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Estimates of wolf density, abundance, and population dynamics in Scandinavia, 2012 - 2021

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Summary

Background The Scandinavian wolf (*Canis lupus*) population is being monitored annually using non-invasive genetic sampling (NGS) and recovery of dead individuals. DNA extracted from faeces, urine, hair, and tissue is used to identify the species, sex, and individual from which each sample originated. These data have been compiled in the Scandinavian large carnivore database Rovbase 3.0 (www.rovbase.se).

Approach Using the Bayesian open-population spatial capture-recapture (OPSCR) model developed by RovQuant (Bischof et al., 2019b, 2020), we estimated annual density and vital rates of the Scandinavian wolf population for nine seasons from 2012/13 to 2020/21. The OPSCR model accounts for individual movements, as well as imperfect and variable detection.

Results The OPSCR model yielded annual density maps and both total and jurisdiction-specific population sizes for wolves from 2012/13 to 2020/21. The estimated number of wolves for October 1, 2020 (start of the 2020/21 monitoring season) was 460 individuals (CrI: 439 - 483), of which 371 (CrI: 351-392) were located in Sweden and 89 (CrI: 80-99) in Norway. In addition to annual density and jurisdiction-specific abundance estimates, we report estimates of survival, recruitment, and detection probabilities.
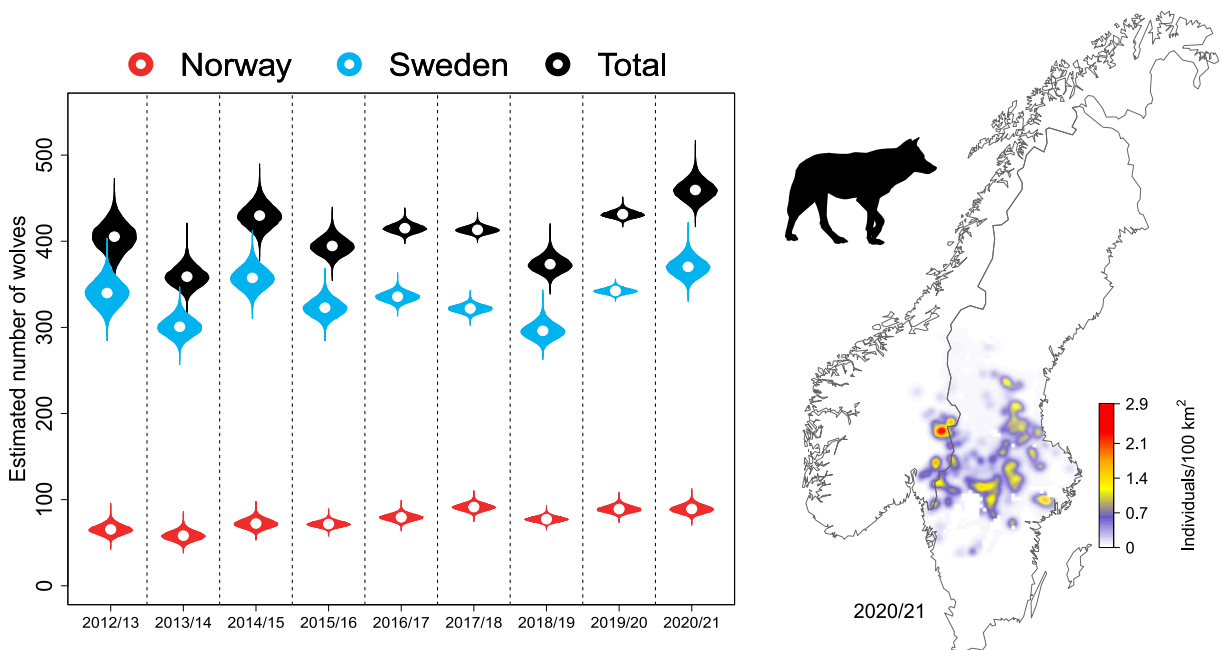
Sammendrag

Bakgrunn Den skandinaviske bestanden av ulv (*Canis lupus*) blir overvåket årlig ved bruk av ikke-invasiv genetisk prøveinnsamling (NGS) og gjenfunn av døde individer. DNA ekstrahert fra skit, urin, hår og vev brukes til å identifisere art, kjønn og individ for hver enkelt prøve. Denne informasjonen samles og ivaretas i den skandinaviske databasen for store rovdyr; Rovbase 3.0 (www.rovbase.se).

Tilnærming Ved bruk av en Bayesiansk åpen romlig fangst-gjenfangst populasjons modell (OPSCR), utviklet av RovQuant (Bischof et al., 2019b, 2020), estimerte vi årlige tettheter og demografiske rater hos den skandinaviske ulvebestanden i ni sesonger fra 2012/13 til 2020/21. OPSCR modellen tar høyde for individers forflytninger, samt variabel oppdagbarhet.

Resultater OPSCR modellen gav årlige kart med tetthet av ulv fra 2012/13 til 2020/21, hvor bestandsstørrelsen både totalt og innenfor ulike administrative enheter kunne avledes. Det estimerte antallet ulver for 1. oktober 2020 var 460 individer (CrI: 439 - 483), hvorav 371 (CrI: 351-392) var lokalisert i Sverige og 89 (CrI: 80-99) i Norge. I tillegg til årlige tettheter og områdespesifikke bestandsestimater, gir rapporten estimater på årlig overlevelse, rekrutering og oppdagbarhet i den skandinaviske bestanden av ulv for perioden 2012/13 til 2020/21.

Contents

1 Introduction

Non-invasive genetic sampling (NGS), in combination with dead recoveries, are a centerpiece of national and regional large carnivore monitoring in Norway and Sweden. Over almost two decades, both countries have accumulated an extensive individual-based data set for wolf (*Canis lupus*), and plan to continue such trans-national monitoring in the future.

Project RovQuant was initiated in 2017 with the objective to develop statistical methods that allow a comprehensive assessment of the status and dynamics of large carnivore populations using NGS data and other sources of information collected and stored in Rovbase (www.rovbase.se) by the national monitoring programs in Sweden and Norway. To do so, a Bayesian open-population spatial capture-recapture (OPSCR) model (Ergon and Gardner, 2014; Bischof et al., 2016; Chandler et al., 2018) was developed by RovQuant (Bischof et al., 2019b, 2020). It addresses three challenges associated with population-level wildlife inventories: 1) Detection is imperfect and sampling effort heterogeneous in space and time: not all individuals present in the study area are detected (Kéry and Schaub, 2012). 2) Individuals that reside primarily outside the surveyed area may be detected within it. Without an explicit link between the population size parameter and geographic space or area, density cannot be estimated and population size is ill-defined (Efford, 2004). 3) Non-spatial population dynamic models often estimate "apparent" survival and recruitment, as these parameters include the probability of permanent emigration and immigration, respectively. By explicitly modelling movement of individuals between years, the OPSCR model can return unbiased estimates of density and demographic parameters (Ergon and Gardner, 2014; Schaub and Royle, 2014).

