

Norwegian University of Life Sciences

Faculty of Environmental Sciences and Natural Resource Management

2020

ISSN 2535-2806

MINA fagrapport 65

Consequences of reduced sampling intensity for estimating population size of wolves in Scandinavia with spatial capture-recapture models

Cyril Milleret
Pierre Dupont
Mikael Åkesson
Linn Svensson
Henrik Brøseth
Richard Bischof



Milleret, C., Dupont, P., Åkesson, M., Svensson, L., Brøseth, H., and Bischof, R. 2020. **Consequences of reduced sampling intensity for estimating population size of wolves in Scandinavia with spatial capture-recapture models** - MINA fagrapport 65. 29pp .

Ås, March 2020

ISSN: 2535-2806

COPYRIGHT

© Norwegian University of Life Sciences (NMBU)

The publication may be freely cited where the source is acknowledged

AVAILABILITY

Open

PUBLICATION TYPE

Digital document (pdf)

QUALITY CONTROLLED BY

The Research committee (FU), MINA, NMBU

PRINCIPAL

Naturvårdsverket, Ref: 323-19-005, Contact person: Jens Andersson

COVER PICTURE

Wolf in Scandinavia. Source: Kjetil Kolbjørnsrud, Shutterstock

NØKKELOORD

ulv, *Canis lupus*, rovdyrforvaltning, tetthet, deteksjonssannsynlighet, ikke-invaderende innsamling av genetisk materiale, romlig fangst-gjenfangst, søkeinnsats

KEY WORDS

wolf, *Canis lupus*, carnivore management, population density, detection probability, non-invasive genetic sampling, spatial capture-recapture, search effort

Cyril Milleret (cyril.milleret@gmail.com), Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway.

Pierre Dupont, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway.

Mikkael Åkesson, Department of Ecology, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station, 73091 Riddarhyttan, Sweden.

Linn Svensson, Wildlife Damage Centre, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station, 73091 Riddarhyttan, Sweden.

Henrik Brøseth, Norwegian Institute for Nature Research, PO Box 5685, NO-7485 Trondheim, Norway.

Richard Bischof (richard.bischof@nmbu.no), Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway.

Summary

Every winter, the Scandinavian wolf population is surveyed using non-invasive genetic sampling (NGS) and snow-tracking to assess its annual status and trends. During 2017/18, search intensity and the proportion of samples genotyped was unusually high, resulting in more than 3000 samples associated with 375 individuals. The boost in sampling was realized in part through intensified structured searches by the management authorities and in part by encouraging hunters and the general public to collect samples opportunistically. Such a high effort is not sustainable for long-term monitoring, but presents an opportunity to evaluate the consequences of reduced sampling intensity. We artificially thinned the number of genetic samples available and evaluated the consequences of thinning on population size estimates derived with spatial capture-recapture (SCR) models.

The original aim of this study was to identify sampling strategies (sampling intensity and spatial configuration) that increased the cost-efficiency of wolf monitoring in Scandinavia for population size estimation using SCR. However, discovery of an apparent bias in population size estimates in response to sample reduction led to a shift in focus to identifying the possible causes of this pattern.

We found population size estimates obtained after sample reduction to be sensitive to different thinning strategies and model specifications. Aside from the expected increase in uncertainty around parameter estimates due to a reduction in sample size, removal of detections collected during structured sampling led to a reduction in mean abundance estimates. Further testing revealed that the apparent negative bias was especially pronounced 1) for the model that included separate submodels for opportunistic and structured sampling, 2) for abundance estimates of females that were not adult scent-marking individuals, 3) for single-season SCR models, as opposed to open-population SCR models (OPSCR), and 4) when thinning was conducted only on samples collected during structured searches.

Our analysis helped us hone in on the conditions under which bias is most prevalent, but further work is needed to identify the mechanisms causing it. As a next step towards a more applicable observation process model and/or data thinning scheme, we recommend a thorough characterization of the data accumulation process, including the potential link between opportunistic and structured sampling and the spatio-temporal relationship between track logs and samples.

Sammendrag

Den Skandinaviska vargpopulationen inventeras varje vinter, främst genom spårning på snö och analys av DNA-prov som samlas in under spårningarna, för att bland annat uppskatta antal och fördelning familjegrupper och revirmarkerande par. Under vintersäsongen 2017/18 utökades insatsen att söka efter och analysera DNA-prov från varg, vilket resulterade i mer än 3000 prov från 375 individer. Insamlingen av prov under vintern utökades dels genom mer intensifierade strukturerade sökinsatser av de förvaltande myndigheterna, dels genom att uppmuntra jägare och allmänheten att opportunistiskt samla in prov. En sådan insats är inte ekonomiskt hållbar för inventeringar på lång sikt, men med det erhållna datamaterialet är möjligt att undersöka och jämföra vad som händer om insatsen skulle varit mindre. Här tunnade vi artificiellt ut antalet tillgängliga prov från vintern 2017/2018 och undersökte konsekvenserna av uttunningen på uppskattningen av populationsstorlek från rumsliga fångst-återfångstmodeller (SCR).

Målet med studien var ursprungligen att identifiera provtagningsstrategier (m.a.p. antal prov och rumslig sammansättning) för att en mer kostnadseffektiv uppskattning av den Skandinaviska vargpopulationens storlek med SCR. Vi upptäckte emellertid att med uttunnade provmaterial fick snedfördelade uppskattningar av populationsstorleken med SCR. Detta gjorde att vi bytte fokus i studien för att undersöka orsaken bakom snedfördelningarna.

Vi fann att uppskattningar av populationsstorlek var känsliga för olika typer av uttunningar av provmaterialet samt olika modelltyper. Som förväntat ökade osäkerheten kring uppskattningarna av parametrarna i modellen med minskat antal prov. Då observationer från den strukturerade insamlingen av prov reducerades blev de uppskattade populationsstorlekarna dessutom lägre. Efter fortsatta undersökningar visade det sig att den negativa avvikelsen i populationsstorlek blev tydligare 1) med modeller som byggde på skilda förklaringsmodeller för opportunistiska och strukturerade provinsamlingar 2) för det uppskattade antalet tikar som inte var revirmarkerande, 3) för SCR-modeller enbart baserade data insamlat inom säsongen till skillnad från fångst-återfångstmodeller som även bygger på data från andra säsonger och 4) när endast prover från den strukturerade insamlingen tunnades ut.

Denna studie hjälpte oss att identifiera de förhållanden som generades de mest snedfördelade uppskattningarna av antalet individer i populationen, men mer analyser behöves för att ta reda mekanismerna bakom dessa resultat. För en mer tillämpbar modell över vargobservationerna och/eller uttunning av befintligt datamaterial, rekommenderar vi en noggrann karakterisering av hur data tas fram, däribland den möjliga kopplingen mellan opportunistisk och strukturerad insamling samt det rumsliga och tidsmässiga sambandet mellan spårningar och insamlade prov.

Contents

1	Introduction	7
2	Methods and Results	9
2.1	Data	9
2.2	Spatial capture-recapture analysis	11
2.3	Analysis overview	13
2.4	Analysis 1: SCR with separate observation models for structured and opportunistic sampling and thinning of search tracks	15
2.5	Analysis 2: SCR with a single observation model and thinning of search tracks	19
2.6	Analysis 3: Sex and state-specific SCR model with thinning of search tracks	20
2.7	Analysis 4: Sex and state-specific SCR model with thinning of samples from structured searches	21
2.8	Analysis 5: Sex and state-specific SCR model with thinning of all samples	22
2.9	Analysis 6: OPSCR model with thinning of search tracks in 2016/17 and 2017/18	25
3	Discussion	27
	References	29

1 Introduction

Norwegian and Swedish authorities have been monitoring the Scandinavian wolf population jointly for more than two decades using mainly non-invasive genetic sampling (NGS) and snow-tracking (Wabakken et al., 1999; Liberg et al., 2011). This has resulted in an extensive long-term data set and allowed the reconstruction of a near-complete pedigree of the population since wolves recolonized Scandinavia in the early 1980's (Åkesson et al., 2016). Monitoring is essential to determine the annual status of the population and to evaluate achievement of population goals in terms of number of packs in Norway (Norwegian Ministry of the Environment, 2003) and total population size in Sweden (Riksdagsbeslut, 2013).

Thus far, wolf population size in Scandinavia has been estimated indirectly using a conversion factor from the number of detected reproductions (Svensson et al., 2013; Chapron et al., 2016; Bischof et al., 2019a). Recently, spatial capture-recapture (SCR) methods have been developed for direct estimation of population size of wolves and other large carnivores in Scandinavia based on non-invasively collected DNA samples (Bischof et al., 2019a,b). SCR uses the spatial configuration of individual detections across the landscape to estimate density and abundance, while accounting for the fact that a) not every individual may be detected during surveys and b) the same individuals may be detected in multiple areas, as large carnivores have a propensity for wide-ranging movements.

A significant amount of resources is dedicated each year to collect and analyze wolf DNA samples in Scandinavia. In recent years, collection effort and the proportion of samples analyzed have been ramped up in Sweden in order to obtain a more complete picture of the structure of the population and to evaluate the reliability of the conversion factor used for deriving population size estimates. In addition to subjecting all samples collected during winter 2017/18 to DNA analysis, sample collection targeted all demographic groups in the population, including those that are not typically the focus of monitoring in Sweden. Such a high level of sampling intensity cannot be sustained in the long term. However, the data collected during the 2017/18 season provide an opportunity to evaluate the consequences of different monitoring schemes for the estimation of abundance using SCR models.

