.02-0.03) ¹	0.03 (0.02-0.04) ¹	0.02 (0.02-0.03) ¹	0.07 (0.05-0.09) ²	0.06 (0.04-0.08) ²	0.07 (0.05-0.09) ²	0.06 (0.04-0.08) ²	0.07 (0.05-0.09) ²	0.06 (0.04-0.08) ²

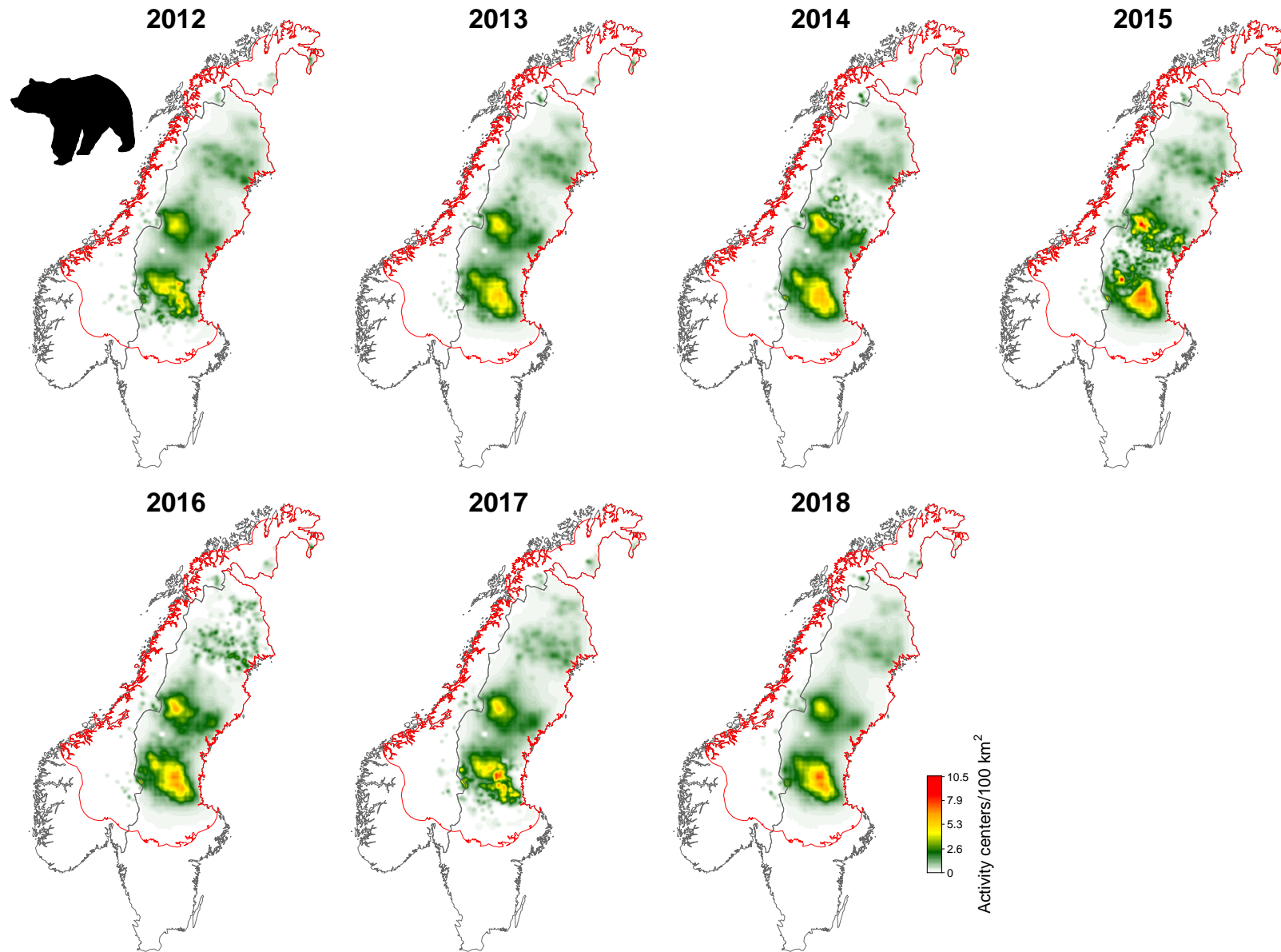


Figure B.1: Annual brown bear density derived from the OPSCR model. The area for which estimates were generated is outlined in red.