Rovquant reported its first results for wolves in March 2019 (Bischof et al., 2019a) and jointly for all three carnivore species in December 2019 (Bischof et al., 2019b, 2020). Here we repeated the analysis for wolves with NGS and dead-recovery data from two additional years, for a total of nine monitoring seasons (2012/13-2020/21). We do so with the goal of providing the following information:

- Number of wolves (with credible intervals) for Sweden, Norway, and both countries combined.

- Proportion of individuals detected through NGS.

- Wolf density maps throughout the species' primary range in Scandinavia.

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

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.

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

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

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

Habitat buffer: buffer surrounding the searched area that is considered 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.

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

2 Methods

2.1 Data

We relied on data from multiple sources, the primary one being the Scandinavian large carnivore database Rovbase 3.0 (rovbase.se and rovbase.no; last extraction: 2021-05-21). 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, and GPS search tracks. In the following sections, we describe the various types of data used in the analysis. We used data collected between 2012 and 2021.

Non-invasive genetic sampling 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 originated 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. 2019a for further details about the data collection procedure). For individual identification, 17-21 microsatellite markers were used throughout the study period . Samples were then 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). Since 2017/2018, 90 single nucleotide polymorphisms (SNPs) were used for individual identification, in addition to microsatellites. Samples were amplified and genotypes visualized twice using nanofluid arrays (Fluidigm Inc.). Consensus SNP genotypes consisted of the markers with the same allele composition from the two amplifications (Åkesson et al., 2018).

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.

GPS search tracks Government employees involved in systematic searches for wolf DNA (e.g. via snowmobiles, skis, snowshoes, etc.) documented their effort with GPS track logs which were registered in Rovbase 3.0. GPS search tracks were included in the OPSCR model to account for spatial and temporal variation in search effort.

Parentage analysis and social status assignation Each year, field observations, genetic sampling data, dead recoveries, and parentage analysis (which resulted in a near-complete pedigree of the Scandinavian wolf population) are used to establish counts of pairs, packs, and reproductions (Svensson et al., 2014, 2015, 2017, 2018; Wabakken et al., 2016). The social status (adult scent-marking member in a pack/pair, or subadult member of a pack and vagrant individuals) was determined on a yearly basis for genetically identified individuals using the pedigree and tracking information from the monitoring. The identity of known adult scent-marking individuals was reported in the yearly monitoring reports (Svensson et al., 2014, 2015,

2017, 2018, 2019, 2021; Wabakken et al., 2016, 2020) and a detailed description of the method used for parental assignment was provided in Åkesson et al. (2016). We assigned individuals to two different states depending on whether the individual had been identified as an adult scent-marking member of a pair or a pack ("adult scent-marking"), or not ("other"). See Bischof et al. (2019a) for further details.

2.2 Analysis

Spatial capture-recapture model We analysed the data using the Bayesian open-population spatial capture-recapture (OPSCR) model developed during project RovQuant (Bischof et al., 2019b), which addresses three challenges associated with population-level wildlife inventories:

1. Detection is imperfect and sampling effort heterogeneous in space and time: not all individuals present in the study area are detected (Kéry and Schaub, 2012).
2. Individuals that reside primarily outside the surveyed area may be detected within it. Without an explicit link between the population size parameter and geographic space or area, density cannot be estimated and population size is ill-defined (Efford, 2004).
3. Non-spatial population dynamic models usually estimate "apparent" survival and recruitment, as these parameters include the probability of permanent emigration and immigration, respectively. By explicitly modelling movement of individuals between years, the OPSCR model can return unbiased estimates of demographic parameters (Ergon and Gardner, 2014; Schaub and Royle, 2014).

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

1. A model for population dynamics and population size.
2. A model for density and movements.
3. A model for detections during DNA searches.

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

Model fitting We fitted the Bayesian OPSCR model using Markov chain Monte Carlo (MCMC) simulation with NIMBLE (Turek et al., 2016; de Valpine et al., 2017; NIMBLE Development Team, 2019) and nimbleSCR (Bischof et al., 2021) in R version 3.3.3 (R Core Team, 2018). We ran 4 chains, each with $32\,500$ iterations, including a $5\,000$-iteration burn-in period. Due to the computing challenge associated with post-processing large amounts of data, we thinned chains by a factor of 10 from which abundance estimates were derived. We considered models as converged when the Gelman-Rubin diagnostics (Rhat, Gelman and Rubin, 1992) was ≤ 1.1 for all parameters and by visually inspecting the trace plots.

Parameter estimation 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 (jurisdictions) add up to the 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.

To obtain an estimate of abundance for any given area, we summed the number of OPSCR-predicted AC locations (live individuals) that fell within that region for each iteration of the MCMC chains, thus generating a posterior distribution of the abundance for that area. In this fashion, abundance estimates and the associated uncertainty can be extracted for any desired spatial unit, including country or county level estimates.

We used both the distribution of model-estimated AC positions and the scale parameter (σ) of the detection function to construct density maps based on individual utilization distributions. These maps are not only based on the position of the center of an individual's home range, but also take into account the area over which that individual's activity is spread, i.e., it's space use (Bischof et al., 2020). To do so, we constructed raster maps of individual utilization distributions, scaled values in each raster to sum to one, and then summed across individual rasters to create a single population-level raster map for each iteration. An overall density map was derived by calculating the average of the posterior utilization density (i.e., across iterations) in each cell (Bischof et al., 2020).

The average proportion of individuals detected and the associated uncertainty were obtained by dividing the number of individuals detected through NGS sampling (Table A.2) by the abundance estimates and their associated credible intervals, respectively.

3 Results

3.1 Non-invasive genetic samples and dead recoveries

A total of 15 172 (6 627 female; 8 545 male) genotyped wolf genetic samples were included in the analysis (Table A.1), of which 75% originated from Sweden. These samples were associated with 1 480 (659 female; 821 male) individuals (Table A.2). We also included 591 dead recoveries of wolves, of which 478 (195 female; 283 male) were due to legal culling and 113 (54 female; 59 male) due to other causes of mortality (Table A.3). The majority of dead recoveries (70%) originated from Sweden.

3.2 Density and abundance

The model-estimated wolf abundance for the entire study area (254 000 km^2, excluding the buffer area) ranged between 359 (CrI: 338-383) in 2013/14 and 460 (CrI: 439-483) in 2020/21 (Figure 1). Estimates refer to the status of the population at the start of the annual sampling period (Oct. 1). The overall proportion of females in the Scandinavian wolf population was 47% (CrI: 43-51%; Table 1), 47% (CrI:46-49%) in 2019/20, and 48% (CrI:44-49%) in 2020/21. Based on the model-predicted location of ACs, we estimated that in 2020/21, 371 wolves (CrI: 351-392) could be attributed to Sweden and 89 (CrI: 80-99) to Norway. A further breakdown into annual county-specific estimates is provided in Table A.4. The greater number of detections associated with the increased survey effort in Sweden during seasons 2016/17, 2017/18, and 2019/20 (e.g., 93-95% of individuals detected in 2019/20; Table A.8) led to higher precision in population size estimates (Figure 1). Note that estimates provided here differ slightly from those provided in Bischof et al. (2020). This is explained by the inclusion of two additional monitoring seasons, 2019/20 and 2020/21, 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 (Bischof et al., 2020; Milleret et al., 2019). In addition, information in Rovbase is continuously updated and corrected as new information emerges (e.g., dead recoveries, correction of genotype assignments, etc.).

