Instrumented individuals are not representative of the population. Survival of wolverines with and without GPS collars

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Abstract

15 Results from biologging studies are often scaled up to population-level inferences and this begs

16 the question: Are instrumented animals representative of the population given the potential bias

17 in individual selectivity, the influence of capture, handling and wearing bio-loggers? The

18 answer is elusive due to the challenges of obtaining comparable data from individuals without

19 bio-loggers. Using non-invasive genetic data of a large carnivore, the wolverine (*Gulo gulo*) in

20 Scandinavia, and an open-population spatial capture-recapture model, we were able to estimate

21 and compare survival rates of individuals fitted with GPS collars versus individuals that had

22 never been captured and collared. We found that mortality of GPS collared individuals was

23 47% lower compared to individuals without GPS collars. While instrumented and non-

24 instrumented wolverines had similar risks of dying from legal culling, GPS collared individuals

25 displayed lower mortality rates due to causes other than legal culling. Reports of positive

26 effects of biologging on the fitness of individuals are rather uncommon and we argue that the

27 most likely explanation is that GPS-collars could shield animals from poaching. Our results

28 highlight the challenges of drawing population level inferences for large carnivores when using

29 data from an instrumented sample of the population.

Introduction

31 Telemetry and biologging systems have been instrumental in furthering our understanding of

32 the ecology and cryptic behavior of wildlife. Technological development and miniaturization

33 of devices have allowed researchers to track animals and obtain a wide range of previously

34 unattainable information, such as fine scale movement data (Bischof et al. 2019), kill rates of

35 predators (Gervasi et al. 2014), and habitat selection (Bouyer et al. 2015). Results from tracking

36 studies are often scaled up to population-level inferences, with the assumption - explicit or

37 implicit - that instrumented animals are representative of the population as a whole

38 (Hebblewhite and Haydon 2010). There are two main reasons why this assumption may be

39 violated: 1) the sample of instrumented individuals is non-random (i.e., a systematic bias in the

40   selection of individuals studied) and 2) biologging and tracking themselves alter the biology of

41   instrumented animals. Despite the long history and widespread use of wildlife telemetry

42   applications, it is challenging to assess the reliability of telemetry studies for inferring

43   processes and patterns in wild populations. This is largely due to the inherent catch-22: the

44   methods whose impact is to be evaluated are often seen as the only reliable methods available

45   for obtaining the parameters that are potentially impacted.

46   *Non-random sampling.* Randomization is an essential requirement for inferring population

47   properties from the properties of a sample. Yet, the selection of animal subjects enrolled in

48   telemetry studies is rarely, if ever, fully randomized (Hebblewhite and Haydon 2010). For

49   example, variation in the vulnerability to physical capture that is non-random with regards to

50   biological attributes (such as behavior or fitness) is bound to lead to biased conclusions if

51   estimates are extrapolated to the population level. Some deviations from representativeness

52   may be easy to detect, such as a different age structure or gender ratio in the sample vs the

53   population. Others, such as individual variation in boldness (Darrow and Shivik 2009) or social

54   standing (Young et al. 2019) may not.

55   *Observer effect.* Aside from animal welfare concerns (Putman 1995), methods that impact the

56   study species will inadvertently introduce bias as the system studied is altered through the

57   process of observation/data collection, the so-called "observer effect" (Canine 1990,

58   MacFarlane and King 2002). First, capturing and handling are stressful for animals (Cattet et

59   al. 2008, Esteruelas et al. 2016). Second, although benign in most cases (Bodey et al., 2018),

60   attaching bio-logger devices can influence behavior or even have long-term detrimental effects

61   on individuals (Lechenne et al. 2012, Bodey et al. 2018).

62   In addition to direct effects of capture, handling, and wearing biologging device, the fitness of

63   instrumented individuals can be impacted indirectly if awareness of the presence of biologging

64   devices alters human decision making in human-wildlife interactions. This may be particularly

65   acute for rare, elusive, and controversial species such as large carnivores. Bio-logging is

66   commonly used to study large carnivores and helps inform debate, policy, and management

67   (Carricondo-Sanchez et al. 2020). Large carnivores are essential for ecosystem functioning but

68   also get into conflict with humans as they prey on wild and domestic animals, and can

69   occasionally injure or kill people (Packer et al. 2019). The resulting controversy and debate

70   extend not only to large carnivore management, but also to the use of biologging in carnivore

71   research. Indeed, this is not always perceived as positive by the public because captures are

72   often costly and require the use of invasive techniques such as helicopter and anesthesia (Mech

73   and Barber 2002). Furthermore, biologging can have indirect consequences for individuals as

74   bio-loggers can interact with management decisions and lead to lethal actions that would have

75   not occurred without the information provided by the logger (Meeuwig et al. 2015, Cooke et

76   al. 2017). Real time information about individual location can also be made publicly available

77   to avoid conflicts (Liberg et al. 2010) or be hacked by poachers ("cyber-poaching",(Cooke et

78   al. 2017)). Additionally, it has been suggested that instrumented animals could be protected

79   from poaching due to the increased risk of detecting poaching events when animals wear a

80   visible bio-logger. As a consequence, biologging of large carnivores may not only interfere

81   directly with the behavior and fitness of individuals, but also indirectly by influencing

82   management actions and illegal activities.