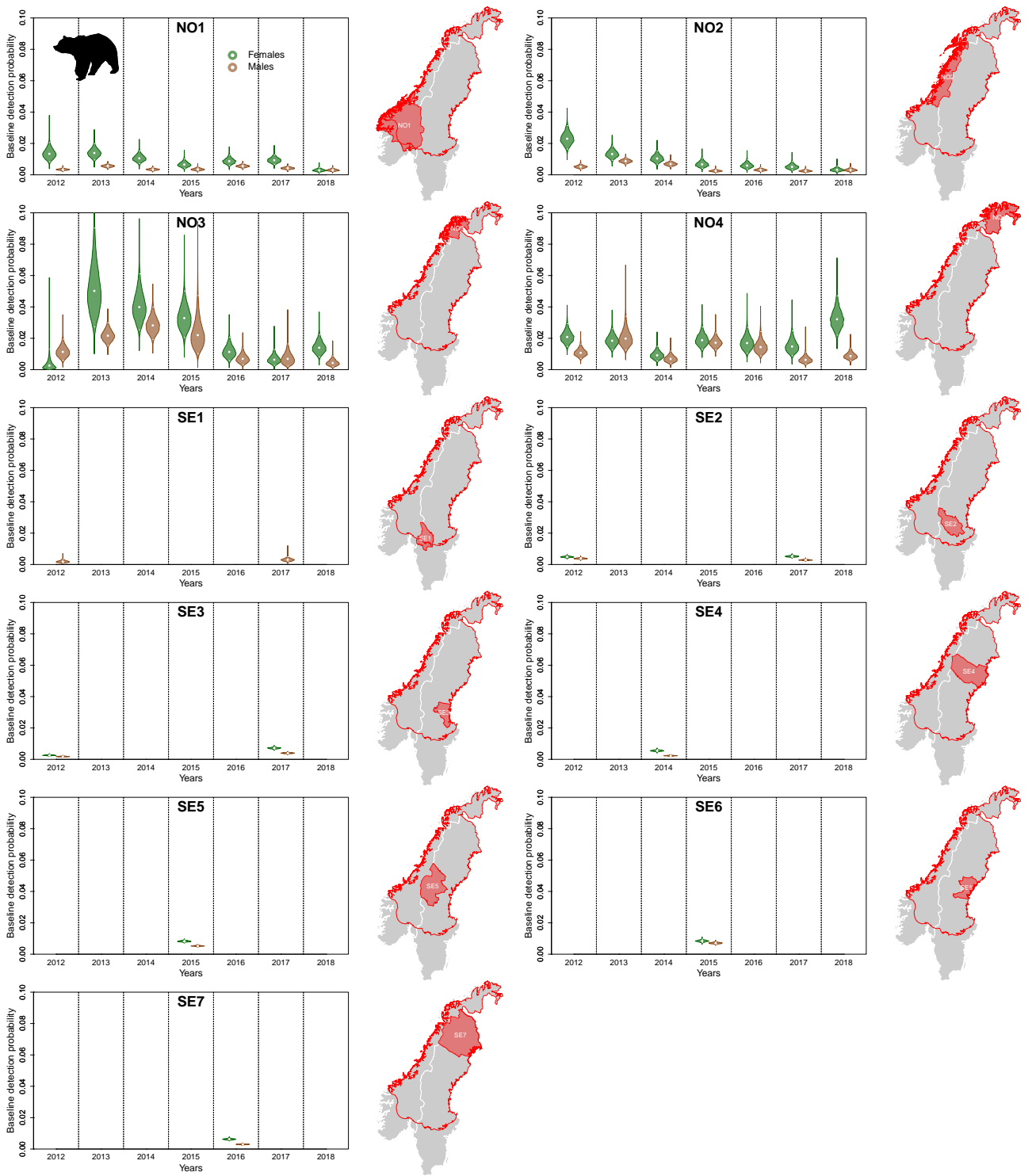


Figure B.2: Baseline detection probability (p_0) estimated by the OPSCR model for brown bears. Violins show the distribution of the posterior samples, white dots indicate the median, and areas with solid shading represent the 95% credible interval. Results are separated into panels based on the regions highlighted with red shading on the maps to the right of each violin plot. Estimates are shown for the mean values of the detection covariates.

Appendix C

Additional results for wolverine

C Wolverine

Table C.1: Annual number of wolverine non-invasive genetic samples included in the OPSCR analysis by country, for females (F) and males (M). We included only samples collected within the study area and during the primary monitoring period (Dec 1 – Jun 30) between 2012 and 2019.

	2013		2014		2015		2016		2017		2018		2019	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	459	546	524	580	416	447	471	581	606	670	465	750	592	733
Sweden	111	174	255	199	284	263	291	319	487	555	622	821	448	515
Total	570	720	779	779	700	710	762	900	1093	1225	1087	1571	1040	1248

Table C.2: Annual number of individual wolverines detected via non-invasive genetic sampling that were included in the OPSCR analysis. Numbers are reported by country, for females (F) and for males (M). We included only individuals associated with samples collected within the study area and during the primary monitoring period (Dec 1 – Jun 30) between 2012 and 2019. Some individuals were detected in both countries during the same year, hence the sum of the national counts can exceed the total number of unique individuals detected in Scandinavia.

	2013		2014		2015		2016		2017		2018		2019	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	174	146	190	136	158	117	182	127	182	132	173	126	193	152
Sweden	70	85	121	98	142	109	147	129	210	177	231	210	232	199
Total	243	225	305	225	292	218	323	248	376	288	393	318	416	338

Table C.3: Number of cause-specific dead recoveries of wolverines in Scandinavia between 2012 and 2019 that were included in the OPSCR analysis. Numbers are reported by country, for males (M) and for females (F).

	Country	2013		2014		2015		2016		2017		2018		2019	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway	0	2	1	1	0	1	2	0	1	0	0	1	0	1
	Sweden	0	0	1	2	0	1	0	1	0	1	0	1	0	1
Legal culling	Norway	42	50	30	21	42	39	33	36	34	44	23	27	33	24
	Sweden	8	14	11	8	15	11	6	9	4	1	2	5	3	3
Total	Total	50	66	43	32	57	52	41	46	39	46	25	34	36	29

Table C.4: Annual abundance estimates for wolverines at three spatial scales: the entire study area, by country, and by management unit. The latter refers to counties (“Län”) in Sweden and large carnivore management regions in Norway (Figure A.1). Estimates are the posterior distribution means of abundance based on OPSCR-estimated activity center locations. 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.