The original goal of this study was to identify sampling strategies (sampling intensity and spatial configuration) that increased the cost-efficiency of wolf monitoring in Scandinavia for population size estimation using SCR. However, discovery of an apparent bias in population size estimates in response to sample reduction (subsection 2.4) led to a shift in focus to identifying the cause of this pattern. This report thus describes a series of analyses that aim to 1) quantify the consequences of reduced sampling intensity on the precision and bias of population size estimates derived using SCR and 2) identify the conditions (sampling schemes and model specifications) under which data thinning leads to unreliable estimates.

Box 1: Definitions and acronyms

Pack: Group of ≥ 3 wolves sharing a territory, including at least one scent-marking adult (Liberg et al. 2012). Also referred to as “family group” by the Scandinavian wolf monitoring program.

Territorial pair: Two scent-marking adults of opposite sex.

Pup: Individual aged 0–12 months, within its natal pack.

Subadult: Individual aged >12 months, remaining in its natal pack.

Scent-marking adult: An individual that was identified at least once, during the current or any previous monitoring period, as a scent-marking member of a pack or a territorial pair.

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.

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.

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

Länsstyrelsen: 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.

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

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

SCR: Spatial capture-recapture.

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

Accuracy: Represents how close estimates are from the reference population size (or from the center of a target, Figure 1)

Precision: Represents how close several population size estimates are from each other (Figure 1).

Bias: Metric representing the distance between the reference population size and estimates. A negative bias means that population size estimates are lower than the reference population size, while a positive bias means larger population size estimates than the reference population size.

Reference population size: Since the true size of the wolf population is unknown, we used the estimates obtained without thinning and for each type of model as the “reference” population size.

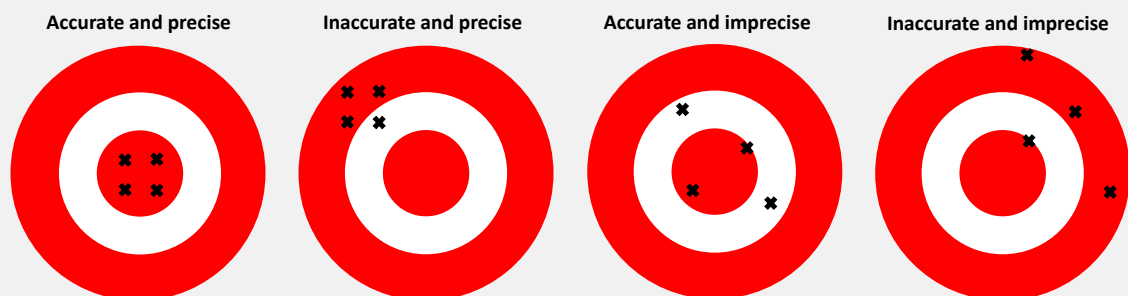


Figure 1: Schematic representation of accuracy and precision. The center of each target represents the reference population size and the four black crosses are population size estimates. We aim to maximize accuracy and precision, as represented on the target to the left.

2 Methods and Results

2.1 Data

We used data from the Scandinavian large carnivore database Rovbase 3.0 (rovbase.no, rovbase.se; last extraction 2019-10-08). This database is used jointly by Norway and Sweden to record information obtained during large carnivore monitoring, including non-invasive genetic sampling (NGS) data and GPS search tracks.

Non-invasive genetic sampling (NGS) Swedish and Norwegian management authorities - Statens naturoppsyn (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 any time of the year, the official survey period starting with the 2014/15 season has been October 1 – March 31. NGS schemes differs between Norway and Sweden. In Norway, the goal is to give all members of the population a chance of being detected via NGS. In Sweden, scent-marking adult individuals from pairs and packs are the primary target of NGS. All collected samples are genetically analyzed in Norway, whereas in Sweden, due to economic constraints, only a subset of the collected samples are generally subjected to genetic analysis based on prioritization of individuals or areas according to monitoring goals.

In order to obtain a better picture of the structure of the population and the robustness of the conversion factor used to estimate wolf population size from the number of detected packs (Chapron et al., 2016; Bischof et al., 2019a), the Swedish authorities increased the monitoring effort during seasons 2016/17 and 2017/18. During 2016/17, field protocols remained unchanged, but all collected samples were genetically analyzed. During 2017/18, NGS field protocols were adjusted so that all members of the population (not only scent-marking adult individuals from pairs and packs) were targeted by NGS, and all genetic material found in the field was collected and analysed. In 2017/18, opportunistic sampling also increased through a higher collection rate from members of the public, including hunters, as the Swedish hunter associations were specifically asked to help with the sample collection. This resulted in 3 112 genotyped samples (1 352 ♀; 1 760 ♂) that were associated with 375 (188 ♀; 187 ♂) individuals during that season. The average number of samples per individual detected was 8.3 (7.2 ♀; 9.4 ♂). Twenty-four individuals were associated with more than 50 detections (5 ♀; 19 ♂) with a maximum of 113 detections for one male (Table 1, Table 2).

Search tracks/logs During official sample collection, authorities recorded the GPS track log of their searches using hand-held GPS units. In 2017/18, >340 000 km of searches associated with wolves were recorded within the study area providing important information about the spatial variation in intensity of the search effort. We associated each sample collected by the authorities with the nearest search track with the same date. If no track of the same date was recorded within a 500 m radius of the sample (\approx 18% of samples), we assigned the sample to the nearest track of any date within that season.

Individual state The long-term and extensive monitoring of the Scandinavian wolf population has allowed the construction of a near complete pedigree of the population (Liberg et al., 2011; Åkesson et al., 2016). Using this information, scent-marking adult individuals (adult scent-marking members in a pack and adult scent-marking members in a pair) could be identified on a yearly basis. The identities of known adult scent-marking individuals are provided in the annual monitoring reports (e.g. Svensson et al. 2019). The state of an individual as either “adult scent-marking” (68 ♀; 68 ♂) or “other” (all others; 120 ♀; 119 ♂) has been shown to affect both ecological parameters and detection probability (Bischof et al., 2019a). We also accounted for this designation in the present study. Adult scent-marking individuals were associated with larger average number of samples (10,7 ♀; 15,8 ♂) compared to other individuals (5,2 ♀; 5,8 ♂).

Table 1: Annual number of wolf non-invasive genetic samples collected in Sweden and Norway, by individual state (“other” and “scent-marking”), for females (F) and males (M), and according to sample origin. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection. We included only samples collected within the study area and during the primary monitoring period (Oct 1 – March 31) between 2016/17 and 2018/19.

		2016/2017				2017/2018				2018/2019			
		Other		Scent-Marking		Other		Scent-Marking		Other		Scent-Marking	
		F	M	F	M	F	M	F	M	F	M	F	M
Total		516	580	588	739	623	689	729	1071	263	347	321	444
Norway	Authorities	70	56	40	38	80	70	48	87	49	69	57	74
	Hunter	14	2	16	15	24	16	18	8	10	55	16	14
	Research	59	21	21	30	28	20	31	35	17	35	16	26
	Random	15	23	29	21	22	17	24	27	46	43	24	23
	Viltskadecenter	0	0	0	0	0	0	0	0	0	0	0	0
	Total	158	102	106	104	154	123	121	157	122	202	113	137
Sweden	Authorities	281	421	420	572	237	292	400	687	126	129	194	292
	Hunter	62	40	47	37	194	169	119	147	6	7	4	4
	Research	4	0	1	0	0	4	4	6	4	4	1	2
	Random	8	12	9	9	37	84	71	67	5	5	6	7
	Viltskadecenter	3	5	5	17	1	17	14	7	0	0	3	2
	Total	358	478	482	635	469	566	608	914	141	145	208	307

Table 2: Annual number of wolf individuals detected in Sweden and Norway, by individual state (“other” and “scent-marking”), for females (F) and males (M), and according to their origin. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection. We included only samples collected within the study area and during the primary monitoring period (Oct 1 – March 31) between 2016/17 and 2018/19. Note that the number of individuals detected does not add up because the same individual can be detected in both countries and/or by different entities.

		2016/2017				2017/2018				2018/2019			
		Other		Scent-Marking		Other		Scent-Marking		Other		Scent-Marking	
		F	M	F	M	F	M	F	M	F	M	F	M
Total		105	118	67	65	120	119	68	68	79	92	59	58
Norway	Authorities	19	17	12	11	23	20	15	17	21	15	10	9
	Hunter	5	2	3	4	12	7	7	1	3	15	4	7
	Research	13	11	7	8	9	8	6	6	5	15	6	5
	Random	7	7	6	7	12	7	6	4	11	16	5	7
	Viltskadecenter	0	0	0	0	0	0	0	0	0	0	0	0
	Total	28	21	18	15	32	27	17	19	26	32	15	14
Sweden	Authorities	81	96	55	53	75	84	56	58	54	57	47	50
	Hunter	25	21	19	16	47	62	34	37	3	6	4	3
	Research	3	0	1	0	0	4	3	5	2	2	1	2
	Random	4	5	5	1	21	33	17	20	3	4	4	5
	Viltskadecenter	3	2	3	4	1	1	2	2	0	0	2	1
	Total	85	101	55	53	92	97	58	59	57	63	48	50