83   To investigate the effect of biologging, we used a decade worth of non-invasive genetic

84   monitoring data of wolverines (*Gulo gulo*) in Scandinavia and compared survival rates of

85   individuals with and without GPS collars using an open-population capture-recapture model.

86   This unique data set contained data from individuals without capturing them, as both

87   instrumented and non-instrumented individuals were sampled during monitoring. We show

88   that instrumented large carnivores may not always constitute a representative sample of the

89   population and call for prudence when extrapolating survival estimates from instrumented

90   individuals to populations.

91   **Material and methods**

92   *GPS collared individuals and study area*

93   Wolverines were equipped with GPS collars after being darted from a helicopter and

94   immobilized with medetomidine–ketamine, following pre-established protocols (Arnemo et al.

95   2012). GPS collars with GSM communication (GPS plus mini; Vectronic Aerospace GmbH,

96   Berlin, Germany) were used. The collars were fitted with a release mechanism in the form of

97   a cotton band that usually breaks apart after ~0.5 -2 years (depending on thickness of band and

98   behavior of the animal). The handling protocols were approved by the Norwegian Experimental

99   Animal Ethics Committee (FOTS ID 2826, FOTS ID 4699, FOTS 7017) and fulfilled their

100   ethical requirements for research on wild animals. In addition, permits for wild animal capture

101   were obtained from the Norwegian Environment Agency. Captures occurred in the winters

102   (Jan-April) of 2010 to 2015. In total, we collared 43 individuals (♀21; ♂22), 18 in the Central

103   (♀8; ♂10), and 25 in the Northern (♀13; ♂12) part of Norway (Appendix S1, Figure 1). Of

104   these 18 (41%) where approximately 1-year old (average birthdate of wolverines 15th of

105   February). The wolverine population is distributed continuously between the two regions

106   where individuals were captured (Bischof et al. 2019). However, we distinguished between the

107   Central and Northern areas so that instrumented and non-instrumented individuals were

108   exposed to similar ecological conditions.

109   The northern study area is situated in Finnmark and Troms County (70°10′ N , 24°70′) and the

110   Central area in Trøndelag County (64°30′ N , 12°50′ E). Troms and Finnmark have a coastal

111   alpine climate, while Trøndelag has a more continental climate. The northern area is dominated

112   by alpine tundra and mountain birch forest (*Betula pubescens*) forms the tree line. Northern

113   boreal forest, dominated by conifer (*Pinus sylvestris, Picea abies*), is common at lower

114   elevations in the central area. High elevations of both areas are usually snow-covered from

115   November to June. Free-ranging semi-domestic reindeer (*Rangifer tarandus*) is the most

116   abundant ungulate in both areas. All reindeer herds migrate seasonally, but different husbandry

117   practices and land use restrictions create variation in the timing, magnitude, and direction of

118   the migrations. The coastal parts of Troms and Finnmark are almost completely devoid of

119   reindeer in winter (Mattisson et al. 2011). In Trøndelag, seasonal migration is short, and most

120   wolverine home ranges include both summer and winter reindeer-grazing areas. Free-ranging

121   domestic sheep (*Ovis aries*) are present to a varying degree in both areas during summer.

122   *Non-invasive genetic sampling*

123   Wolverines are monitored annually by Swedish and Norwegian authorities using non-invasive

124   genetic sampling (NGS) and dead recoveries (Gervasi et al. 2016). Scat and hair samples were

125   collected on snow along wolverine tracks from December to June, covering the entire

126   distribution range of the species in Scandinavia. Non-invasive genetic samples were collected

127   from individuals (≥1 year old), but not from young of the year. For further details on the DNA

128   analysis procedure see (Flagstad et al. 2004, Brøseth et al. 2010, Gervasi et al. 2016). To ensure

129   that the studied individuals with and without a GPS collars were exposed to similar conditions,

130   we only considered non-invasive genetic samples collected within 70km of any genetic

131   samples from collared individuals.

132   We used data from eight consecutive monitoring seasons (December-June) between 2009/10

133   (i.e. the winter when wolverine captures started) and 2016/17. After the winter 2016/17, none

134   of the wolverines were wearing a GPS collar. The non-invasive dataset contained a total of

135   4989 (♀2446; ♂2543) genetically identified samples of which 2753 (♀1360; ♂1393) and 2236

136   (♀1183; ♂1053) were collected in the Central- and Northern areas, respectively (Appendix S1

137   Table S1). This corresponded to 1036 (♀555; ♂481) different individuals of which 616 (♀321;

138   ♂295) and 421 (♀235; ♂186) were detected in the Central- and Northern areas, respectively

139   (Appendix S1 Table S1). Note that only one individual was detected in both study areas. We

140   also obtained recovery locations and genetic identification data from 424 (♀219; ♂ 205)

141   individuals legally culled during the study period. Occasionally, individuals recovered dead

142   due to other reasons (e.g. poaching, car collision) were also reported (♀6; ♂ 5).