	2013	2014	2015	2016	2017	2018	2019
TOTAL	980.1 (904-1061)	896.6 (848-951)	885.4 (843-931)	943.3 (900-988)	941.7 (909-977)	944.5 (914-977)	1034.8 (985-1088)
NORWAY	442.4 (411-476)	394.6 (371-419)	393.1 (371-416)	397.1 (377-419)	376 (358-395)	360.1 (342-379)	374.7 (353-397)
Region 1	12.2 (7-18)	10.9 (6-16)	11.8 (8-16)	6.6 (4-10)	6.3 (3-11)	5.8 (3-10)	6 (2-11)
Region 2	4.2 (1-9)	2.8 (0-6)	2.2 (0-5)	2.1 (0-5)	2.4 (1-5)	2.5 (0-5)	2.8 (0-6)
Region 3	30.5 (24-38)	35.7 (29-43)	38.3 (31-46)	35.1 (29-41)	30.8 (25-37)	25.7 (21-31)	27.3 (22-33)
Region 4	1.4 (0-4)	0.8 (0-3)	0.7 (0-3)	0.7 (0-3)	0.5 (0-2)	0.4 (0-2)	0.9 (0-3)
Region 5	72.6 (63-84)	67.9 (59-77)	72.1 (63-82)	73.2 (65-82)	75.1 (67-84)	81.8 (74-90)	87.3 (79-96)
Region 6	89.9 (77-104)	83.5 (73-95)	85.6 (74-97)	92.2 (82-103)	90 (80-100)	95.5 (86-106)	97.6 (87-109)
Region 7	98.9 (89-110)	77.6 (68-87)	69.1 (61-78)	78.6 (70-87)	65.3 (58-73)	59.5 (52-67)	62.4 (54-71)
Region 8	132.8 (117-149)	115.5 (105-127)	113.5 (102-126)	108.7 (98-121)	106 (97-116)	88.9 (79-99)	90.4 (80-102)
SWEDEN	537.7 (481-598)	502 (463-543)	492.3 (459-528)	546.2 (511-583)	565.7 (538-594)	584.5 (560-611)	660.1 (619-703)
Östergötland	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Dalarna	30.6 (22-40)	26.3 (19-34)	25.9 (19-34)	26.2 (19-33)	33.7 (27-41)	42.7 (36-49)	41.6 (34-50)
Gävleborg	11 (5-18)	10.9 (5-17)	11.8 (7-17)	14.3 (9-20)	16.4 (11-23)	19.6 (14-25)	33 (27-40)
Jämtland	159.9 (138-182)	160.2 (142-180)	158 (142-176)	179.6 (164-196)	190.2 (174-207)	196.3 (182-211)	211.3 (192-231)
Norrbottn	176.7 (150-206)	151.6 (132-172)	151.5 (133-171)	170 (150-190)	164.4 (154-176)	162.1 (152-173)	194.4 (175-215)
Örebro	2.2 (0-5)	1.2 (0-4)	0.8 (0-3)	0.8 (0-3)	1.1 (0-3)	1.2 (0-3)	1.5 (0-4)
Södermanland	0 (0-1)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Uppsala	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Värmland	9.8 (5-15)	7.5 (4-12)	5.4 (2-9)	8.9 (5-13)	11 (7-16)	8.6 (5-12)	8.4 (4-13)
Västerbotten	124.5 (104-146)	126.8 (113-142)	120.1 (110-131)	127.5 (115-141)	121.6 (110-135)	120.9 (107-135)	133.5 (117-151)
Västernorrland	22.1 (15-29)	17.1 (11-24)	18.3 (12-25)	18.5 (12-26)	26.6 (19-34)	32.7 (26-40)	35.5 (28-43)
Västmanland	0.7 (0-3)	0.4 (0-2)	0.3 (0-2)	0.3 (0-2)	0.3 (0-2)	0.2 (0-1)	0.6 (0-2)
Västra Götaland	0.1 (0-1)	0.1 (0-1)	0 (0-1)	0.1 (0-1)	0 (0-1)	0.1 (0-1)	0.2 (0-1)

Table C.5: Estimates of the demographic parameters obtained from the wolverine OPSCR model. Parameters represent transition rates from the start of one monitoring season to the start of the next one. Median estimates and 95% credible intervals (in parentheses) for recruitment rate (ρ), survival (ϕ), mortality due legal culling (h), and mortality due to other causes (w) are presented for males (M) and females (F). See Bischof et al. (2019) for a full description of the model parameters.

	2013-2014		2014-2015		2015-2016		2016-2017		2017-2018		2018-2019	
	M	F	M	F	M	F	M	F	M	F	M	F
ρ	0.29 (0.20-0.39)	0.30 (0.19-0.43)	0.35 (0.26-0.44)	0.22 (0.15-0.31)	0.35 (0.27-0.43)	0.31 (0.23-0.40)	0.36 (0.29-0.42)	0.24 (0.18-0.31)	0.38 (0.33-0.44)	0.23 (0.18-0.29)	0.43 (0.37-0.49)	0.29 (0.24-0.35)
ϕ	0.51 (0.44-0.58)	0.64 (0.58-0.71)	0.62 (0.56-0.68)	0.73 (0.68-0.78)	0.65 (0.58-0.70)	0.77 (0.72-0.83)	0.64 (0.58-0.69)	0.74 (0.68-0.78)	0.61 (0.56-0.67)	0.73 (0.68-0.78)	0.64 (0.58-0.70)	0.76 (0.69-0.83)
h	0.14 (0.11-0.18)	0.08 (0.06-0.11)	0.08 (0.06-0.12)	0.07 (0.05-0.10)	0.13 (0.10-0.17)	0.10 (0.08-0.13)	0.12 (0.09-0.15)	0.07 (0.05-0.09)	0.12 (0.09-0.15)	0.06 (0.04-0.08)	0.09 (0.06-0.12)	0.04 (0.03-0.06)
w	0.35 (0.28-0.41)	0.28 (0.21-0.35)	0.29 (0.23-0.35)	0.20 (0.14-0.25)	0.22 (0.17-0.28)	0.13 (0.08-0.18)	0.24 (0.19-0.29)	0.20 (0.15-0.25)	0.27 (0.22-0.32)	0.21 (0.16-0.26)	0.27 (0.22-0.33)	0.20 (0.13-0.26)