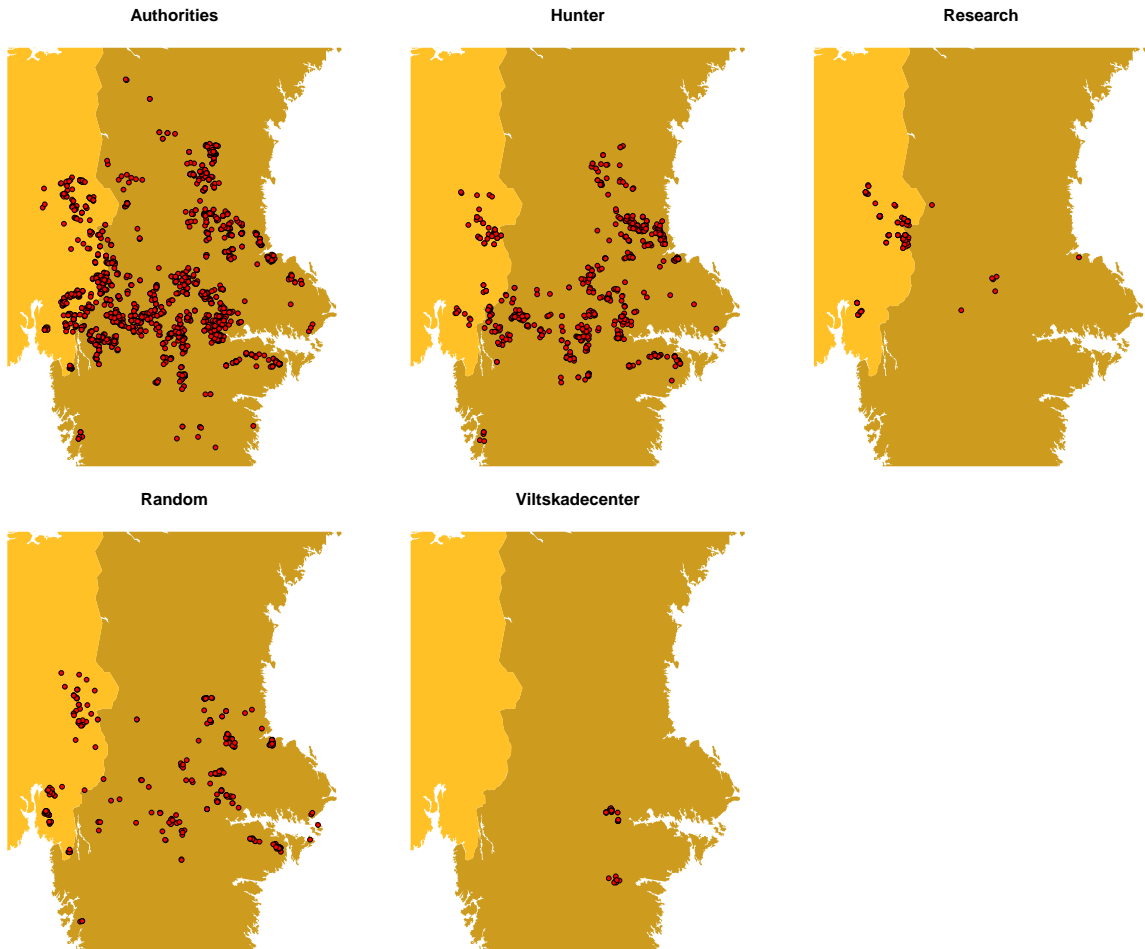


Figure 2: Spatial distribution of 3112 genetic samples collected between Oct 1 2017 – March 31 2018 in Scandinavia according to their origin. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection.

2.2 Spatial capture-recapture analysis

For the majority of the analyses conducted as part of this study, we used a single-season spatial capture recapture (SCR) model. This model differs from the open population SCR (OPSCR) model used during RovQuant (Bischof et al., 2019a,b) in that it does not include population dynamics, uses only a single year of data, and therefore only estimates density and abundance for a single year. We chose a simpler model for this study for two main reasons: 1) the step-wise procedure used to track down the cause of the bias in abundance estimates required the fitting of thousands of models and would have been computationally prohibitive using the much more complex and data-hungry OPSCR model, and 2) the single season model presented a more controlled setting (e.g. no propagation of information between years, Milleret et al. 2019b) to explore the implications of thinning. However, for comparison, we also conducted an analysis using the OPSCR model (see subsection 2.9).

Basic SCR model The single season SCR model is composed of two sub-models:

1. A model for the spatial distribution of individuals.
2. A model for individual detections during noninvasive genetic sampling.

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 notations to Milleret et al. (2018); Dupont et al. (2019); Milleret et al. (2019a,b); Bischof et al. (2019a,b) and other references provided in the following sections.

In SCR, the position of an individual in space is described by the location of its activity center (AC), which is equivalent to the center of a circular home range. The AC location of a detected individual is informed by the spatial configuration of detections of that individual. The AC location of individuals that were not detected are determined based on the spatial heterogeneity in detection probability and a spatial covariate describing the distribution of activity centers (density) within the study area. Both detected and undetected individuals are thus less likely to be placed in areas with high detection probability and/or low density. We constructed an intensity surface for density by applying a smoothing kernel to locations of detected wolf packs during the previous year (Figure A2.5 in Bischof et al., 2019a).

Although individual detections can occur continuously in the landscape, it is common to aggregate detections to the closest grid cell center (Milleret et al., 2018). Detectors in our study were 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 (Milleret et al., 2018).

We added a 40km wide buffer around the detector grid that allowed placement of individual ACs but did not contain any detections (Bischof et al., 2019a). This is an important component of SCR models, as it allows the detection of individuals with ACs located outside the detector grid (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.

We used a half-normal detection function that represents a decline in detection probability with increasing distance from individual AC location (Royle et al., 2014). This function has two parameters, the baseline probability (p_0) and the scale parameter (σ) of the detection function that can be under the influence of individual and spatial (detector-specific) factors. 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., 2019a): this variable was included as a logit-linear covariate on the baseline detection probability.
- Average distance from the nearest road (Bischof et al., 2019a): the distance from each detector to the closest road (1:100 000, Lantmäleriet, Sweden; N50 kartdata, Statens kartverk, Norway). This variable represents accessibility, which we predicted to facilitate detectability, and was included as a logit-linear covariate on the baseline detection probability
- 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. 2019a) between October 1–March 31. As NGS during winter relies heavily on the presence of snow, we predicted that greater snow cover increases detectability. This variable was included as a logit-linear covariate on the baseline detection probability.
- Countries: to control for differences in monitoring regimes between countries (i.e. Sweden and Norway), we estimated independent baseline detection probabilities for each country.

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 logit-linear predictor of the baseline detection probability.
- 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 “scent-marking adult” and “other” (Bischof et al., 2019a).

Detection probability and the effect of the aforementioned individual and spatial factors were estimated separately for males and females in the sex-specific SCR models (Bischof et al., 2019a), but also sex and state-specific models (subsection 2.6).

Model fitting We fitted Bayesian SCR 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) and used various techniques to increase efficiency of the models (Milleret et al. 2018, 2019a, Turek et al. in prep.). We ran three chains, each with 10 000 iterations, including a 2 000-iteration burn-in period. A description of the MCMC process and its outcome is provided in Box 2 in Bischof et al. (2019a). 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.

To obtain an estimate of abundance excluding the buffer region, we summed the number of SCR-predicted AC locations of alive individuals that fell within the focal area for each iteration of the MCMC chains, thus generating a posterior distribution of the abundance for this area. We calculated the median and the 95% credible interval limits of the posterior distribution of abundance. Total population size estimates were obtained by merging the posterior samples obtained from the sex-specific models. For each of the 25 model repetitions (Table 3), we calculated “relative bias” (RB) in abundance (N) using $RB = \frac{\bar{N} - N}{N}$, where \bar{N} is the median estimated abundance after thinning, and N , the abundance obtained without thinning. Abundance estimates derived from the full (not thinned) data set were used as reference values for calculating relative bias for simulation scenario, because true abundance was unknown. We also calculated the width of the 95%CrI of N for each model repetition, by subtracting the value of the 2.5% quantile from the value of the 97.5% quantile of the posterior distribution. Higher 95%CrI widths indicate higher uncertainty around the estimates and thus lower precision.

2.3 Analysis overview

Scent-marking adult individuals from pairs and packs constitute only a small portion of a wolf population (Chapron et al., 2016), which means that NGS sampling needs to also target other members of the population (i.e. pups, dispersers, lone individuals) to obtain robust estimates of total population size (Bischof et al., 2019a). Since the original aim of this study was to quantify the minimum effort necessary to obtain reliable estimates of population size using SCR models, we only used data from season 2017/18, where authorities were instructed to target all demographic groups during structured searches.

We report methods and results from six separate analytical steps (Table 3) with different thinning strategies and model configurations. Each analysis was implemented with the intent to fix issues or answer questions raised by the preceding one. The primary focus of this stepwise procedure was to identify the causes for and attempt to eliminate issues with biased estimates of abundance resulting from thinning.

Table 3: Summary of the different models and thinning strategies presented in this report

Analysis	Thinning Type	Thinning target	% Removal	Model type
1	Track removal	Structured searches	25, 50, 75%	Double observation model for each sex
2	Track removal	Structured searches	25, 50, 75%	Single observation model for each sex
3	Track removal	Structured searches	25, 50, 75%	Single observation model for each sex/state
4	Sample removal	Structured searches	25, 50, 75%	Single observation model for each sex/state
5	Sample removal	All samples	25, 50, 75%	Simple observation model for each sex/state
6	Track removal	Structured searches	25, 50, 75%	OPSCR model for each sex

2.4 Analysis 1: SCR with separate observation models for structured and opportunistic sampling and thinning of search tracks

Model We extended the basic SCR model described in subsection 2.2 by including separate observation process models for structured and opportunistic sampling. NGS sampling conducted by the authorities is associated with a detailed record of effort in space and time (GPS search tracks, subsection 2.2). By contrast, samples submitted by other entities (e.g. the public and hunters) lack a direct measure of associated search effort. By utilizing a double-observation model, we accounted for the difference in available information on search effort. This also allowed us to account for different probabilities of being detected during structured searches and opportunistically, which might be especially important when we artificially removed samples from only one origin. The double-observation process model estimated separate baseline detection probabilities and covariate effects on detection for each sampling type, while both models shared the same σ , as this is related to home range size. Note that this feature was not implemented in the OPSCR models described in (Bischof et al., 2019a,b) due to the significant computational cost of using a double observation model when estimating spatial population dynamics.