143   *GPS covariate*

144   All collared individuals were genetically identified from tissue collected during the capture

145   which allowed us to match them with the NGS dataset. We created an individual and time-

146   dependent binary covariate (*GPS*) coding 1 if the individual was wearing a GPS collar at any

147   time during the monitoring season, and 0 otherwise. The latter included individuals that were

148   never captured, and individuals before they were collared or after losing their collar. With the

149   use of this covariate, we intended to account for any contemporary effect caused by the GPS

150   collar.

151   *OPSCR model*

152   To estimate the survival rates of wolverines, we built an open population spatial capture-

153   recapture (OPSCR) model (Ergon and Gardner 2014, Bischof et al. 2016, Chandler et al. 2018),

154   which addresses three challenges associated with the analyses of population-level NGS data:

155   1) detection is imperfect and heterogeneous in space and time (Kery and Schaub 2011), 2)

156   individuals that reside primarily outside the surveyed area may be detected within it (Efford

157   2004), and 3) estimation of true survival rate (Ergon and Gardner 2014).

158   We estimated separate model parameters for each region and sex, except for the parameters

159   that concerned the quantification of the differences between GPS-collared versus not GPS-

160   collared individuals. Due to sample size limitations, we did not break estimates down further

161   and assumed that differences between collared versus non-collared animals were consistent

162   across regions and sex.

163   The OPSCR model is a hierarchical state-space model composed of three sub-models: 1) a

164   model for detections during DNA searches, 2) a model for population dynamics, and 3). a

165   model for density and movements.

166   ***The detection model*** the detection model describes the relationship between individual

167   detection probability and distance to its activity center (AC). We used the half-normal detection

168   model that assumes that the probability p of detecting individual i at detector j and time t

169   decreases with distance (D_{ijt}) between the detector and the AC:

170     $p_{i,j,t} = p_{0_{i,j,t}} . exp\left(\frac{-D_{i,j,t}^2}{2\sigma^2}\right)$ *eqn 1*

171   where p_0 represents the detection probability at the location of the AC, and σ represents the

172   width of the utilization distribution.

173   We placed a detector grid within a buffer of 70 km surrounding all detections of captured

174   individuals for each region (Appendix S1, Figure 1). The spatial domain was defined as the

175   detector grid surrounded by a 60 km buffer. We used grid cells as detectors and aggregated

176   detections to the closest grid cell center. We used a partially aggregated binomial model that

177   divided detectors (10 km resolution) into 25 subdetectors (2 km) and modeled the frequency

178   of subdetectors with more than one detection as a binomial response with a sample size of 25

179   (for additional details see Milleret et al. 2018). To account for individual, spatial, and temporal

180   heterogeneity in detection probability we included several linear effects on a logistic scale on

181   the baseline detection probability (p_0) (Appendix S2):

182   ***The multistate model*** We used a multistate formulation for the population dynamics model

183   (Lebreton and Pradel 2002) where each individual life history is represented by a succession

184   of discrete states z_{it} that arises from a Markov process. Between two consecutive years, an

185   individual i can either remain in its current state or transition to another one, with transition

186   probabilities corresponding to vital rates. We considered four different states: "unborn" if the

187 individual has not yet been recruited in the population. "alive" if it is alive. "dead legal" if it

188 has died from legal culling between the start of the previous and current monitoring seasons.

189 "Dead": if it has a) died from any other cause of mortality between the start of the previous and

190 current monitoring seasons or b) died earlier, regardless of the cause.

191 During the first occasion, individuals can only be designated as "unborn" or "alive" so that

192 $z_{i,1} \sim dcat(1- \psi, \psi, 0, 0)$, where ψ represents the probability to be already part of the population

193 at t=1.

194 For $t \geq 2$, $z_{i,t}$ is conditional on the state of individual i at $t-1$:

- If $z_{i,t-1} = 1$, individual i is available to be recruited (transition to state 2), so $z_{i,t} \sim dcat(1-$

196 $\gamma_t, \gamma_t, 0, 0)$.

197 - If $z_{i,t-1} = 2$ individual i can survive and remain $z_{it}=2$ with probability Φ_t, die from culling

198 and transition to $z_{it}=3$ with probability h_t or die from other causes and transition to $z_{i,t}$

199 $=4$ with probability h_t, so that $z_{i,t} \sim dcat(0, \Phi_t, h_t, w_t)$, where $\Phi_t = 1-h_t-w_t$

200 - Finally, all individuals in dead states ($z_{i,t-1} = 3$ or 4) transition to $z_{i,t-1} = 4$, the absorbing

201 state, with probability 1.