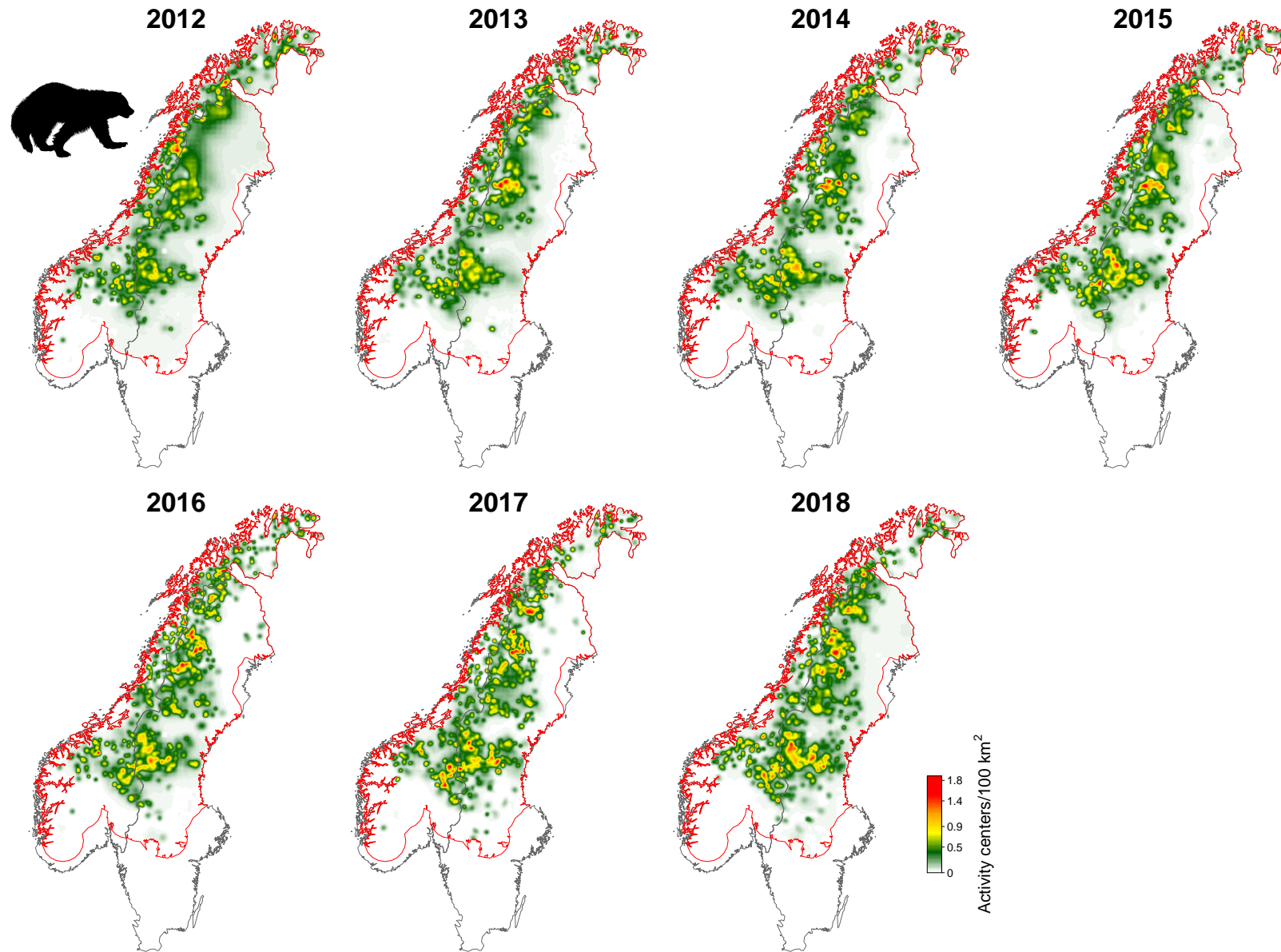


Figure C.1: Annual wolverine density derived from the OPSCR model. The area for which estimates were generated is outlined in red.