The OPSCR model yielded annual density maps, which illustrate changes in the distribution of wolves over time (Figure A.2). Average density in 2020/21 was estimated at 0.18 wolves per 100 km^2 (CrI: 0.17 − 0.19) throughout the 259 700 km^2 study area (Figure 2).

Table 1: Wolf population size estimates by sex and jurisdiction (Norway: carnivore management regions, Sweden: counties; Figure A.1) during the two most recent monitoring seasons (2019/20 and 2020/21). Numbers are 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 for constituent regions.

|	2019/2020			2020/2021		
	F	M	Total	F	M	Total
TOTAL	206.1 (201-212)	225.3 (220-232)	431.4 (424-440)	214.1 (200-231)	245.4 (231-262)	459.5 (439-483)
NORWAY	43.5 (38-50)	45.6 (41-51)	89.1 (82-97)	41.1 (34-49)	48.1 (43-54)	89.2 (81-99)
Region 2	0.3 (0-2)	0.5 (0-2)	0.8 (0-3)	0.1 (0-1)	0 (0-1)	0.1 (0-1)
Region 3	0.7 (0-3)	2.3 (1-4)	3 (1-6)	1.1 (0-4)	0.6 (0-2)	1.6 (0-5)
Region 4	13.8 (11-17)	14.5 (12-18)	28.3 (24-33)	13.3 (10-17)	6.4 (3-10)	19.7 (15-24)
Region 5	27.6 (23-33)	26.7 (23-32)	54.4 (48-61)	24.2 (19-30)	40.1 (36-45)	64.3 (58-72)
Region 6	1.1 (0-4)	2.1 (1-5)	3.2 (1-7)	2.3 (0-6)	1.4 (0-4)	3.8 (1-8)
SWEDEN	162.6 (159-167)	179.7 (175-185)	342.3 (336-349)	173 (160-188)	197.3 (183-214)	370.3 (351-392)
Örebro	20.2 (17-24)	23.5 (19-28)	43.7 (38-49)	18.6 (14-24)	27 (22-33)	45.6 (39-53)
Östergötland	5.1 (5-6)	3.2 (3-5)	8.3 (8-10)	4.3 (3-7)	3.7 (2-7)	8 (5-12)
Dalarna	34.1 (30-38)	33.1 (30-37)	67.3 (62-73)	33.6 (28-40)	35.9 (29-44)	69.5 (60-80)
Gävleborg	34 (31-37)	40.1 (37-43)	74.1 (70-78)	33 (28-38)	31.9 (27-38)	64.9 (58-73)
Jämtland	4.3 (2-7)	9.5 (6-13)	13.7 (10-18)	11.3 (7-17)	11.2 (6-17)	22.5 (16-30)
Jönköping	0 (0-1)	0.5 (0-2)	0.5 (0-2)	0.6 (0-2)	0.6 (0-2)	1.2 (0-4)
Kalmar	0 (0-0)	0 (0-1)	0.1 (0-1)	0.2 (0-1)	0.3 (0-2)	0.5 (0-2)
Södermanland	3.8 (3-5)	5 (3-6)	8.8 (7-10)	9.1 (7-12)	7.9 (5-12)	17 (13-22)
Stockholm	0.3 (0-1)	2.1 (1-4)	2.5 (1-4)	2.6 (1-5)	3.6 (1-7)	6.2 (3-10)
Uppsala	2.5 (2-4)	1.1 (1-2)	3.6 (3-5)	4.5 (2-7)	5.3 (3-8)	9.8 (7-14)
Värmland	43.2 (39-47)	43.6 (39-48)	86.8 (81-93)	35 (30-41)	42.9 (37-50)	77.8 (69-87)
Västerbotten	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Västernorrland	0.3 (0-2)	1 (0-3)	1.3 (0-4)	2.7 (0-6)	2.7 (0-6)	5.4 (1-10)
Västmanland	12.5 (10-15)	14 (10-18)	26.5 (22-31)	10.7 (6-16)	10.2 (7-15)	20.9 (15-27)
VästraGötaland	2.2 (1-4)	2.5 (1-5)	4.7 (2-8)	6.8 (4-11)	13.9 (10-19)	20.6 (15-27)
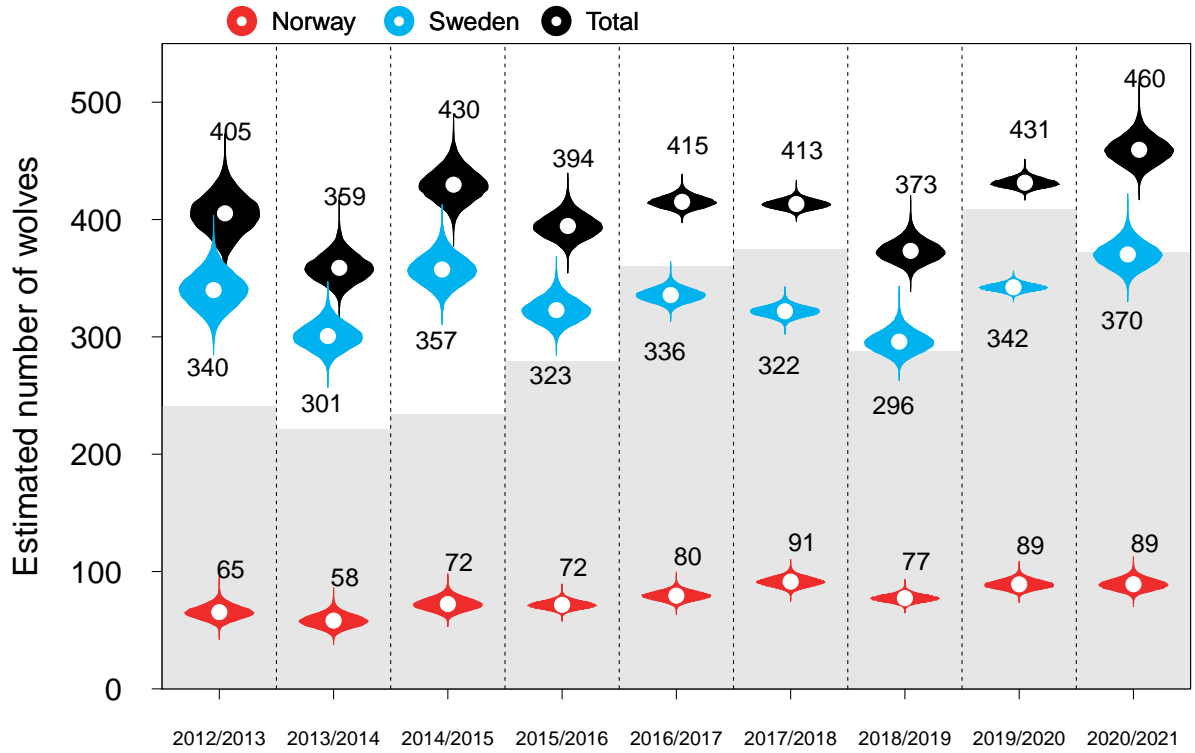
Figure 1: Total (black) and country-specific (blue: Sweden, red: Norway) annual wolf population size estimates from the OPSCR model within the study area. Violins show the posterior distribution of the annual population size estimates (points: mean estimates). Gray vertical bars indicate the total number of individuals detected during noninvasive genetic sampling. Values indicate rounded mean estimates of abundance.
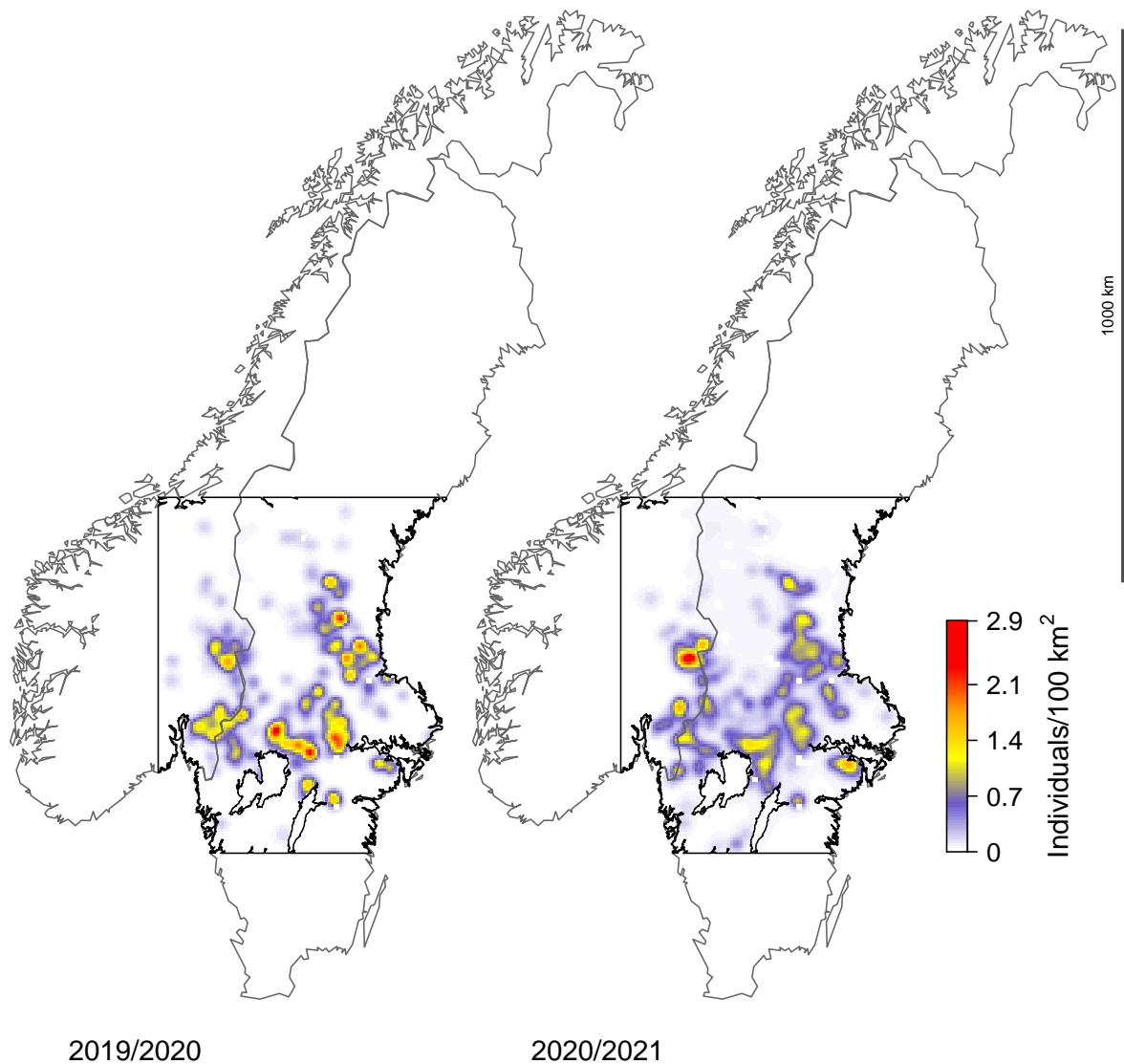
Figure 2: OPSCR-estimated wolf density based on individual utilization distributions throughout the study area (black outline) in Scandinavia during the two most recent monitoring seasons.