202 To quantify differences in mortality rates between collared and non-collared individuals,

203 we included the effect of the *GPS* covariate as a linear effect on the logistic scale for both

204 culling (*h*) and other (*w*) mortality rates:

$$logit(w_{i,t}) = w0_t + \beta w_{GPS} * GPS_{i,t}$$

$$logit(h_{i,t}) = h0_t + \beta h_{GPS} * GPS_{i,t} \qquad \text{eqn 3}$$

207 Note that we estimated separate β parameters for each region and sex.

208 The detection data y_{ijt} was modelled as the realization of a Binomial process based on the

209 individual, detector, and time specific detection probability $p_{i,j,t}$, the number of trials defined

210   as the number subdetectors K, and conditional on individual state $z_{i,t}$ (only individuals with the

211   state "*alive*" can be detected.):

212    $y_{i,j,t} \sim Binomial(p_{0_{i,j,t}} * I(z_{i,t} = 2),\ K_j)$ eqn 4

213   ***The movement model*** We used an inhomogeneous binomial point process to model the

214   distribution of individual ACs (Illian et al. 2008). This formulation allows the density of ACs

215   to vary according to a spatial intensity function. ACs (*s*) at $t = 1$ were placed according to the

216   intensity function $\lambda(s_1)$, that was based on a spatial covariate (*Dens;* locations of known dens

217   from den visits conducted by authorities in their effort to document reproductions per 20 km

218   habitat cell) that roughly reflects the species distributions $\lambda(s_1) = e^{\beta_{dens} \cdot Dens(s_1)}$. For *t≥2,* the

219   intensity function was a combination of the intensity surface representing AC distribution

220   (β_{Dens}) and an isotropic multivariate normal distribution centered around the source

221   coordinates (location of the AC at *t-1*) with standard deviation τ (see (Milleret et al. 2020) for

222   more details). As a consequence, individual movement from year to year was modelled as a

223   Markovian spatial point process. This feature of the model improves survival estimates as it

224   takes into account the impact of animals moving within and out of the sampled area (Ergon

225   and Gardner 2014, Gardner et al. 2018).

226   *Parameter estimation*

227   We fitted the Bayesian OPSCR models using Markov chain Monte Carlo (MCMC) simulation

228   with NIMBLE (de Valpine et al. 2017, NIMBLE Development Team 2019) in R version 3.3.3

229   (R Core Team 2018). We implemented different modelling techniques to increase MCMC

230   efficiency (available in the nimbleSCR package (Bischof et al. 2020); see (Milleret et al. 2018,

231   2019, 2020, Turek et al. 2020) for details). We ran 4 chains, each with 42,500 iterations

232   including a 12,500-iteration burn-in period. We considered models as converged when the

233   Gelman-Rubin diagnostic (Rhat, (Gelman and Rubin 1992)) was < 1.1 for all parameters and

234   by visually inspecting the trace plots. We summarized posterior distributions using their

235   median and 95% credible interval (CrI).

236   **Results**

237   Collared wolverines had a 47% (95% CrI: [21%;68%]) lower overall mortality rate compared

238   to non-collared individuals (Figure 1). This difference was attributable mainly to lower

239   mortality rate due to causes other than legal culling (βw_{GPS}= -1.08 [-1.86; -0.46]), and to a

240   lesser extent to a lower mortality rate due to culling (βh_{GPS}= -0.37 [-1.09; 0.25]; Figure 1). On

241   average, individuals with a collar had 58% [29; 80%] reduced probability to die from mortality

242   due to causes other than legal culling than individuals without a GPS collar. Individuals

243   wearing a GPS collar had a lower detectability rate compared to individuals without GPS collar

244   ($\beta p_{0_{GPS}}$= -0.80 [-1.04;-0.60]). Additional details are presented in Appendix S1 Figure S2-6.

245   **Discussion**

246   Using a single individual-based dataset containing wolverines both with and without a GPS

247   collar, and an open population spatial capture-recapture model, we were able to provide a

248   quantitative answer to a question that has eluded wildlife ecologists: can we extrapolate results

249   obtained from a limited number of instrumented individuals to the population? We found that

250   wolverines with a GPS collar had a lower mortality rate compared to individuals without a

251   collar. Although collared individuals seemed to have slightly lower mortality associated with

252   legal culling, the difference was mainly manifested through a lower mortality rate due to other

253   causes. Our results call for prudence when extrapolating vital rate estimates from a sample of

254   instrumented large carnivores to the population.

255   There are three main potential, not mutually exclusive, explanations for the observed difference

256   in mortality between wolverines with and without GPS collar: a) wolverines selected for GPS-

257   collaring had mortality that differed from the population average ("non-random sample"), b)

258 instrumentation altered wolverine survival ("observer effect"), and c) that our NGS and

259 OPSCR-based approach to mortality estimation inadvertently introduced a bias ("analytical

260 artifact"). Being observational in nature, our study does not allow us to isolate an explanation

261 unequivocally. However, we argue that the observer effect could be the primary cause for the

262 observed difference in mortality between instrumented and non-instrumented animals.

263 *Analytical artifact* – Our OPSCR model aimed at quantifying population dynamics of

264 wolverines while accounting for imperfect detection inherent to NGS data. To reduce the

265 chances of introducing a bias with our OPSCR model by inadvertently comparing different

266 parts of the population, we restricted the spatial (Appendix S1, Figure S1) and temporal extents

267 of the analysis to limit the differences in ecological conditions that individuals with and without

268 collars are exposed to. Furthermore, we accounted for individual, temporal, and spatial

269 heterogeneity in detectability in the population-level OPSCR model, including potential

270 differences in detectability between GPS collared and non-collared individuals. All OPSCR

271 model parameters, except parameters linked with the effect of wearing a GPS collar, were also

272 sex- and region-specific thereby accounting for possibly important sources of variation.