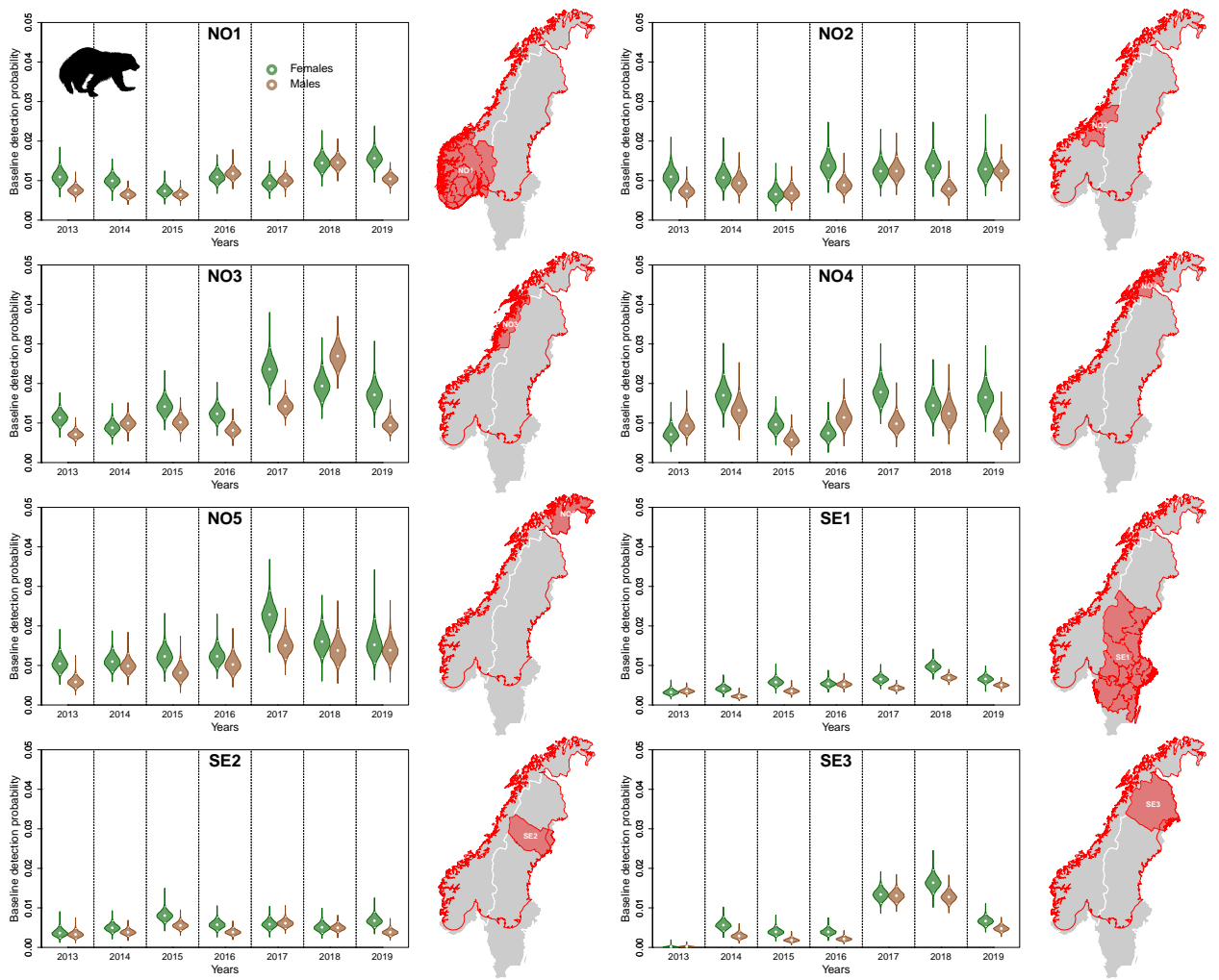


Figure C.2: Baseline detection probability (p_0) estimated by the OPSCR model for wolverines. Violins show the distribution of the posterior samples, white dots indicate the median, and areas with solid shading represent the 95% credible interval. Results are separated into panels based on the regions highlighted with red shading on the maps to the right of each violin plot. Estimates are shown for the mean values of the detection covariates.

Appendix D

Additional results for wolf

D Wolf

Table D.1: Annual number of wolf non-invasive genetic samples included in the OPSCR analysis by country, for females (F) and males (M). We included only samples collected within the study area and during the primary monitoring period (Oct 1 - Mar 31) between 2012 and 2019.

	2012/2013		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	81	146	53	81	94	108	147	184	264	206	275	280	235	339
Sweden	139	225	183	231	180	223	239	366	840	1113	1077	1480	349	452
Total	220	371	236	312	274	331	386	550	1104	1319	1352	1760	584	791

Table D.2: Annual number of individual wolves detected via non-invasive genetic sampling that were included in the OPSCR analysis. Numbers are reported by country, for females (F) and for males (M). We included only individuals associated with samples collected within the study area and during the primary monitoring period (Oct 1 - Mar 31) from 2012 to 2019. Some individuals were detected in both countries during the same year, hence the sum of the national counts can exceed the total number of unique individuals detected in Scandinavia.

	2012/2013		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Norway	25	35	18	27	28	33	29	44	46	36	49	46	41	46
Sweden	81	107	84	103	87	96	91	124	140	154	150	156	105	113
Total	103	137	97	124	111	123	115	161	172	183	188	187	138	150

Table D.3: Number of cause-specific dead recoveries of wolves in Scandinavia between 2012 and 2019 that were included in the OPSCR analysis. Numbers are reported by country, for females (F) and for males (M).

		Country	2012/2013		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019	
			F	M	F	M	F	M	F	M	F	M	F	M	F	M
Other	Norway		0	1	1	3	0	0	1	2	0	0	1	4	2	0
	Sweden		8	8	4	5	7	11	7	5	4	2	5	2	3	5
Legal culling	Norway		1	13	5	7	4	8	6	6	7	7	19	14	10	11
	Sweden		11	19	12	13	33	32	8	20	20	26	15	31	3	5
Total	Total		20	41	22	28	44	51	22	33	31	35	40	51	18	21

Table D.4: Annual abundance estimates for wolves at three spatial scales: the entire study area, by country and by management unit. The latter refers to counties (“Län”) in Sweden and large carnivore management regions in Norway (Figure A.1). Estimates are the posterior distribution means of abundance based on OPSCR-estimated activity center locations. 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.