3.3 Vital rates

The model produced annual estimates of legal hunting mortality, mortality associated with other causes, and per capita recruitment rates (Figure 3; Table A.6). 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 3). With the exception of the 2017/18 season in males, legal culling mortality was consistently lower than mortality due to other causes (Figure 3).
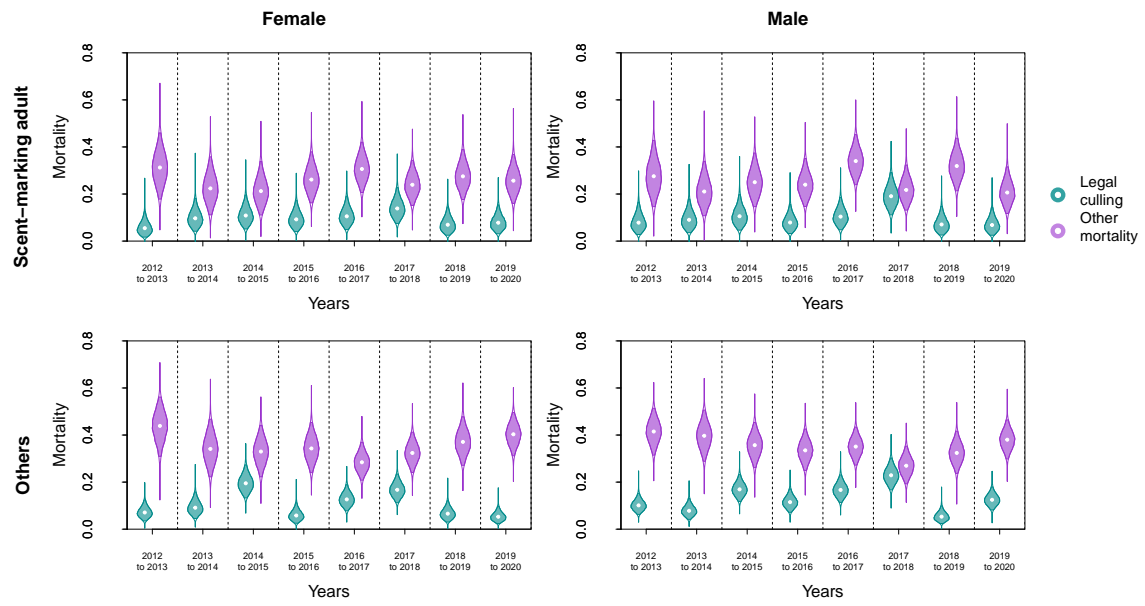
Figure 3: Mortality probabilities due to legal culling and other causes for female and male wolves. Shown are overall estimates throughout the study area. Violins show the posterior distribution of mortality estimates (points: median estimates; solid colors: 95% credible interval). Estimates refer to deaths occurring between the start of one sampling season and the start of the next (hence estimates for mortality between 2020/21 and 2021/22 are not yet available).