273 *Non-random sampling* – Non-invasive genetic sampling and the collaring of wolverines

274 targeted all segments of the population (except cubs of the year). Captures from helicopter also

275 occurred opportunistically by following any fresh wolverine tracks encountered on snow,

276 without intentional focus on a specific part of the population. Captures may have been

277 unintentionally biased towards individuals whose tracks are likely to be encountered (e.g.,

278 animals moving in open areas and traveling longer distances) and those that are more

279 vulnerable to capture once detected (e.g. young individuals). Indeed, the proportion of 1-year

280 old among collared individuals (41%) was higher than their expected prevalence in the

281 population (29%; Landa et al. 1998). With a negative age-mortality relationship (Persson et al.

282 2009)(Persson et al. 2009), the proportion of young individuals among GPS-collared individual

283   being higher than expected for this wolverine population, we would expect higher mortality

284   among GPS tagged animals than the population average. Yet, we detected the opposite effect,

285   which suggests that the explanation for the mortality difference lies elsewhere.

286   *Observer effect* –. A third possibility is that wearing a GPS collar itself impacts mortality of

287   instrumented wolverines. Mortality due to other causes includes three main causes that our

288   study can not differentiate: 1) natural (e.g., age, diseases, intra and inter-specific killing), 2)

289   traffic, and 3) illegal killing. The literature generally reports negative or neutral effect of the

290   capture, handling, and wearing of bio-logger on the survival of individuals (Sergio et al. 2015,

291   Bodey et al. 2018), and we are not aware of any mechanisms that could give a competitive

292   advantage to GPS collared wolverines to a magnitude that would decrease their natural or

293   traffic mortality rates. Although patterns of carnivore mortality due to causes other than culling

294   remain cryptic, we know that illegal culling account for a large part of carnivore mortality in

295   Scandinavia (Persson et al. 2009, Liberg et al. 2011, Milleret et al. 2016, Rauset et al. 2016).

296   Therefore, a plausible explanation for the observed result is that GPS collars could shield

297   individuals against illegal killing. First, the collar in itself can act as a deterrent as the likelihood

298   of detecting poaching events increases. Secondly, the wolverines were captured as part of a

299   wildlife-human conflict project studying predation on semi-domestic reindeer and sheep (e.g.

300   Mattisson et al. 2016). In Norway, compensation for livestock losses to carnivores is estimated

301   based on the number of detected domestic preys that could be documented as killed by a

302   carnivore. As information provided by the GPS collar is partly used to conduct predation

303   studies, it generally results in a higher number of documented kills, which could give an

304   incentive to keep GPS collared individuals alive.

305   Instrumented versus non-instrumented individuals have been suggested to have different

306   survival rates in other large carnivore populations (Schmidt et al. 2015, Borg et al. 2016, Treves

307   et al. 2017), but evaluating the representativeness of instrumented individuals is particularly

308   challenging as it also requires to obtain data on non-instrumented individuals. Using a

309   comprehensive spatially explicit population-level model taking into account imperfect

310   detection inherent to non-invasive genetic sampling, we showed that GPS collared large

311   carnivores may not always constitute a representative sample of the population for the

312   estimation of survival rates. Although our OPSCR model would greatly benefit from

313   incorporating age structure, age information was not available for individuals detected solely

314   with NGS. To our knowledge, this study is the first to compare survival rates of carnivores

315   with and without telemetry collars, using an independent source of data collected at the

316   individual level, and a comprehensive statistical framework that takes into account imperfect

317   detection. Regardless of the exact mechanisms behind the non-representativeness of the

318   instrumented sample, it has important implication for management and conservation, as many

319   studies use data from GPS collared individuals to draw population-level inferences

320   (Hebblewhite and Haydon 2010) and to parameterize population level models (Liberg et al.

321   2011).

322   **Authors contribution**

323   C.M developed the concept of this study with input from R.B and P.D. J.M and J.O provided

324   data on captured wolverines. Wolverine genetic data extraction and preparation were

325   coordinated by H.B. C.M led the analysis with help from R.B and P.D. C.M led the writing

326   with contributions from R.B, P.D, H.B, J.O and J.M. All authors gave final approval for

327   publication.

328   **Data**

329   Data, R script and nimble codes are available on github repository https://github.com/Cyril-

330   Milleret/Public/tree/master/WolverineGPSSurvival

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483

484

485   **Figures legend:**

486   **Figure 1.**

487   Posterior distributions of wolverine mortality rates with and without a GPS collar obtained

488   using a Bayesian open population spatial capture-recapture model and data from non-invasive

489   genetic sampling in Scandinavia. Proportional differences (95% credible interval) in

490   mortality rates between individuals with and without a GPS collar are depicted for males in

491   the northern area and between the monitoring season 2010/11-2011/12. Proportional

492   differences in mortality rates between individuals with and without a GPS collar depended on

493   the baseline probabilities $(h0, w0)$ that varied with year, sex, and regions because the effect

494   of capture on mortality rates $(\beta w_{GPS}, \beta h_{GPS})$ were quantified on the logit scale. The picture

495   shows one of the studied wolverines wearing a GPS collar (©Thomas Strømseth).