In theory, samples can be collected opportunistically within the entire study area. We therefore placed a 10 km x 10 km detector grid that covered the full spatial domain (except within the buffer area) for the *opportunistic* observation model. We added the same covariates on p_0 as described in paragraph subsection 2.2, except the length of search tracks and the effect of prior detection as they should not affect opportunistic detection probability. During structured sampling, samples can only be collected where authorities have searched. For the *structured* observation model, we therefore placed detectors and subdetectors only in searched grids and sub grid cells, respectively. We then added the same covariates on p_0 as described in subsection 2.2. Separate SCR models were fitted for males and females.

Search effort reduction We randomly removed a certain proportion of search tracks and their associated samples from the data set. This means that only samples collected during structured searches by authorities (SNO, Länsstyrelsen) were removed; all opportunistically collected samples were retained in the dataset even after thinning. We created 25 different datasets (i.e. repeated random thinning) for each level of thinning (i.e. 25%, 50%, 75% of tracks removed; Figure 3).

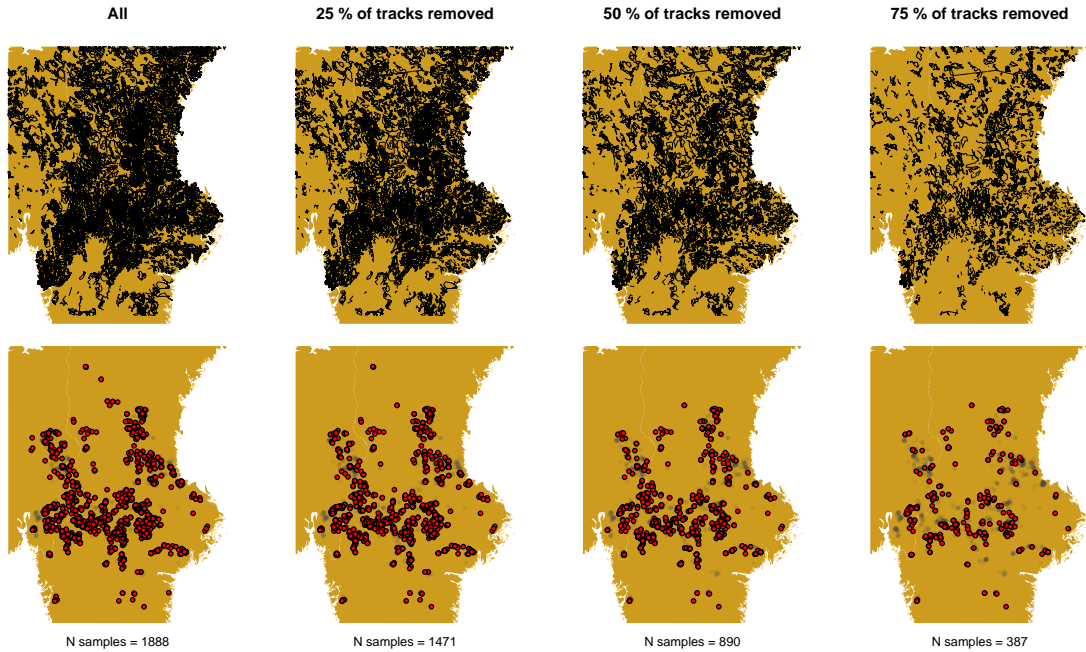


Figure 3: Example of thinning based on track-removal. The top row shows the spatial configuration of the tracks and the bottom row shows the distribution of detections after different levels of thinning. “All” shows all samples and tracks registered in 2017/18. Track removal only reduced the number of detections collected during structured searches (bottom row; red points with black contours). “N samples” corresponds to the number of samples from structured searches that remain in the thinned data set. Samples collected opportunistically (bottom row; transparent black points) were not affected by thinning. For each level of thinning, we repeated the random removal process 25 times, creating a total of 75 different data sets.

Results The removal of 25% of the tracks reduced the total number of samples (all origins combined) by approximately 15% (Table 4), and the number of detected individual by 3% (Table 5). This pattern was similar for males and females (Table 5). However, track-removal caused a considerably higher reduction in the number of “other” individuals detected than the number of “scent-marking” individuals (Table 5).

Table 4: Annual number genetic samples (detections) of wolves in Sweden and Norway, by individual state (“other” and “scent-marking”), for females (F) and males (M), and according to sample origin. Numbers are provided for three levels of random thinning of tracks (25%, 50%, 75% of track removed). Values represent samples left after one thinning replicate. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection. We included only samples collected within the study area and during the primary monitoring period Oct 1 2017 – March 31 2018.

		Other								Scent-Marking							
		F				M				F				M			
		0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%
Total		623	524	459	397	689	586	516	426	729	607	521	398	1071	866	667	476
Norway	Authorities	80	54	33	28	70	51	33	22	48	34	26	14	87	54	30	19
	Hunter	24	24	24	24	16	16	16	16	18	18	18	18	8	8	8	8
	Random	22	22	22	22	17	17	17	17	24	24	24	24	27	27	27	27
	Research	28	28	28	28	20	20	20	20	31	31	31	31	35	35	35	35
	Viltskadecenter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	154	128	107	102	123	104	86	75	121	107	99	87	157	124	100	89
Sweden	Authorities	237	164	120	63	292	208	156	77	400	292	214	103	687	515	340	160
	Hunter	194	194	194	194	169	169	169	169	119	119	119	119	147	147	147	147
	Random	37	37	37	37	84	84	84	84	71	71	71	71	67	67	67	67
	Research	0	0	0	0	4	4	4	4	4	4	4	4	6	6	6	6
	Viltskadecenter	1	1	1	1	17	17	17	17	14	14	14	14	7	7	7	7
	Total	469	396	352	295	566	482	430	351	608	500	422	311	914	742	567	387

Table 5: Number of wolves detected in Sweden and Norway, by individual state (“other” and “scent-marking”), for females (F) and males (M), and according to sample origin. Numbers are provided for three levels of random thinning of tracks (25%, 50%, 75% of track removed). Values represent individuals left in the data set after one thinning replicate. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection. We included only samples collected within the study area and during the primary monitoring period Oct 1 2017 – March 31 2018. Note that the number of individuals detected does not add up because the same individual can be detected in different countries and/or by different entities.

		Other								Scent-Marking							
		F				M				F				M			
		0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%
Total		120	111	105	91	119	114	110	102	68	66	66	60	68	67	65	63
Norway	Authorities	23	17	16	15	20	18	15	10	15	11	10	9	17	15	9	7
	Hunter	12	12	12	12	7	7	7	7	7	7	7	7	1	1	1	1
	Random	12	12	12	12	7	7	7	7	6	6	6	6	4	4	4	4
	Research	9	9	9	9	8	8	8	8	6	6	6	6	6	6	6	6
	Viltskadecenter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	32	29	29	29	27	25	24	22	17	16	16	15	19	18	14	13
Sweden	Authorities	75	64	56	28	84	78	65	42	56	53	51	39	58	56	48	41
	Hunter	47	47	47	47	62	62	62	62	34	34	34	34	37	37	37	37
	Random	21	21	21	21	33	33	33	33	17	17	17	17	20	20	20	20
	Research	0	0	0	0	4	4	4	4	3	3	3	3	5	5	5	5
	Viltskadecenter	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2
	Total	92	84	78	64	97	92	89	81	58	56	55	49	59	58	56	54

The model fitted to data with 25% of tracks removed led to reduced population size estimates compared with the model fitted to the complete data set (negative relative bias, Figure 4). This bias was more pronounced for females than for males. At a higher level of thinning, negative bias was also visible for males (Figure 4).

At very low sample sizes (and recaptures), SCR studies may produce biased results (Patterson et al., 2019); however, bias at the level of thinning tested here (especially at 25% and 50% thinning) is unexpected. There are various potential explanation, one of them being a mismatch between the process by which detections (samples) accumulate across space and the representation of the observation process in the model. For example, the prioritization of search areas and selection of samples for analysis by the authorities may lead to an artificial detection process favoring certain individuals, thus biasing overall detection probability estimates and thus estimates of abundance. Furthermore, in this analysis, opportunistic and structured sampling were considered as independent processes but may actually be mutually influencing each other. This may be facilitated by the fact that most observations in Rovbase are public, authorities are transparent about the location of wolf territories, and hunters are encouraged to report findings to the authorities.

Spatial autocorrelation between samples associated with a given individual may be another cause for bias: removal of entire transects, especially long ones, is liable to remove all or most detections of an individual, without a corresponding reduction in detection probability of individuals that remain in the dataset. However, this potential problem should in theory be mitigated for by the use of the covariate on detection probability coding for the effect of variable effort (search transect length within a given detector grid cell).