	2012/2013	2013/2014	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019
TOTAL	404.4 (375-436)	357.4 (337-381)	423.6 (400-450)	384.2 (366-404)	402.6 (394-413)	407.5 (400-416)	375.4 (352-402)
NORWAY	65.1 (55-77)	57.6 (47-69)	70.9 (62-82)	71.1 (65-78)	78 (71-86)	89.3 (82-97)	78.6 (72-86)
Region 2	1.8 (0-5)	1.6 (0-4)	0.4 (0-2)	0.1 (0-1)	0.3 (0-2)	0.2 (0-1)	0.5 (0-2)
Region 3	1.9 (0-5)	3.1 (1-6)	2.6 (1-5)	0.7 (0-3)	0.7 (0-3)	1 (0-3)	1.1 (0-4)
Region 4	12.7 (8-18)	8.4 (5-13)	6.3 (4-10)	8.5 (7-11)	15.8 (12-20)	20 (17-24)	20.3 (16-25)
Region 5	44.3 (38-52)	41.5 (34-50)	58.9 (51-68)	60.2 (55-66)	60 (54-67)	66.4 (60-73)	53.5 (47-60)
Region 6	3.9 (1-8)	2.7 (0-6)	2.3 (0-6)	1.2 (0-4)	0.9 (0-3)	1.4 (0-4)	2.8 (1-6)
SWEDEN	339.3 (312-368)	299.9 (280-321)	352.7 (330-378)	313.1 (295-333)	324.6 (315-335)	318.2 (310-327)	296.7 (274-322)
Östergötland	5.2 (2-10)	4 (1-8)	3.3 (0-7)	3 (0-7)	1.5 (1-3)	3.5 (2-5)	4.7 (2-8)
Dalarna	80.9 (69-93)	68 (57-80)	72.2 (61-84)	71.5 (63-81)	75.5 (69-82)	57.3 (52-63)	53.1 (44-63)
Gävleborg	25.4 (18-33)	24.8 (18-32)	30 (23-38)	42.8 (36-50)	56.5 (51-62)	60.4 (56-65)	50.4 (43-59)
Jämtland	23.6 (16-33)	18.5 (12-25)	18.2 (11-26)	18.3 (12-25)	12.3 (8-17)	6.2 (3-10)	17.5 (11-25)
Jönköping	1.4 (0-4)	0.7 (0-3)	0.6 (0-2)	0.4 (0-2)	0.1 (0-1)	0.2 (0-1)	0.4 (0-2)
Kalmar	0.5 (0-2)	0.4 (0-2)	0.3 (0-2)	0.3 (0-2)	0 (0-1)	0.1 (0-1)	0.4 (0-2)
Örebro	43.7 (34-54)	32.5 (26-40)	57.2 (45-71)	42.5 (32-53)	33.8 (29-39)	31.9 (28-36)	34.1 (27-42)
Södermanland	3.1 (0-7)	2 (0-5)	3 (0-7)	3.1 (1-6)	2.8 (2-5)	13.3 (11-16)	5.1 (2-9)
Stockholm	4.1 (2-7)	1.3 (0-4)	2.8 (1-6)	2.7 (0-5)	1.9 (1-3)	3.5 (2-6)	2.4 (0-5)
Uppsala	3.6 (0-8)	2.2 (0-5)	3.6 (1-7)	4.3 (2-8)	3.8 (1-6)	4.9 (2-8)	5.2 (2-9)
Värmland	101.4 (88-115)	114.3 (102-128)	117 (103-132)	94.4 (84-106)	102.6 (94-112)	96.8 (90-103)	84.9 (76-95)
Västerbotten	0 (0-1)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Västernorrland	7.5 (3-13)	5.3 (2-9)	5.7 (2-10)	5.1 (2-9)	2.7 (1-5)	0.6 (0-2)	5.5 (2-11)
Västmanland	21.1 (15-28)	11.9 (8-17)	22 (16-28)	14.6 (10-20)	23.9 (21-27)	30.4 (27-34)	18.8 (14-25)
Västra Götaland	18.4 (13-25)	14.3 (9-20)	17.3 (12-24)	10.5 (6-15)	7.4 (3-12)	9.5 (6-13)	14.5 (9-21)

Table D.5: Estimates of the demographic parameters obtained from the wolf OPSCR model. Parameters represent transition rates from Oct 1 to Sep 30 in the following year. Median estimates and 95% credible intervals (in parentheses) for per capita recruitment rate (ρ), survival (ϕ), mortality due legal culling (h) and mortality due to other causes (w) are presented for males (M) and females (F). For wolves, separate alive states were used in the model for “Scent-marking adult” (State 3) and “other” (State 2) individuals. Therefore, in addition to recruitment and survival, the model also estimates transition probability from “Other” to “Scent-marking adult” (ψ); see Bischof et al. (2019) for a full description of the model parameters.