496

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Figure 1

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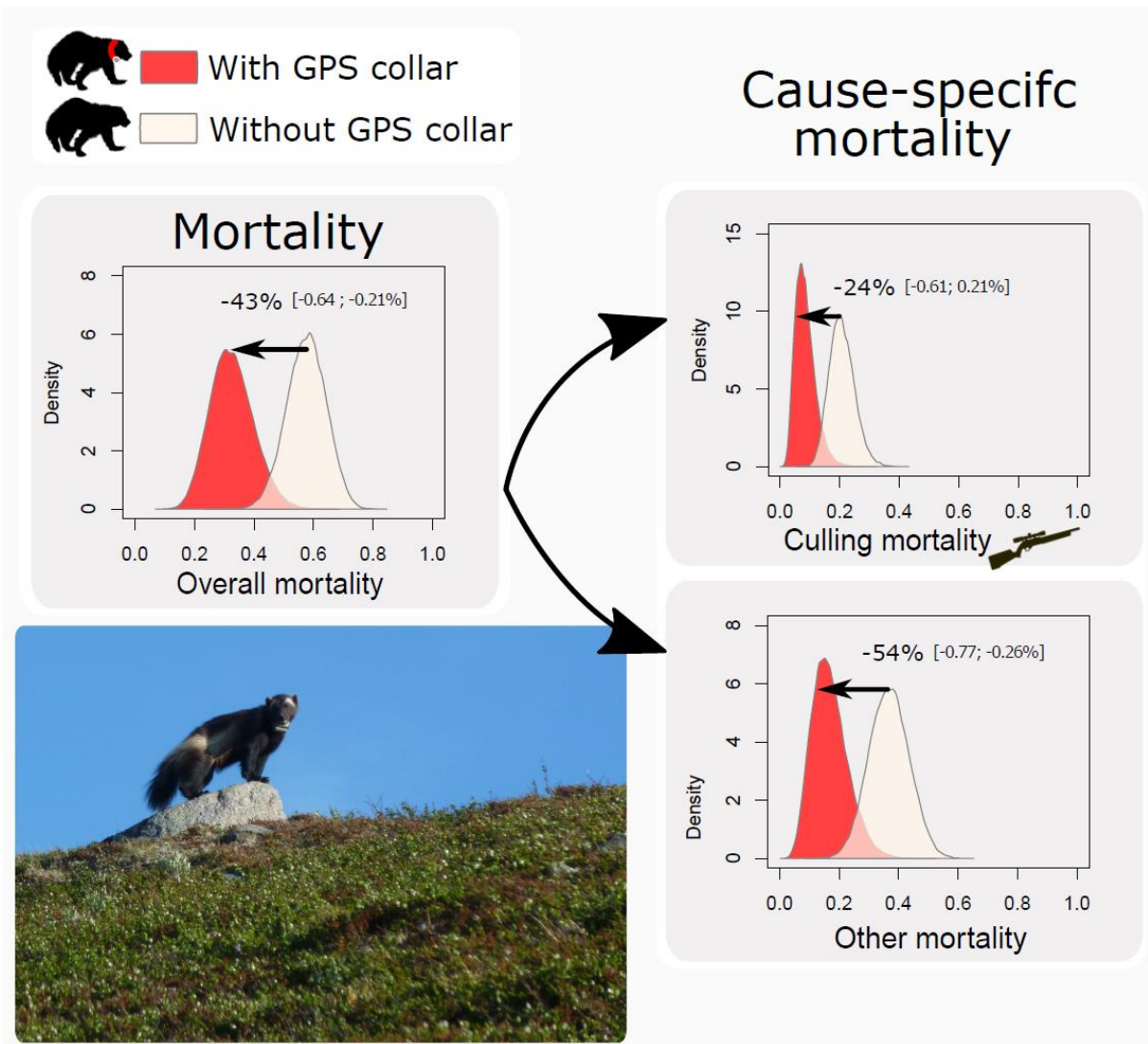
500 **Appendix S1 : Instrumented individuals are not representative of the population.**
501 **Survival of wolverines with and without GPS collars**

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504 **Cyril Milleret, Richard Bischof, Pierre Dupont, Henrik Brøseth, John Odden, Jenny**
505 **Mattisson**

506

507 **Table S1**. Summary of the number of non-invasive genetic samples from wolverines and
508 individuals genetically identified from 2009/10-2016/17 in the Central and Northern study
509 areas (see Figure 1) for females (F) and males (M).

510

Year	2009	2010	2011	2012	2013	2014	2015	2016	Total
N detections									
Sex				**Central**					
M	129	109	145	176	177	187	213	257	1393
F	169	108	149	149	199	162	212	212	1360
				North					
M	124	113	148	116	168	98	121	165	1053
F	124	99	167	107	182	139	134	231	1183
N individuals detected									
				Central					
M	55	49	64	70	61	64	72	73	508
F	71	53	67	75	80	73	87	91	597
				North					
M	50	39	49	34	43	32	31	35	313
F	55	48	77	48	69	62	59	72	490