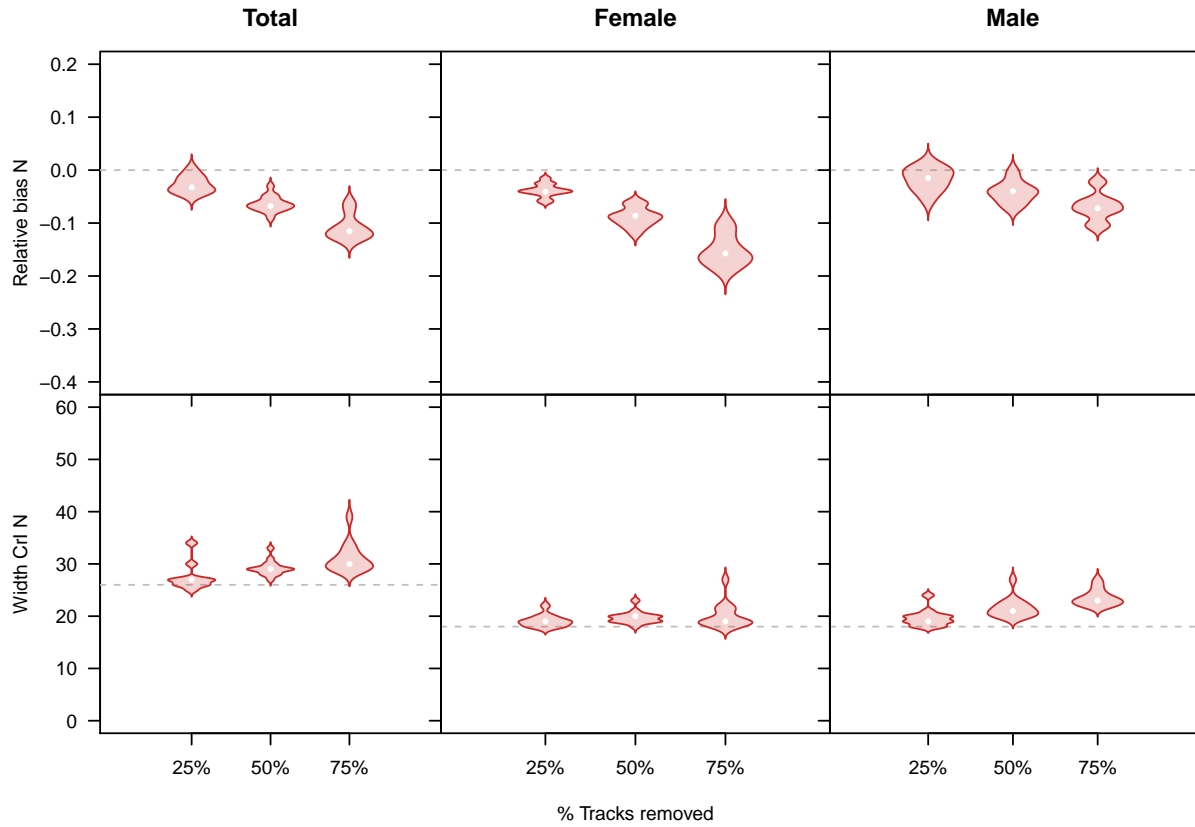


Figure 4: Violin plots showing the average relative bias in abundance (N) estimates (top row) and width of the credible interval (CrI, bottom row) for the 25 replicated datasets for each level of thinning. Estimates were obtained using a double observation model and by removing tracks and associated samples (step 1, Table 3). Dashed lines represent the reference estimates obtained using the same model, but with all the data (no thinning).

2.5 Analysis 2: SCR with a single observation model and thinning of search tracks

Model To determine whether the negative bias observed in subsection 2.4 was linked with the use of the double-observation model, we repeated the analysis with a single observation process that pooled structured and opportunistic sampling. This led to the basic SCR model described in subsection 2.2, with an observation process model that was equivalent to the the one used in the OPSCR models during RovQuant (Bischof et al., 2019a,b).

Search effort reduction Thinning proceeded as in subsection 2.4. We randomly removed a certain proportion of search tracks (i.e. 25%, 50%, 75% of tracks) and their associated samples from the data set. Only samples collected during structured searches by authorities (SNO, Länsstyrelsen) were removed. We created 25 random datasets for each thinning scenario.

Results Relative bias in abundance estimates was less pronounced than in subsection 2.4 but still present, especially for females and at high levels of subsampling (75% samples removed, Figure 5). Merging structured and opportunistic data collection into a single observation model reduced the bias from thinning, but the mechanism behind this phenomenon is unclear and requires further investigation. We also observed an increase in the widths of the CrI after thinning. This pattern is expected, as with fewer detections uncertainty becomes larger.

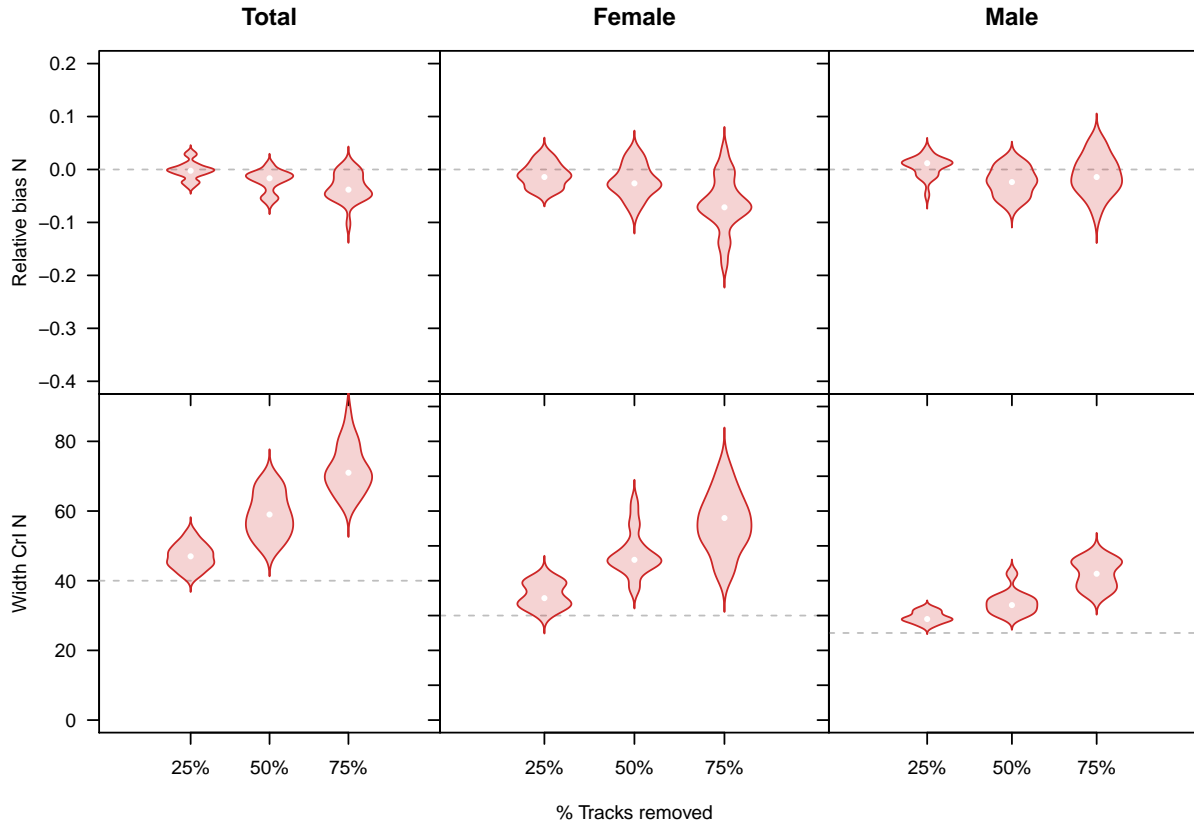


Figure 5: Violin plots showing the average relative bias in abundance (N) estimates (top row) and width of the credible interval (CrI, bottom row) for the 25 replicated datasets for each level of thinning. Estimates were obtained using a single observation model and by thinning tracks and associated samples (analysis 2, Table 3). Dashed lines represent the reference estimates obtained using the same model, but with all the data (no thinning).

2.6 Analysis 3: Sex and state-specific SCR model with thinning of search tracks

Model The bias observed in subsection 2.4 and, to a lesser degree in subsection 2.5, was more pronounced for females than for males. The model further estimates separate detection probabilities (p_0) between adult scent-marking individuals and those that are not. Deviations between the SCR observation process model and true detection process may be more pronounced for one category of individual than the other. To further hone in on the cause of the bias, we used the model described in subsection 2.5, but fitted separate models by sex and state (i.e. “Female scent-marking”, “Male scent-marking”, “Female other”, “Male other”). As a consequence, all parameters were estimated separately for every sex-state combination. We displayed abundance estimates for each sex-state combination and summed estimates obtained from the four models to obtain total abundance estimates.

Search effort reduction Thinning proceeded as in subsection 2.5. We randomly removed a certain proportion of search tracks (i.e. 25%, 50%, 75% of tracks) and their associated samples from the data set. Only samples collected during structured searches by authorities (SNO, Länsstyrelsen) were removed to create 25 random datasets for each thinning scenario (Figure 3).

Results We found that bias in abundance estimates was most pronounced for the “female other” category. For non-scent-marking females a 5% negative bias was apparent already when only 25% of tracks and associated samples had been removed, whereas for the other sex-state combinations bias remained low until 50% (females scent-marking) or 75% (males scent-marking and other) of tracks and associated samples were removed. As expected, the width of the 95% CrI increased with decreasing number of tracks and samples for all sex-state combinations.