State		2012-2013		2013-2014		2014-2015		2015-2016		2016-2017		2017-2018	
		M	F	M	F	M	F	M	F	M	F	M	F
ρ	-	0.46 (0.35-0.59)	0.47 (0.32-0.68)	0.83 (0.67-1.02)	0.93 (0.70-1.21)	0.55 (0.44-0.69)	0.51 (0.38-0.67)	0.53 (0.43-0.63)	0.87 (0.69-1.05)	0.70 (0.63-0.77)	0.71 (0.63-0.79)	0.67 (0.55-0.81)	0.53 (0.41-0.68)
	2	0.48 (0.39-0.58)	0.47 (0.36-0.59)	0.52 (0.42-0.63)	0.56 (0.44-0.68)	0.46 (0.37-0.55)	0.46 (0.36-0.57)	0.55 (0.46-0.64)	0.58 (0.47-0.69)	0.49 (0.41-0.58)	0.57 (0.48-0.66)	0.51 (0.41-0.61)	0.50 (0.40-0.60)
ϕ	3	0.63 (0.49-0.77)	0.62 (0.48-0.77)	0.69 (0.56-0.81)	0.67 (0.54-0.80)	0.64 (0.51-0.76)	0.68 (0.55-0.80)	0.69 (0.57-0.79)	0.64 (0.52-0.75)	0.55 (0.44-0.66)	0.58 (0.47-0.69)	0.60 (0.48-0.71)	0.64 (0.52-0.75)
	-	0.28 (0.19-0.40)	0.40 (0.26-0.54)	0.24 (0.15-0.36)	0.37 (0.24-0.52)	0.34 (0.24-0.46)	0.37 (0.25-0.52)	0.29 (0.19-0.40)	0.39 (0.27-0.52)	0.42 (0.31-0.54)	0.43 (0.32-0.55)	0.32 (0.22-0.44)	0.28 (0.18-0.40)
h	2	0.10 (0.06-0.15)	0.07 (0.03-0.12)	0.08 (0.04-0.13)	0.09 (0.04-0.16)	0.18 (0.12-0.24)	0.19 (0.13-0.27)	0.12 (0.07-0.18)	0.06 (0.03-0.12)	0.18 (0.12-0.25)	0.13 (0.08-0.19)	0.23 (0.17-0.30)	0.17 (0.12-0.24)
	3	0.08 (0.03-0.17)	0.05 (0.02-0.13)	0.09 (0.04-0.18)	0.10 (0.04-0.18)	0.11 (0.05-0.20)	0.11 (0.05-0.19)	0.08 (0.03-0.16)	0.09 (0.04-0.17)	0.10 (0.05-0.19)	0.11 (0.05-0.19)	0.19 (0.11-0.29)	0.14 (0.07-0.23)
w	2	0.41 (0.31-0.51)	0.46 (0.33-0.58)	0.40 (0.29-0.50)	0.35 (0.23-0.47)	0.36 (0.27-0.46)	0.34 (0.23-0.45)	0.32 (0.24-0.42)	0.36 (0.25-0.47)	0.33 (0.25-0.41)	0.29 (0.21-0.38)	0.26 (0.17-0.36)	0.32 (0.23-0.42)
	3	0.28 (0.15-0.42)	0.32 (0.18-0.46)	0.21 (0.11-0.34)	0.22 (0.11-0.36)	0.25 (0.14-0.37)	0.21 (0.10-0.33)	0.22 (0.14-0.33)	0.26 (0.16-0.38)	0.34 (0.23-0.45)	0.31 (0.21-0.42)	0.21 (0.12-0.31)	0.22 (0.13-0.32)