3.4 Detection probability

The average proportion of individuals detected ranged between 55% (CrI: 51-65%) in 2014/15 and 95% (CrI: 93-96%) in 2019/20 (Table A.8). The baseline detection probability varied between jurisdictions, generally increased with time, and was higher for individuals that had been identified as scent-marking members of a pair or pack vs. those that had not (Figure A.3, see Bischof et al. 2019a for details). Detection probability increased with the length of recorded search trails (males: $\beta = 0.30$, CrI: 0.28 - 0.33; females: $\beta = 0.30$, CrI: 0.28 - 0.33) and decreased in areas further away from roads for both males ($\beta = -0.52$, CrI: -0.68 - -0.37) and females ($\beta = -0.69$, CrI: -0.91 - -0.49, Table A.7). The average proportion of snow cover had no significant effect on the baseline detection probability for either sex (males: $\beta = -0.00$, CrI: -0.07 - 0.06; females: $\beta = 0.02$, CrI: -0.06 - 0.10). Detection probability increased significantly in Sweden during the three seasons with intensified NGS (Figure A.3). Detection probability was also generally higher for individuals if they had already been detected during a previous sampling season (males: $\beta = 0.21$, CrI: 0.13 - 0.28; females: $\beta = 0.37$, CrI: 0.29 - 0.44).

4 Acknowledgements

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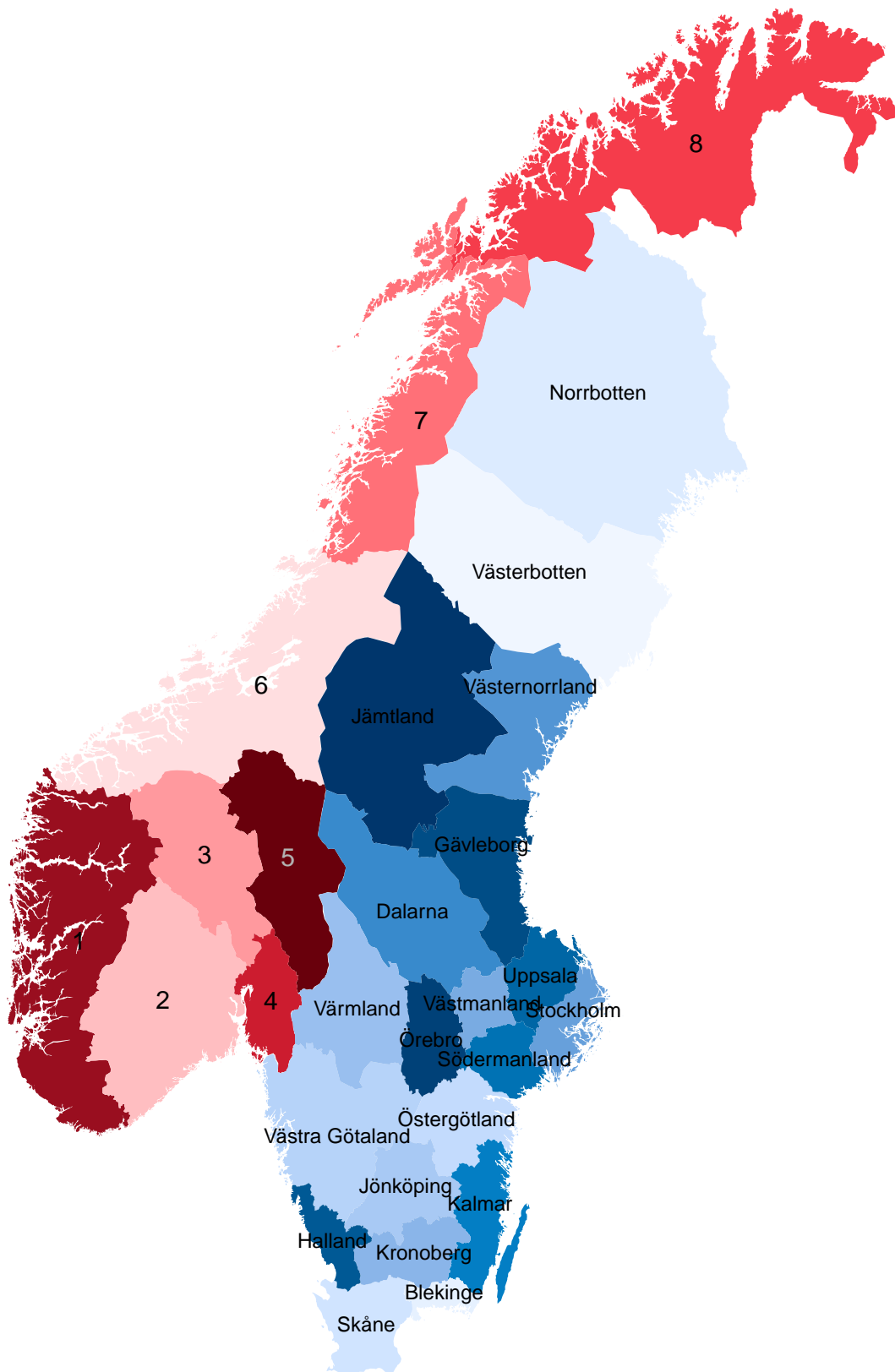
Appendices

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

Table A.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 2012/13 and 2020/21.

	2012/2013		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021	
	F	M	F	M	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	273	282	231	345	240	332	310	444
Sweden	140	226	183	231	180	223	239	370	840	1122	1077	1480	349	457	1428	1546	498	762
Total	221	372	236	312	274	331	386	554	1104	1328	1350	1762	580	802	1668	1878	808	1206

Table A.2: Annual number of individual wolves detected via non-invasive genetic sampling and included in the OPSCR analysis. We included only individuals associated with samples collected within the study area and during the primary monitoring period (Oct 1 - Mar 31) from 2012/13 to 2020/21. 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		2019/2020		2020/2021	
	F	M	F	M	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	48	47	39	48	39	46	39	58
Sweden	81	108	84	103	87	96	91	127	140	159	150	156	105	113	162	182	138	153
Total	103	138	97	124	111	123	115	164	172	188	187	188	136	152	194	215	172	200

Table A.3: Number of cause-specific dead recoveries of wolves in Scandinavia between 2012 and 2021 that were included in the OPSCR analysis. Numbers are reported by country, for females (F) and for males (M). Note that dead recovery data from the final season (2020/21) were not used in this analysis because survival is modeled as part of the transition from one season to the next.