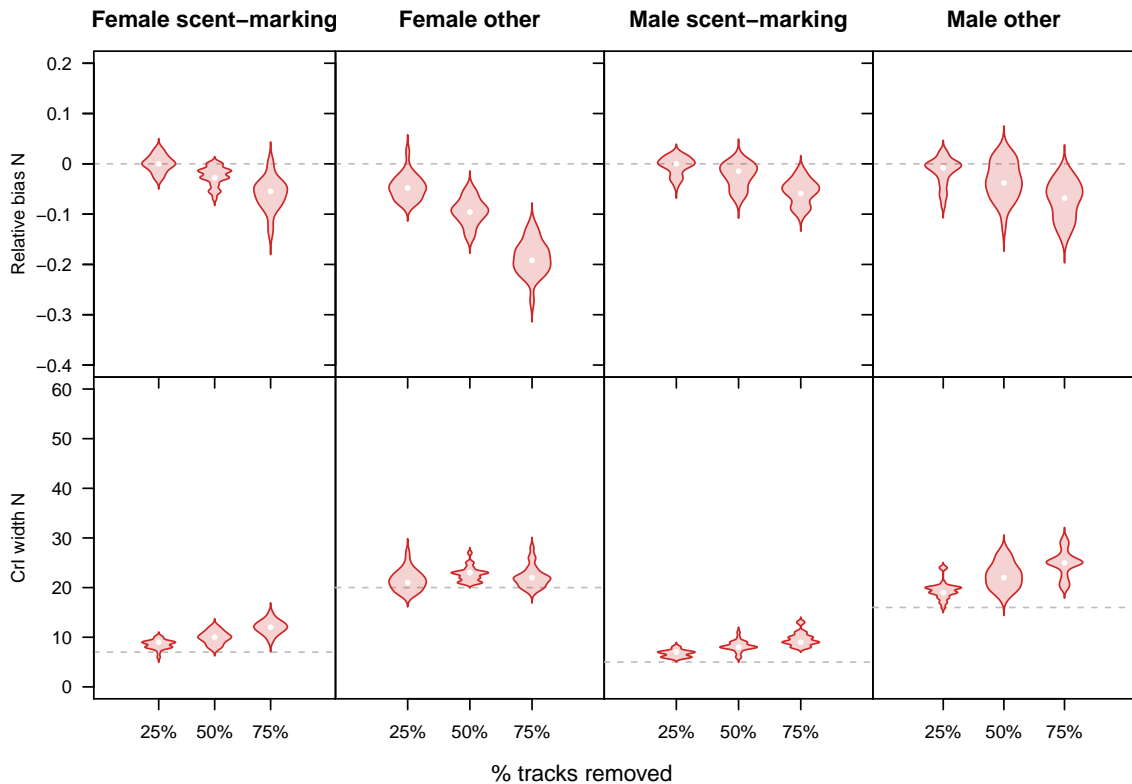


Figure 6: Violin plots showing the average relative bias in abundance (N) estimates (top row) and width of the credible interval (CrI, bottom row) for the 25 replicated datasets for each level of thinning. Estimates were obtained using a SCR model for each state and sex and by thinning tracks and associated samples (analysis 3, Table 3). Dashed lines represent the reference estimates obtained using the same model, but with all the data (no thinning).

2.7 Analysis 4: Sex and state-specific SCR model with thinning of samples from structured searches

Model Here we used the SCR model described in subsection 2.6 with a single observation process fitted separately to all sex and state combinations.

Search effort reduction A possible explanation for biased abundance estimates following thinning is that detections of an individual are likely linked with one or a few search tracks, thus leading to selective removal of all detections associated with an individual without a corresponding reduction in detection probability of individuals remaining in the data set. If the effort covariate (track length) does not sufficiently account for spatial variation in detection probability, this may result in overestimation of detection probability and thus a negative bias in abundance. In order to explore this possibility, we repeated the analysis described in subsection 2.6, but performed thinning at the level of samples, instead of search tracks. Instead of removing tracks, we randomly removed a portion of all samples obtained during structured searches, regardless of location. As in the previous analyses, all opportunistic samples were retained. We created 25 random datasets for each thinning scenario (i.e. 25%, 50%, 75% of samples).

Results Patterns in bias and uncertainty resemble those from the analysis with thinning of search transects subsection 2.6.

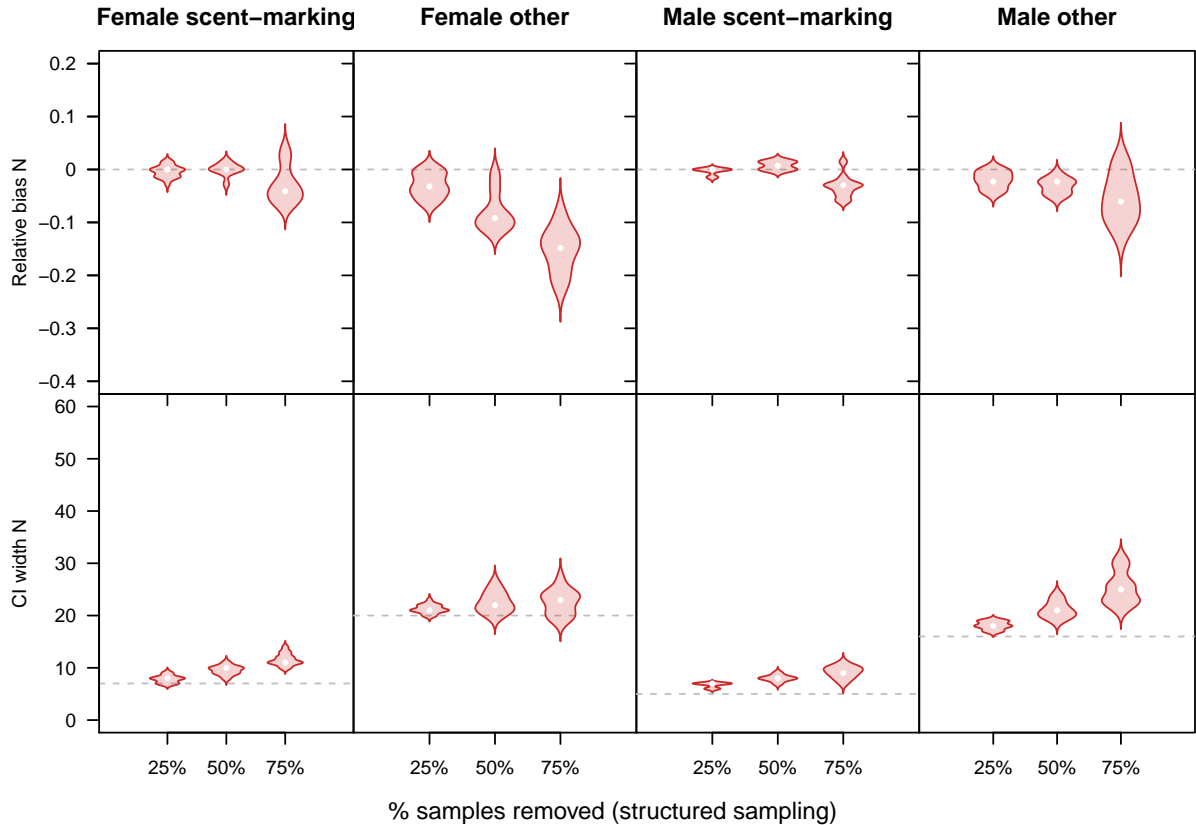


Figure 7: Violin plots showing the average relative bias in abundance (N) estimates (top row) and width of the credible interval (CrI, bottom row) for the 25 replicated datasets for each level of thinning. Estimates were obtained using a SCR model for each state and sex and by thinning randomly only the samples collected during structured sampling (analysis 3, Table 3). Dashed lines represent the reference estimates obtained using the same model, but with all the data (no thinning).

2.8 Analysis 5: Sex and state-specific SCR model with thinning of all samples

Model Here we used the SCR model described in subsection 2.6 and subsection 2.7 with a single observation process fitted separately to all sex and state combinations.

Search effort reduction The results from one search type (opportunistic vs. structured) may influence the other (subsection 2.4). This non-independence between the sample accumulation processes could lead to biases in abundance estimates if only data obtained with one methods are subjected to thinning. In order to explore this possibility, we repeated the analysis described in subsection 2.7, but subjected all samples to thinning, regardless of their origin (opportunistic vs. structured). We created 25 random datasets for each thinning scenario (i.e. 25%, 50%, 75% of samples).

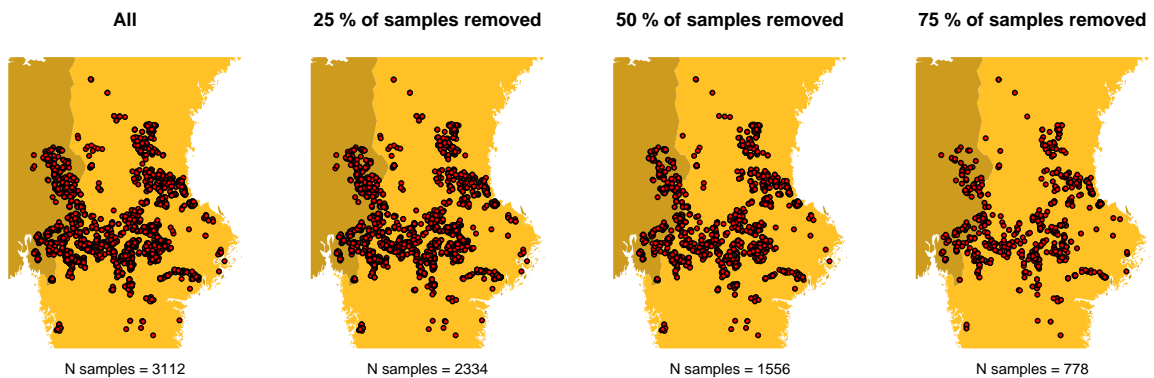


Figure 8: Example of thinning based on removal of samples regardless of origin (structured vs. opportunistic). “All” shows all samples registered in 2017/18. “N samples” corresponds to the number of samples that remain in the data set after thinning. For each level of thinning, we repeated the random removal process 25 times, creating a total of 75 different data sets.