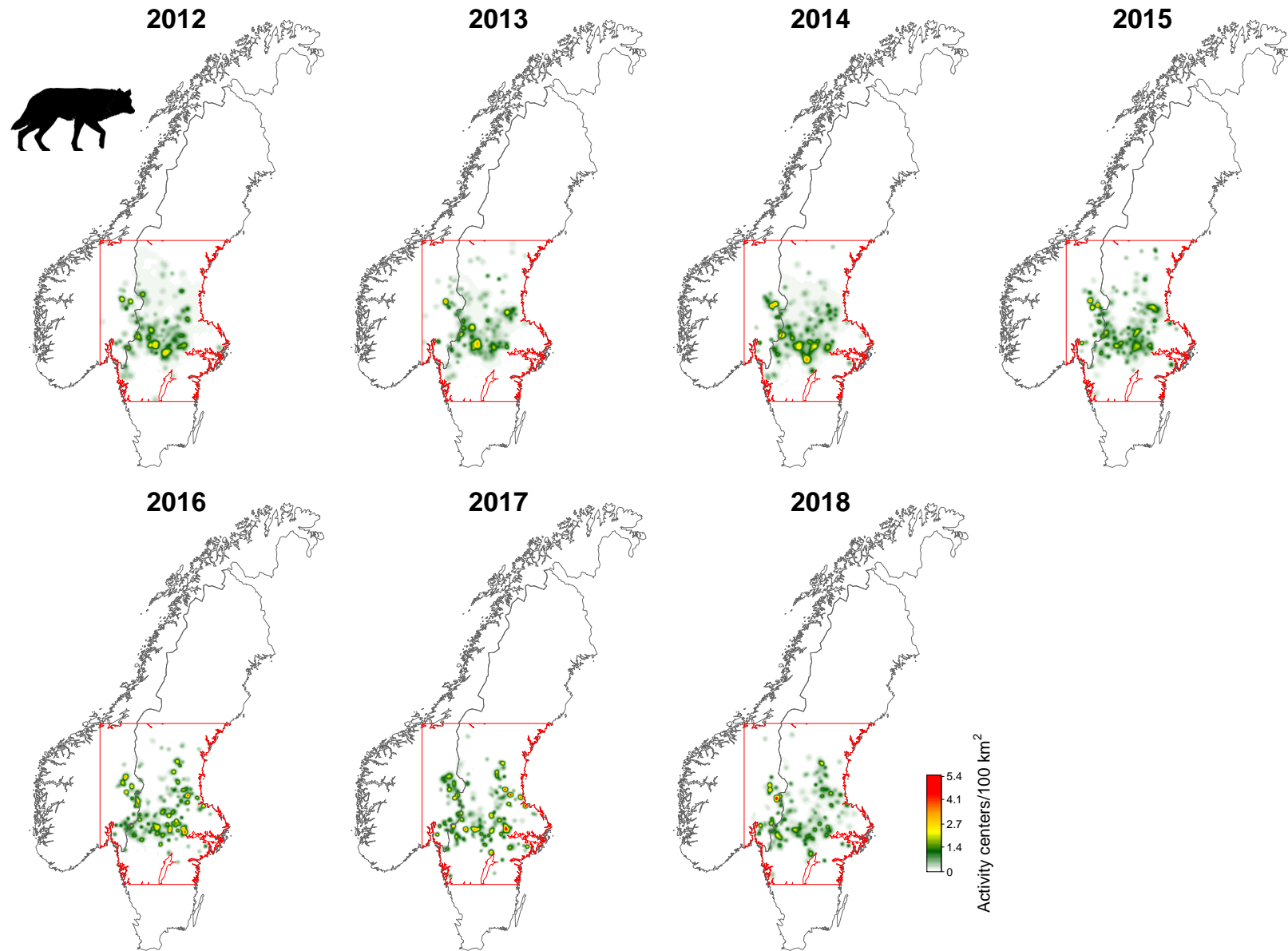


Figure D.1: Annual wolf density derived from the OPSCR model. The area for which estimates were generated is outlined in red.

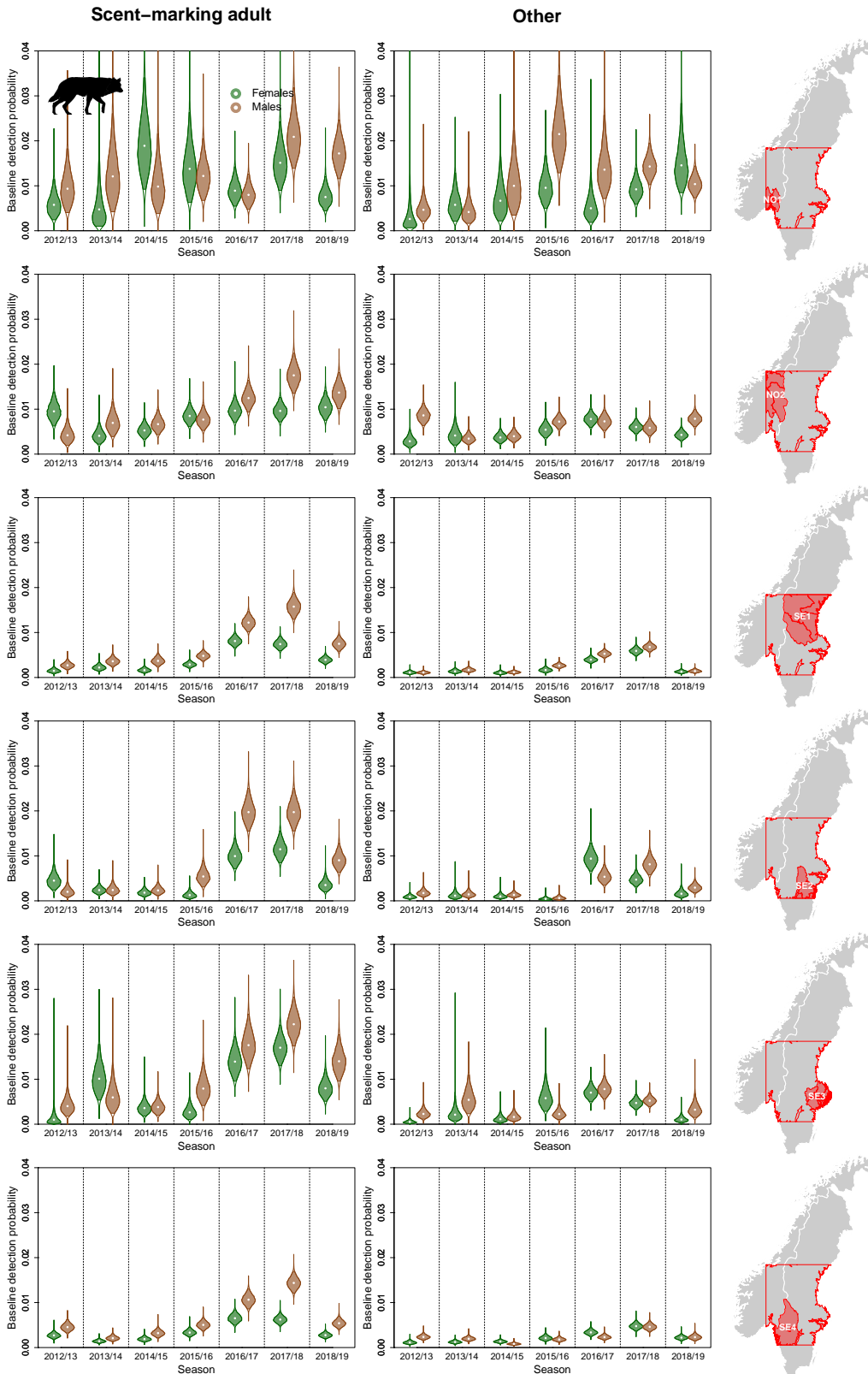


Figure D.2: Baseline detection probability (p_0) estimated by the OPSCR model for wolves. Violins show the distribution of the posterior samples, white dots indicate the median, and areas with solid shading represent the 95% credible interval. Results are separated into panels based on regions (rows: counties or groups of counties, as shown in the maps to the left) and based on social status (columns: scent marking adults vs. other individuals). Estimates are shown for the mean values of the detection covariates.