	Country	2012/2013		2013/2014		2014/2015		2015/2016		2016/2017		2017/2018		2018/2019		2019/2020		2020/2021	
		F	M	F	M	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	1	1	1	1	0	0
	Sweden	8	8	4	5	8	11	7	6	4	2	5	2	5	5	5	7	4	1
Legal culling	Norway	1	13	5	7	4	8	6	6	7	7	18	15	10	11	6	14	11	14
	Sweden	11	19	12	13	33	32	8	20	20	26	15	31	4	5	6	13	18	29
Total		20	41	22	28	45	51	22	34	31	35	39	52	19	22	18	35	33	44

Table A.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	2019/2020	2020/2021
TOTAL	405.3 (374-438)	358.9 (338-383)	429.8 (405-457)	394.5 (376-415)	415.1 (406-426)	413.2 (406-422)	373.3 (357-393)	431.4 (424-440)	459.5 (439-483)
NORWAY	65.4 (55-77)	58.2 (48-70)	72.3 (62-83)	71.7 (65-79)	79.5 (72-88)	91.4 (84-100)	77.3 (71-84)	89.1 (82-97)	89.2 (81-99)
Region 2	1.9 (0-5)	1.7 (0-4)	0.4 (0-2)	0.1 (0-1)	0.4 (0-2)	0.2 (0-1)	0.4 (0-2)	0.8 (0-3)	0.1 (0-1)
Region 3	2 (0-5)	3.1 (1-6)	2.7 (1-6)	0.8 (0-3)	0.8 (0-3)	1.2 (0-4)	1 (0-3)	3 (1-6)	1.6 (0-5)
Region 4	12.7 (8-19)	8.4 (5-13)	6.4 (4-10)	8.4 (7-11)	16 (12-20)	20 (17-24)	20.4 (17-25)	28.3 (24-33)	19.7 (15-24)
Region 5	44.6 (38-52)	42.1 (34-51)	60.1 (52-69)	60.9 (55-67)	61 (55-68)	69.4 (63-76)	53.7 (48-60)	54.4 (48-61)	64.3 (58-72)
Region 6	4 (1-8)	2.8 (0-7)	2.6 (0-6)	1.4 (0-4)	1.1 (0-4)	1.5 (0-4)	2 (1-4)	3.2 (1-7)	3.8 (1-8)
SWEDEN	339.9 (311-370)	300.7 (280-323)	357.4 (334-383)	322.8 (304-344)	335.7 (325-347)	321.9 (313-331)	296 (279-315)	342.3 (336-349)	370.3 (351-392)
Örebro län	45 (35-56)	34.2 (27-42)	59.5 (47-73)	43.9 (34-55)	37 (32-42)	31.7 (28-36)	36 (29-44)	43.7 (38-49)	45.6 (39-53)
Östergötlands län	5.2 (1-10)	4.1 (1-9)	3.4 (0-8)	3.4 (0-7)	1.8 (1-4)	3.6 (2-5)	4.8 (2-8)	8.3 (8-10)	8 (5-12)
Dalarnas län	80.3 (68-93)	67.9 (57-80)	73.1 (62-85)	72.5 (64-82)	76 (70-83)	57.9 (52-64)	53.8 (45-64)	67.3 (62-73)	69.5 (60-80)
Gävleborgs län	25.4 (18-33)	24.3 (18-32)	30.2 (23-38)	43.9 (37-51)	57.4 (52-63)	60 (55-64)	50.9 (44-59)	74.1 (70-78)	64.9 (58-73)
Jämtlands län	23.9 (16-33)	18.7 (13-26)	19.2 (12-27)	19.5 (14-26)	12.8 (8-18)	6.6 (3-10)	15.1 (10-21)	13.7 (10-18)	22.5 (16-30)
Jönköpings län	2.3 (0-5)	1 (0-3)	0.8 (0-3)	0.7 (0-3)	0.3 (0-2)	0.3 (0-2)	0.4 (0-2)	0.5 (0-2)	1.2 (0-4)
Kalmar län	0.6 (0-2)	0.5 (0-2)	0.4 (0-2)	0.4 (0-2)	0.1 (0-1)	0.1 (0-1)	0.2 (0-1)	0.1 (0-1)	0.5 (0-2)
Södermanlands län	3.1 (0-7)	2.1 (0-5)	3.2 (0-7)	3.3 (1-6)	3.2 (2-5)	14.1 (12-16)	5.1 (3-8)	8.8 (7-10)	17 (13-22)
Stockholms län	4.1 (2-7)	1.4 (0-4)	2.7 (0-6)	2.6 (0-5)	1.6 (0-3)	2.8 (1-5)	1.4 (0-4)	2.5 (1-4)	6.2 (3-10)
Uppsala län	4.3 (1-9)	2.4 (0-6)	4.3 (1-8)	4.7 (2-8)	4 (2-7)	6.2 (4-9)	6.3 (3-10)	3.6 (3-5)	9.8 (7-14)
Värmlands län	100.8 (88-115)	112.9 (100-126)	115.2 (101-130)	97.4 (87-109)	105.2 (96-115)	96 (89-103)	87.5 (78-98)	86.8 (81-93)	77.8 (69-87)
Västerbottens län	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Västernorrlands län	7.6 (3-13)	5.2 (2-9)	6 (2-11)	5 (1-9)	2.8 (1-6)	0.6 (0-2)	3.8 (1-8)	1.3 (0-4)	5.4 (1-10)
Västmanlands län	20 (14-27)	11.7 (8-16)	21.5 (16-28)	14.4 (10-19)	25.6 (23-29)	30.4 (26-35)	16.6 (12-22)	26.5 (22-31)	20.9 (15-27)
Västra Götalands län	17.7 (12-24)	14.6 (9-21)	18 (13-24)	11.2 (7-16)	8.2 (4-13)	10.5 (7-15)	13.9 (9-19)	4.7 (2-8)	20.6 (15-27)

Table A.5: Annual population growth rates for Norway, Sweden, and Norway and Sweden combined ("Total"). Estimates are derived from the same posterior distribution than the one used to extract abundance estimates (Table A.4). Credible intervals (95%) are shown in parentheses.

	2012-2013	2013-2014	2014-2015	2015-2016	2016-2017	2017-2018	2018-2019	2019-2020
Norway	0.90 (0.69-1.13)	1.25 (0.99-1.57)	1.00 (0.83-1.18)	1.11 (0.97-1.27)	1.15 (1.01-1.31)	0.85 (0.75-0.95)	1.15 (1.02-1.30)	1.00 (0.87-1.15)
Sweden	0.89 (0.79-0.99)	1.19 (1.08-1.31)	0.90 (0.83-0.99)	1.04 (0.97-1.11)	0.96 (0.92-1.00)	0.92 (0.86-0.98)	1.16 (1.08-1.23)	1.08 (1.02-1.15)
Total	0.89 (0.80-0.98)	1.20 (1.10-1.30)	0.92 (0.85-0.99)	1.05 (1.00-1.11)	1.00 (0.96-1.02)	0.90 (0.86-0.95)	1.16 (1.10-1.21)	1.07 (1.01-1.12)

Table A.6: 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. (2019a) for a full description of the model parameters. Credible intervals (95%) are shown in parentheses.