Results The most pronounced result of this analysis is the marked increase in uncertainty with thinning, compared with the previous analyses (Figure 9). This is not unexpected, as thinning affected both structured and opportunistic samples, thus leading to a more substantial reduction in sample size. Bias is less pronounced than in the previous analyses.

Table 6: Annual number genetic samples (detections) of wolves in Sweden and Norway, by individual state (“other” and “scent-marking”), for females (F) and males (M), and according to sample origin. Numbers are provided for three levels of random thinning of all samples, regardless of origin (25%, 50%, 75% of samples removed). Values represent samples left after one thinning replicate. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection. We included only samples collected within the study area and during the primary monitoring period (Oct 1 2017 – March 31 2018.).

		Other								Scent-Marking							
		F				M				F				M			
		0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%
Total		623	457	308	145	689	505	337	178	729	561	361	191	1071	811	550	264
Norway	Authorities	80	56	36	19	70	52	35	17	48	36	27	16	87	56	30	10
	Hunter	24	21	14	6	16	11	6	3	18	13	8	5	8	4	3	1
	Random	22	15	12	5	17	14	9	1	24	14	9	4	27	20	11	7
	Research	28	23	15	11	20	14	8	5	31	23	16	12	35	24	18	7
	Viltskadecenter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	154	115	77	41	123	91	58	26	121	86	60	37	157	104	62	25
Sweden	Authorities	237	174	115	55	292	223	152	81	400	307	208	106	687	540	379	192
	Hunter	194	136	95	37	169	121	80	47	119	94	52	24	147	109	70	34
	Random	37	31	21	12	84	58	36	18	71	61	37	21	67	51	35	12
	Research	0	0	0	0	4	3	3	3	4	3	2	2	6	3	1	0
	Viltskadecenter	1	1	0	0	17	9	8	3	14	10	2	1	7	4	3	1
	Total	469	342	231	104	566	414	279	152	608	475	301	154	914	707	488	239

Table 7: Annual number of wolf individuals detected annually in Sweden and Norway, by individual state (“other” and “scent-marking”), for females (F) and males (M), and according to sample origin. Numbers are provided for three levels of random thinning of all samples, regardless of origin (25%, 50%, 75% of samples removed). Values represent individuals that remained in the data set after one thinning replicate. Samples were collected during structured searches by the authorities (mainly by SNO, Länsstyrelsen). Samples collected by hunters, universities and research institutes (research), the wildlife damage center at SLU (Viltskadecenter), and other members of the public (random) represent the opportunistic part of the sample collection. We included only samples collected within the study area and during the primary monitoring period (Oct 1 2017 – March 31 2018.). Note that the number of individuals detected does not add up because the same individual can be detected in different countries and/or by different entities.

		Other								Scent-Marking							
		F				M				F				M			
		0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%	0%	25%	50%	75%
Total		120	112	98	72	119	111	103	84	68	68	65	57	68	67	66	61
Norway	Authorities	23	18	13	11	20	19	16	13	15	13	13	11	17	16	14	7
	Hunter	12	11	9	6	7	7	4	3	7	6	3	3	1	1	1	1
	Random	12	8	7	4	7	7	5	1	6	5	5	3	4	3	2	2
	Research	9	7	5	5	8	7	5	4	6	6	5	5	6	6	6	5
	Viltskadecenter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	32	27	22	18	27	26	22	17	17	17	16	14	19	18	17	11
Sweden	Authorities	75	70	59	39	84	77	70	50	56	56	54	43	58	57	54	47
	Hunter	47	43	39	22	62	56	49	34	34	31	25	17	37	35	30	22
	Random	21	20	14	9	33	25	18	10	17	17	13	9	20	19	18	10
	Research	0	0	0	0	4	3	3	3	3	3	2	2	5	3	1	0
	Viltskadecenter	1	1	0	0	1	1	1	1	2	2	1	1	2	2	1	1
	Total	92	87	78	56	97	89	82	67	58	58	56	49	59	58	55	52



Figure 9: Violin plots showing the average relative bias in abundance (N) estimates (top row) and width of the credible interval (CrI, bottom row) for the 25 replicated datasets for each level of thinning. Estimates were obtained using a SCR model for each state and sex and by thinning samples (step 4, Table 3). Dashed lines represent the reference estimates obtained using the same model, but with all the data (no thinning).

2.9 Analysis 6: OPSCR model with thinning of search tracks in 2016/17 and 2017/18

Model During analyses 1-5, we used single-season SCR models because the single season model presented a more controlled setting to explore the implications of subsampling. However, because individual information is propagated between years in the OPSCR model, it is likely that this model is more robust to subsampling. For example, as we have shown previously (Milleret et al., 2019b), OPSCR models can produce reliable abundance estimates in years that are entirely void of sampling, i.e. when there are gaps in the monitoring time series. To determine how a reduction in effort would impact inferences drawn from the model developed and used by RovQuant for Scandinavian wolf density estimation, we conducted one additional analysis using the OPSCR model described in (Bischof et al., 2019a) that uses a single observation process model such as in subsection 2.5.

Search effort reduction This analysis was based on the 7-year monitoring time series (2012/13 - 2018/19) also used in (Bischof et al., 2019a). We thinned the data collected as part of structured searches based on tracks during the monitoring seasons with intensified inventory in Sweden (2016/17 and 2017/18) to reach similar sample sizes as during the surrounding years with normal sampling intensity (Figure 10). This meant removal of approximately 60% of tracks during the two seasons with higher than usual search effort. Thinning was repeated five times, resulting in five alternative data sets to which the OPSCR model was fitted.

Results Similar to results obtained using a single year SCR model, sub-sampling based on tracks led to lower population size estimates compared to estimates obtained without thinning. However, bias was less pronounced than when using single-season SCR models subsection 2.4. The uncertainty in population size estimates remained comparatively low during 2016/17 and 2017/18 even after thinning, because the number of detections collected opportunistically (not thinned) was higher than in surrounding years (Table 4, Table 5).

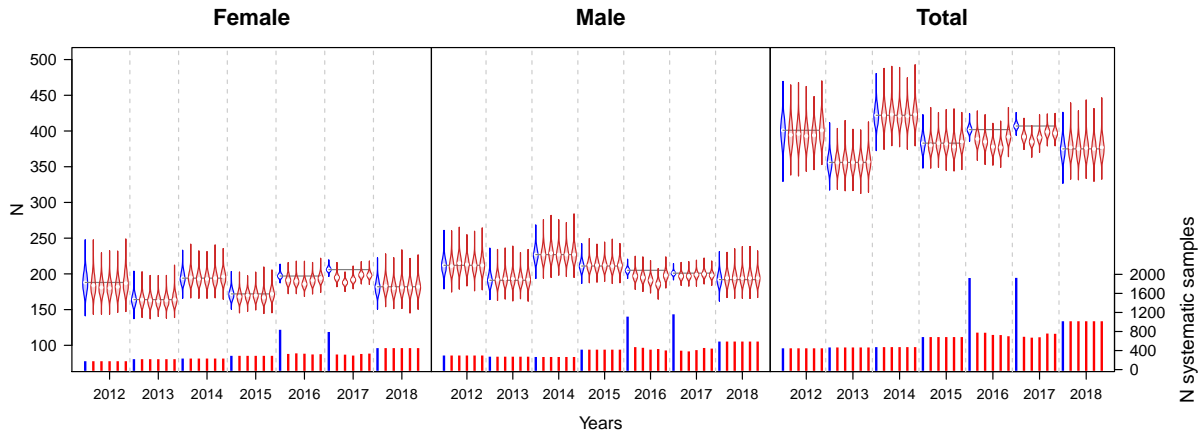


Figure 10: Violin plots showing wolf abundance estimates obtained using the OPSCR model presented in Bischof et al. (2019a) on the complete data set (blue violins), and after five track-based thinning replicates (red violins), for the period 2012-2018. Vertical bars correspond to the number of samples from structured searches used in the analysis (blue: full data set; red: thinned data). Note that samples collected opportunistically were not thinned.

3 Discussion

As expected, simulated reduction in the number of available samples led to a decrease in precision of abundance estimates. However, it appears that even in single-season SCR models, and more so in the OPSCR model, precision remains relatively high even when a drastic reduction in effort associated with structured searches is simulated.

On the other hand, the apparent negative bias resulting from thinning is of concern. Under certain conditions, even low levels of thinning (25% of tracks and associated samples) can lead to bias, which becomes increasingly pronounced as effort decreases. We found that bias was: 1) most pronounced for females not identified as scent-marking members of a pair or pack, 2) higher for the analysis that used separate vs. joint observation process models for opportunistic and structured sample collections, 3) less pronounced in the OPSCR model than the single-season SCR model, 4) and more pronounced when thinning was conducted only on samples collected during structured searches.

There are a number of possible explanations for the thinning-caused bias. At very low sample sizes (and recaptures), SCR studies may produce biased results (Paterson et al., 2019); however, bias at the level of thinning tested here is unexpected because the number of detections per individual remains relatively high even at the highest level of thinning employed here (average of >2.5 samples per detected individual at 75% tracks removed).