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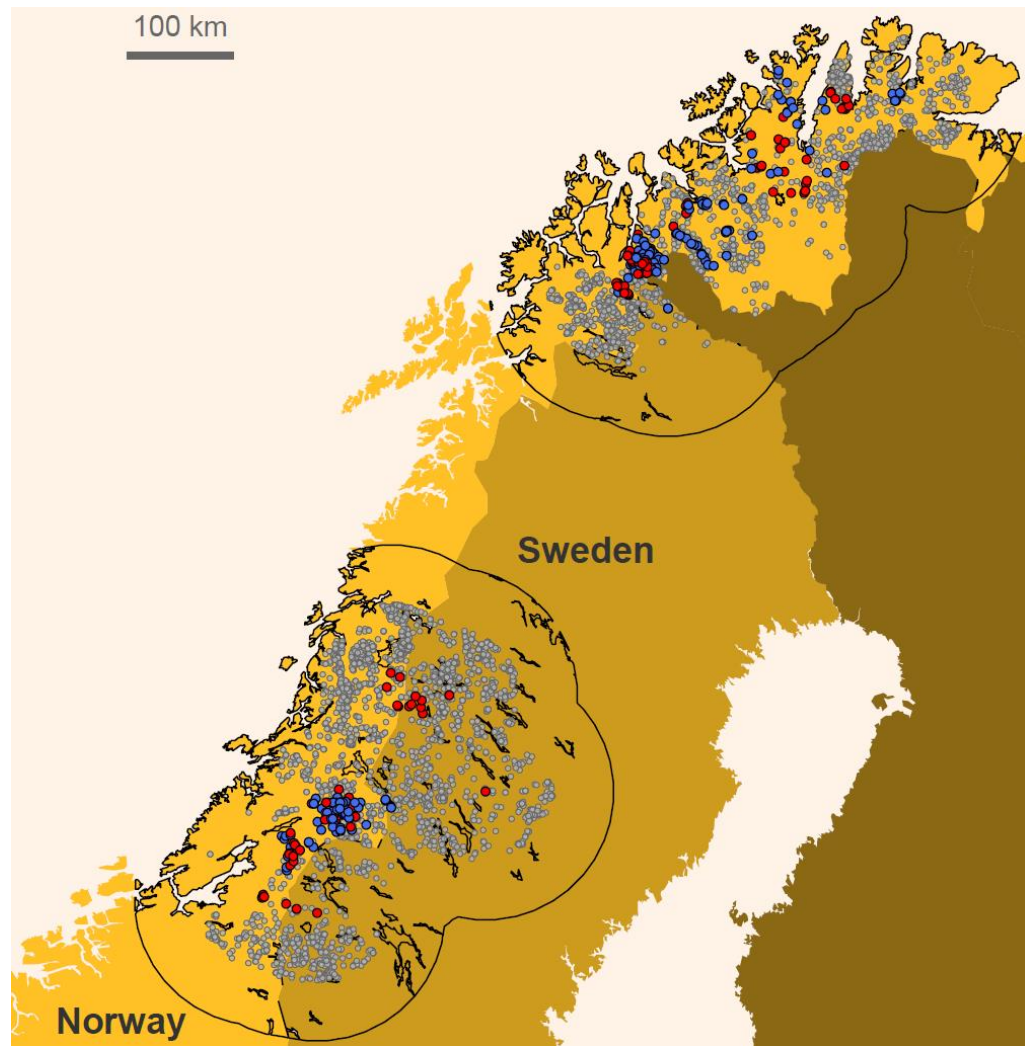
Figure S1.

Locations of non-invasive genetic samples of wolverines collected during eight consecutive monitoring seasons (December– June; 2009/10-2016/17) in Sweden and Norway. Blue and red dots show genetically identified samples from male and female individuals with GPS-collars, respectively. Grey dots represent detections from all other individuals. Polygons with a black outline represent the two study areas (North and Center) and include the buffer (area of the polygon without detections) considered in the open-population spatial capture-recapture analysis.