	State	2012-2013		2013-2014		2014-2015		2015-2016	
		M	F	M	F	M	F	M	F
ρ	-	0.45 (0.34-0.59)	0.47 (0.31-0.68)	0.85 (0.68-1.06)	0.95 (0.72-1.22)	0.55 (0.43-0.68)	0.53 (0.40-0.69)	0.55 (0.44-0.65)	0.85 (0.68-1.02)
ϕ	2	0.48 (0.39-0.58)	0.49 (0.37-0.61)	0.52 (0.42-0.63)	0.56 (0.44-0.69)	0.47 (0.38-0.57)	0.47 (0.37-0.58)	0.55 (0.46-0.64)	0.60 (0.49-0.70)
	3	0.64 (0.49-0.78)	0.63 (0.48-0.77)	0.69 (0.56-0.81)	0.67 (0.54-0.80)	0.64 (0.51-0.76)	0.67 (0.54-0.79)	0.68 (0.56-0.78)	0.64 (0.52-0.75)
ψ	-	0.27 (0.18-0.38)	0.39 (0.26-0.54)	0.24 (0.14-0.35)	0.38 (0.25-0.52)	0.34 (0.24-0.45)	0.37 (0.24-0.51)	0.28 (0.19-0.38)	0.37 (0.25-0.50)
h	2	0.10 (0.06-0.15)	0.07 (0.03-0.13)	0.08 (0.04-0.13)	0.09 (0.05-0.16)	0.17 (0.12-0.23)	0.19 (0.13-0.27)	0.11 (0.07-0.17)	0.06 (0.02-0.11)
	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 (0.05-0.20)	0.08 (0.03-0.16)	0.09 (0.04-0.17)
w	2	0.41 (0.31-0.51)	0.44 (0.31-0.56)	0.40 (0.29-0.51)	0.34 (0.22-0.47)	0.36 (0.26-0.45)	0.33 (0.22-0.44)	0.33 (0.25-0.43)	0.34 (0.24-0.45)
	3	0.28 (0.15-0.43)	0.31 (0.18-0.46)	0.21 (0.11-0.34)	0.22 (0.11-0.36)	0.25 (0.15-0.38)	0.21 (0.11-0.34)	0.24 (0.15-0.35)	0.26 (0.16-0.38)

	State	2016-2017		2017-2018		2018-2019		2019-2020	
		M	F	M	F	M	F	M	F
ρ	-	0.66 (0.60-0.73)	0.66 (0.59-0.74)	0.63 (0.54-0.75)	0.44 (0.36-0.54)	0.77 (0.63-0.91)	0.94 (0.78-1.10)	0.77 (0.67-0.88)	0.71 (0.59-0.85)
ϕ	2	0.48 (0.40-0.56)	0.59 (0.50-0.67)	0.50 (0.41-0.59)	0.51 (0.42-0.60)	0.62 (0.53-0.71)	0.56 (0.46-0.66)	0.49 (0.41-0.58)	0.54 (0.45-0.63)
	3	0.55 (0.44-0.66)	0.58 (0.47-0.69)	0.59 (0.47-0.70)	0.62 (0.50-0.72)	0.60 (0.48-0.72)	0.65 (0.53-0.76)	0.72 (0.60-0.82)	0.66 (0.54-0.77)
ψ	-	0.40 (0.29-0.52)	0.41 (0.31-0.52)	0.31 (0.21-0.42)	0.26 (0.17-0.37)	0.30 (0.21-0.41)	0.43 (0.30-0.56)	0.33 (0.24-0.44)	0.35 (0.25-0.47)
h	2	0.17 (0.11-0.23)	0.13 (0.08-0.19)	0.23 (0.17-0.30)	0.17 (0.11-0.23)	0.05 (0.02-0.10)	0.07 (0.03-0.12)	0.12 (0.08-0.18)	0.05 (0.02-0.10)
	3	0.10 (0.05-0.19)	0.11 (0.05-0.19)	0.19 (0.11-0.29)	0.14 (0.07-0.23)	0.07 (0.03-0.15)	0.07 (0.02-0.15)	0.07 (0.02-0.14)	0.08 (0.03-0.15)
w	2	0.35 (0.27-0.43)	0.28 (0.21-0.37)	0.27 (0.19-0.35)	0.32 (0.24-0.41)	0.32 (0.24-0.42)	0.37 (0.27-0.48)	0.38 (0.30-0.46)	0.40 (0.31-0.50)
	3	0.34 (0.24-0.45)	0.31 (0.21-0.42)	0.22 (0.13-0.32)	0.24 (0.15-0.34)	0.32 (0.21-0.44)	0.24 (0.15-0.39)	0.21 (0.12-0.32)	0.26 (0.16-0.37)

Table A.7: Estimates of detection and spatial process parameters obtained from the wolf OPSCR model for males (M) and females (F). β_1 corresponds to the effect of previous detection of an individual on detection probability, β_2 on the effect of distance to the nearest roads on detection probability, β_3 on the effect of search-effort (track length) on detection probability β_4 on the effect of average snow cover during the monitoring period on detection probability. τ represents the standard deviation of the bivariate normal describing individual movement distances between years and β the effect of the density of known wolf packs on AC locations (Bischof et al., 2020). The units of the parameters σ and τ are kilometers; coefficients are associated with scaled covariates. Credible intervals (95%) are shown in parentheses.

	Parameters	M	F
Spatial process	τ	81.46 (78.29-85.48)	55.71 (53.28-58.40)
	β	0.44 (0.42-0.47)	0.48 (0.45-0.50)
Detection process	σ	7.98 (7.86-8.09)	7.68 (7.56-7.80)
	β_1	0.21 (0.13-0.28)	0.37 (0.29-0.44)
	β_2	-0.52 (-0.68-(-)0.37)	-0.69 (-0.91-0.49)
	β_3	0.30 (0.28-0.33)	0.30 (0.28-0.33)
	β_4	0.00 (-0.07-0.06)	0.02 (-0.06-0.10)

Table A.8: Average proportion of individuals detected calculated as the number of individuals detected with NGS (Table A.2) divided by the total abundance estimates (Table A.4). Credible intervals (95%) are shown in parentheses.