Another possible explanation concerns the subampling itself. Detections associated with a given individual are inherently autocorrelated; this is the premise behind the detection function used in the SCR model. The removal of entire transects, especially long ones, is liable to remove all or most detections of an individual, without a corresponding reduction in detection probability of the other individuals that remain in the dataset. This, in turn, could lead to an overestimation of overall detectability and thus underestimation of abundance. However, this potential problem should in theory be mitigated by the use of the covariate on detection probability which accounts for variable effort (search transect length within a detector grid cell).

The two types of sampling may not be completely independent, but rather complementary to each other. The information obtained during opportunistic data collection may inform the structured searches and vice-versa, which could induce some bias when thinning is performed only on one type of data. As expected, due to the more severe reduction in sample size, thinning all samples, rather than just samples obtained during structured sampling, led to a more drastic increase in uncertainty.

Another explanation for the observed bias is a mismatch between the process by which detections (samples) accumulate across space and the observation process model used in the analysis. For example, the prioritization of search areas may lead to an artificial detection process favoring certain individuals, thereby biasing overall detection probability estimates and thus estimates of abundance. We explored two alternative observation process models in this analysis, one that separated structured and opportunistic sample collections and one that treated them as part of the same process. The double observation process model, while in theory more closely reflecting the true observation process, led to more pronounced bias. This, together with the fact that one category of animals (non-scent-marking females) is associated with the strongest thinning-caused bias, may provide another clue as to the cause of the problem and requires further investigation.

Due the discovery of an unexpected bias arising from thinning, we had to divert from our original analytical aim. As a consequence, we are not yet able to provide concrete recommendations for sampling configurations and intensities that would maximize the cost-efficiency of NGS for the purpose of estimating wolf population size using SCR. However, in addition to the suggestions we have already made concerning NGS-based monitoring (see Anon 2017), we make the following recommendations based on the findings of the present study and assuming the intention to estimate population size using SCR models:

1. Avoid any undocumented non-random thinning and individual-based prioritization in search areas and samples designated for analysis. Even though there is no expectation to detect every individual in the population, wolves in every demographic group (e.g. pups, scent marking individuals, dispersers, lone territorial individuals) should have a chance of being detected. The more pronounced thinning-caused bias in abundance estimates for individuals in state “other” could be due to the significantly lower detection probability of this segment of the population (Table 4). This is the most common demographic group in the population Chapron et al. (2016) and additional thinning of the already comparatively low number of samples may have a disproportional effect on abundance estimates.
2. Until a solid explanation for the bias observed in this study can be found, we suggest the continued use of a single-observation process model that combines opportunistic and structured sampling during SCR analysis.
3. Continue analyzing the wolf NGS data using the OPSCR model (Bischof et al., 2019b) as this model appears to be more robust to the bias phenomenon than the single-season SCR models that were the focus of the present analysis. The reason for the lower thinning-caused bias in the OPSCR model is likely the more effective use of information due to its propagation between years through the population dynamic component of the model.
4. Conduct a detailed characterization of the spatio-temporal relationship between track logs and samples obtained via structured searches, and between structured and opportunistic samples. Furthermore, attempt to identify potential mechanisms that lead to prioritization of samples and non-random sampling in the field with respect to individuals, classes, and search areas.
5. Maintain the pedigree of the wolf population (Åkesson et al., 2016) as it allows the distinction between scent-marking and others individuals, which is especially important as they have different detection probabilities.

Acknowledgements

This work would not have been possible without the large carnivore monitoring programs and the extensive monitoring data collected by Swedish (Länstyrelsen) and Norwegian (SNO) wildlife management authorities, as well as the public in both countries. Our analyses relied on genetic analyses conducted by the laboratory personnel at the DNA laboratories at the Swedish University of Agricultural Sciences (SLU) and the Norwegian Institute for Nature Research (NINA). The study was funded by Miljødirektoratet, Naturvårdsverket, and the Research Council of Norway (NFR 286886; project WildMap). The computations/simulations were performed on resources provided by NMBU’s computing cluster “Orion”, administered by the Centre for Integrative Genetics and by UNINETT Sigma2 - the National Infrastructure for High Performance Computing and Data Storage in Norway. We are grateful to P. de Valpine and D. Turek for extensive help with the formulation of the OPSCR model in Nimble. J. Vermaat provided helpful comments on drafts of this report.

References

- Åkesson, M., Liberg, O., Sand, H., Wabakken, P., Bensch, S., and Flagstad, Ø. (2016). Genetic rescue in a severely inbred wolf population. *Molecular Ecology*, 25(19):4745–4756.
- Anon (2017). Estimating population size of wolves in sweden using spatial capture-recapture based on noninvasive genetic sampling: suggestions for sampling design. *Rapport från SKANDULV*, (5s).
- Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Åkesson, M., Brøseth, H., and Kindberg, J. (2019a). Estimating the size of the scandinavian wolf population with spatial capture recapture and conversion factors. *MINAflagrapport57*, 80pp.
- Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Brøseth, H., and Kindberg, J. (2019b). Rovquant:estimating density, abundance and population dynamics of bears, wolverines, and wolves in scandinavia. *MINAflagrapport63*, 79pp.
- Chapron, G., Wikenros, C., Liberg, O., Wabakken, P., Flagstad, Ø., Milleret, C., Månsson, J., Svensson, L., Zimmermann, B., Åkesson, M., and Sand, H. (2016). Estimating wolf (*canis lupus*) population size from number of packs and an individual based model. *Ecological Modelling*, 339:33 – 44.
- de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., and Bodik, R. (2017). Programming with models: writing statistical algorithms for general model structures with nimble. *Journal of Computational and Graphical Statistics*, 26(2):403–413.
- Dupont, P., Milleret, C., Gimenez, O., and Bischof, R. (2019). Population closure and the bias-precision trade-off in spatial capture–recapture. *Methods in Ecology and Evolution*, 10(5):661–672.
- Efford, M. G. (2011). Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. *Ecology*, 92(12):2202–2207.
- Gardner, B., Sollmann, R., Kumar, N. S., Jathanna, D., and Karanth, K. U. (2018). State space and movement specification in open population spatial capture-recapture models. *Ecology and Evolution*, 8(20).
- Gelman, A. and Rubin, D. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7:457–511. <http://www.stat.columbia.edu/~gelman/research/published/itsim.pdf>.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Hobbs, N. T., and Sand, H. (2011). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in europe. *Proceedings of the Royal Society B: Biological Sciences*, 279(1730):910–915.
- Milleret, C., Dupont, P., Bonenfant, C., Brøseth, H., Flagstad, y., Sutherland, C., and Bischof, R. (2019a). A local evaluation of the individual state-space to scale up bayesian spatial capture recapture. *Ecology and Evolution*, 9(1):352–363.
- Milleret, C., Dupont, P., Brøseth, H., Kindberg, J., Royle, J. A., and Bischof, R. (2018). Using partial aggregation in spatial capture recapture. *Methods in Ecology and Evolution*, 9(8):1896–1907.
- Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., de Valpine, P., and Bischof, R. (2019b). Estimating abundance with interruptions in data collection using open population spatial capture-recapture models. *bioRxiv*.
- NIMBLE Development Team (2019). *NIMBLE: MCMC, Particle Filtering, and Programmable Hierarchical Modeling*. <https://cran.r-project.org/package=nimble>.
- Norwegian Ministry of the Environment (2003). Rovvilt i norsk natur [carnivores in norwegian nature]. stortingsmelding 15 (2003–2004). <https://www.regjeringen.no/no/dokumenter/stmeld-nr-15-2003-2004/id403693/>.
- Paterson, J. T., Proffitt, K., Jimenez, B., Rotella, J., and Garrott, R. (2019). Simulation-based validation of spatial capture-recapture models: A case study using mountain lions. *PLOS ONE*, 14(4):1–20.
- R Core Team (2018). R: A language and environment for statistical computing. vienna, . *Austria: R Foundation for Statistical Computing*.
- Riksdagsbeslut (2013). En hållbar rovdjurspolitik. proposition 2012/13:191. <https://bit.ly/2xPuZcF>.
- Royle, J. A., Chandler, R. B., Sollmann, R., and Gardner, B. (2014). *Spatial Capture-Recapture*. Academic Press.
- Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., Flagstad, ., and Hedmark, E. (2013). Varg i skandinavien och finland: Slutrapport fraøninventering av varg vintern 2013–2014. *Høgskolan i Hedmark*.
- Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., Flagstad, ., and Hedmark, E. (2019). Inventering av varg vintern 2018-2019. bestandsövervakning av ulv vintren 2018-2019. *Bestandsstatus for store rovdyr i Skandinavia. Bestandsstatus for stora rovdjur i Skandinavien*, 1(53s).
- Turek, D., de Valpine, P., and Paciorek, C. J. (2016). Efficient markov chain monte carlo sampling for hierarchical hidden markov models. *Environmental and Ecological Statistics*, 23(4):549–564.
- Turek, D., Milleret, C., Ergon, T., Brøseth, H., and de Valpine, P. ("in prep."). Efficient mcmc for spatial capture-recapture models.
- Wabakken, P., Aronson, Å., Sand, H., Steinset, O. K., and Kojola, I. (1999). The wolf in scandinavia: Status report of the 1998-1999 winter.(in norwegian with english summary). 19:40.
- Williams, B. K., Nichols, J. D., and Conroy, M. J. (2002). *Analysis and management of animal populations*. Academic Press.