|	2012/2013	2013/2014	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021
M	0.63 (0.57-0.70)	0.64 (0.58-0.69)	0.53 (0.48-0.57)	0.75 (0.70-0.80)	0.88 (0.85-0.91)	0.92 (0.89-0.94)	0.77 (0.72-0.82)	0.95 (0.93-0.98)	0.82 (0.76-0.87)
F	0.55 (0.49-0.62)	0.59 (0.54-0.64)	0.57 (0.52-0.61)	0.66 (0.61-0.71)	0.85 (0.83-0.88)	0.90 (0.87-0.92)	0.78 (0.72-0.82)	0.94 (0.92-0.97)	0.80 (0.74-0.86)
Total	0.60 (0.55-0.64)	0.62 (0.58-0.65)	0.55 (0.51-0.58)	0.71 (0.67-0.74)	0.87 (0.85-0.89)	0.91 (0.89-0.92)	0.77 (0.73-0.81)	0.95 (0.93-0.96)	0.81 (0.77-0.85)
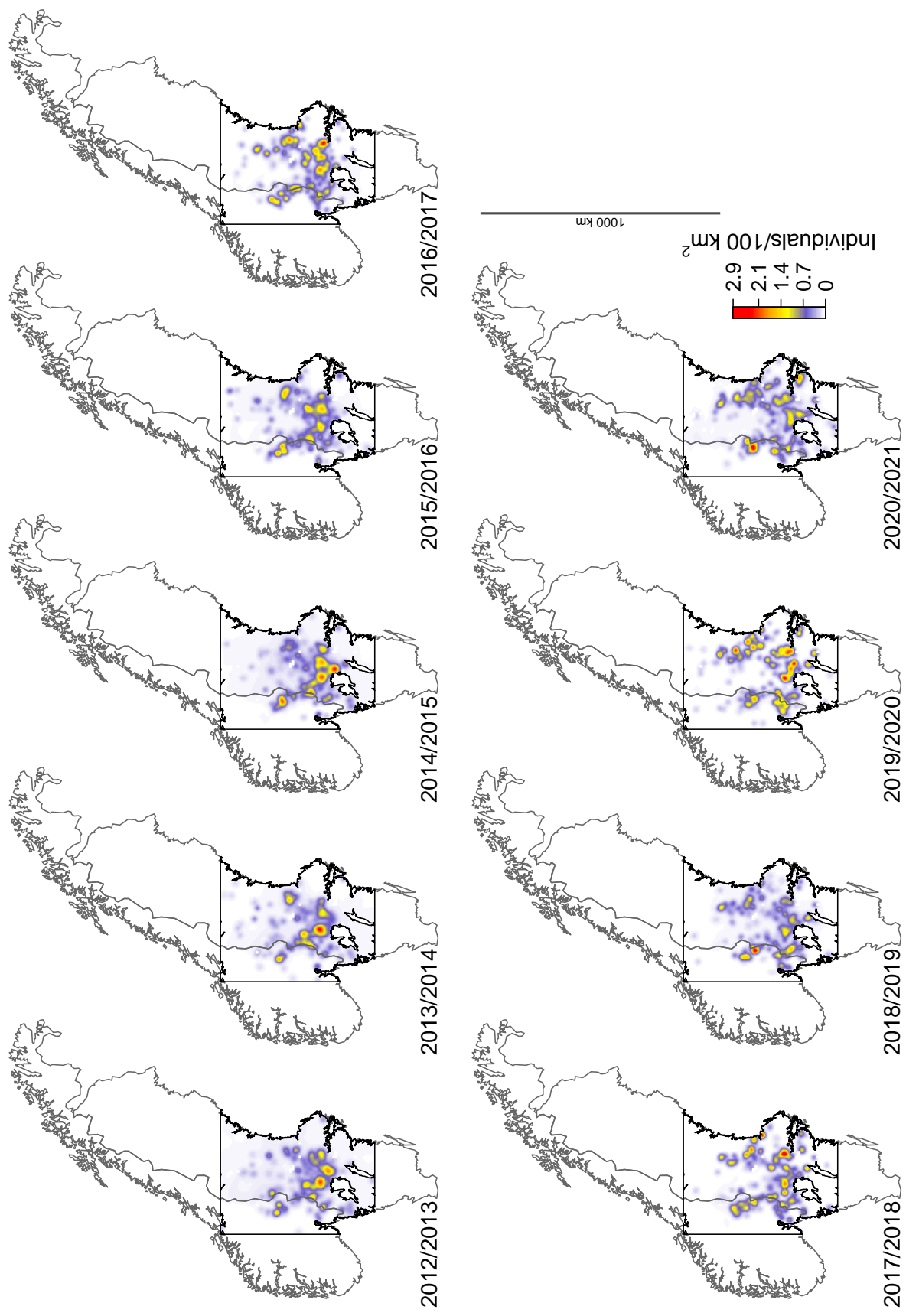
Figure A.2: Annual wolf density based on individual utilization distributions derived from the OPSCR model. The area for which estimates were generated is outlined in black.
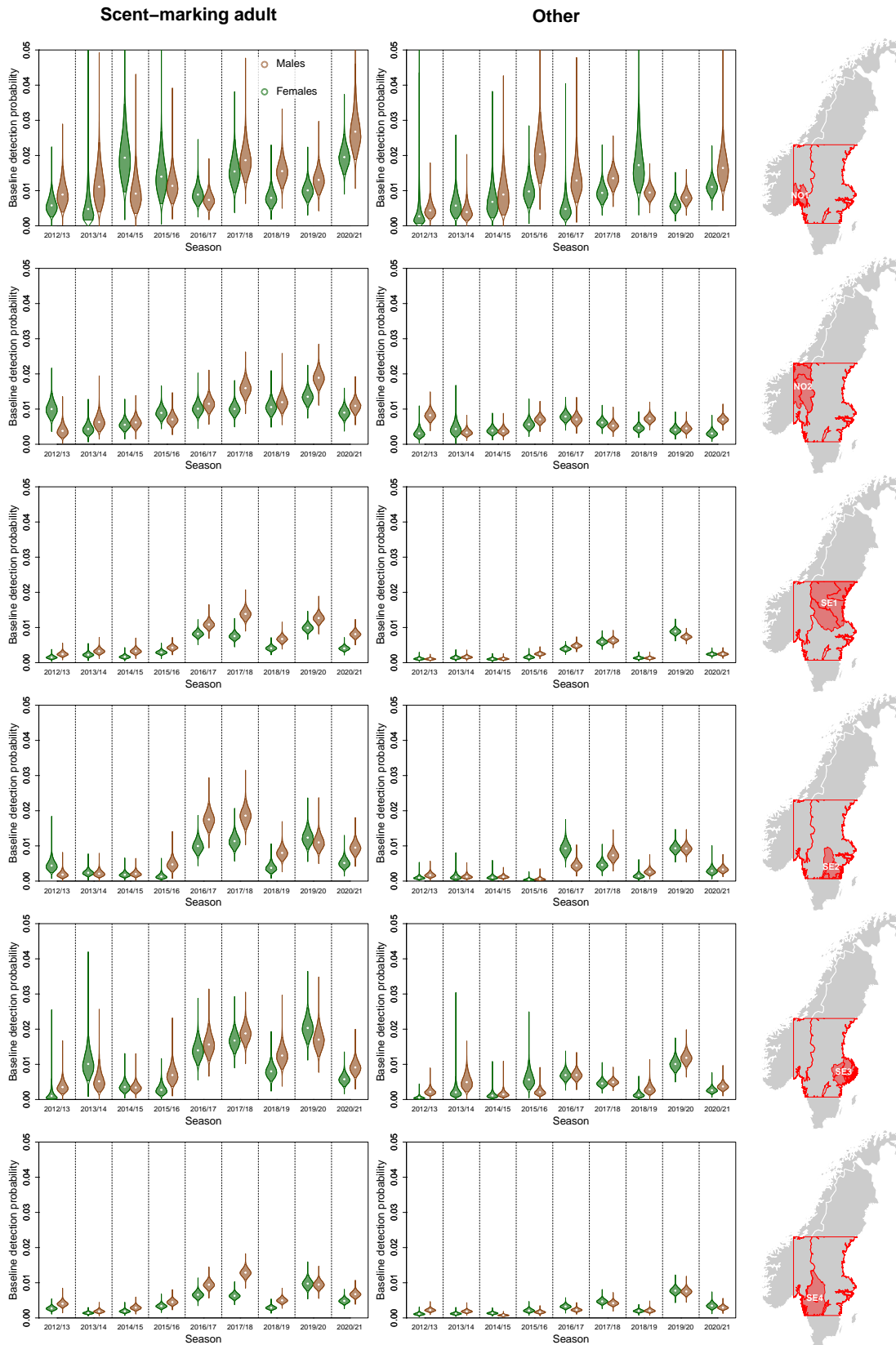
Figure A.3: Baseline detection probability (p_0) estimated by the OPSCR model for wolves. Violins show the distribution of the posterior samples, white dots indicate the median, and areas with solid shading represent the 95% credible interval. Results are separated into panels based on regions (rows: 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.