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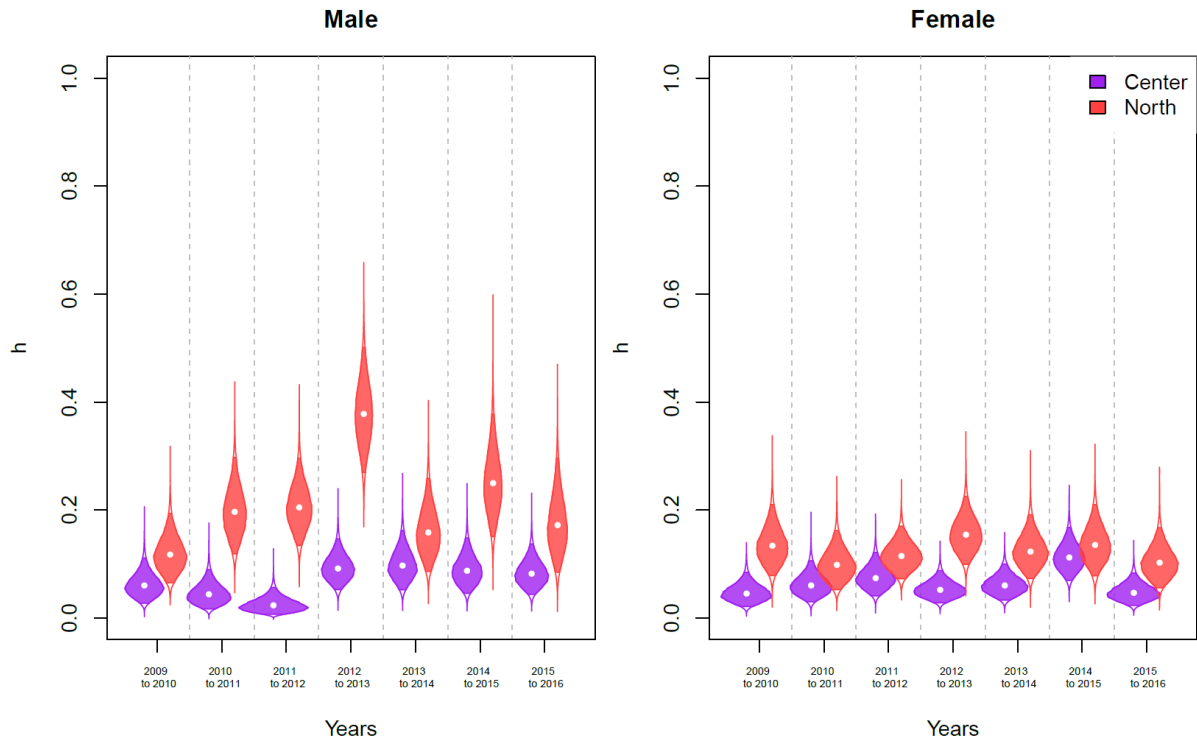
Figure S2. Mortality probabilities due to legal culling (*h*) for male and female wolverines. Shown are overall estimates throughout the Central and Northern study areas (Figure 1). Violins show the posterior distribution of mortality estimates (points: median estimates; solid colors: 95% credible interval). Estimates reflect mortalities occurring between the start of one sampling season and the start of the next.
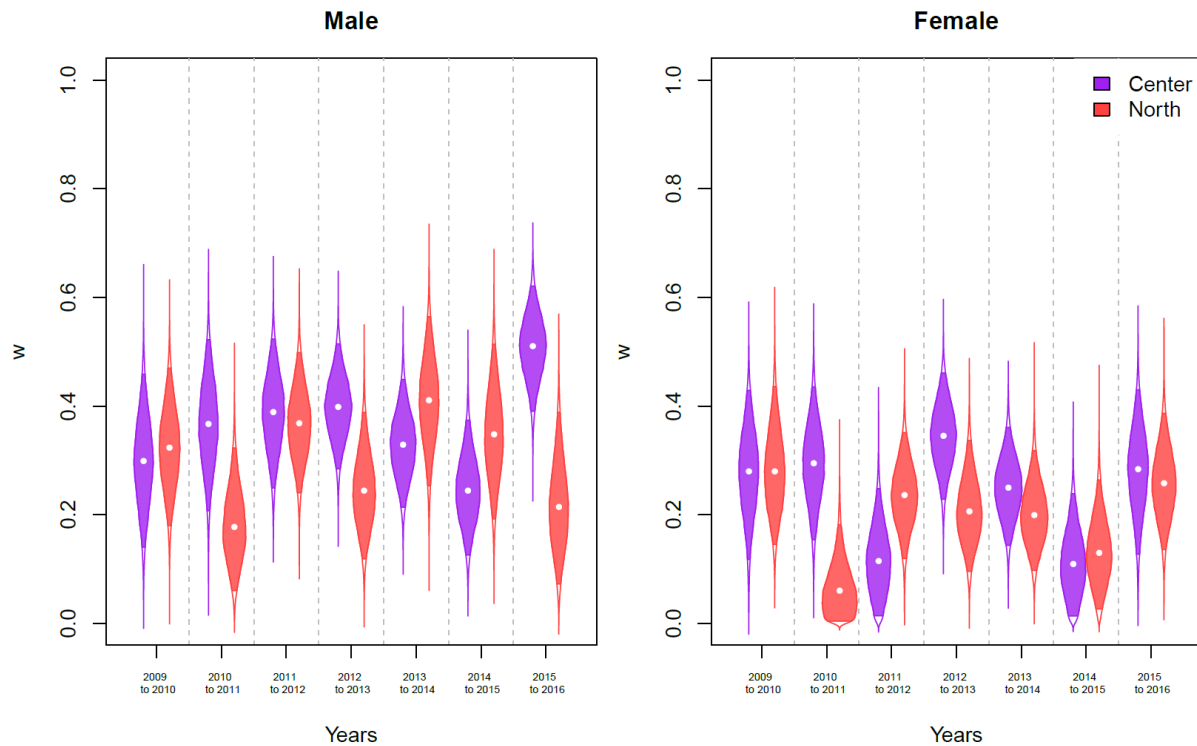
520

521 **Figure S3.** Mortality probabilities due to causes other than legal culling (w) for male and
522 female wolverines. Shown are overall estimates throughout the Central and Northern study
523 areas (Figure 1). Violins show the posterior distribution of mortality estimates (points:
524 median estimates; solid colors: 95% credible interval). Estimates reflect mortalities occurring
525 between the start of one sampling season and the start of the next.

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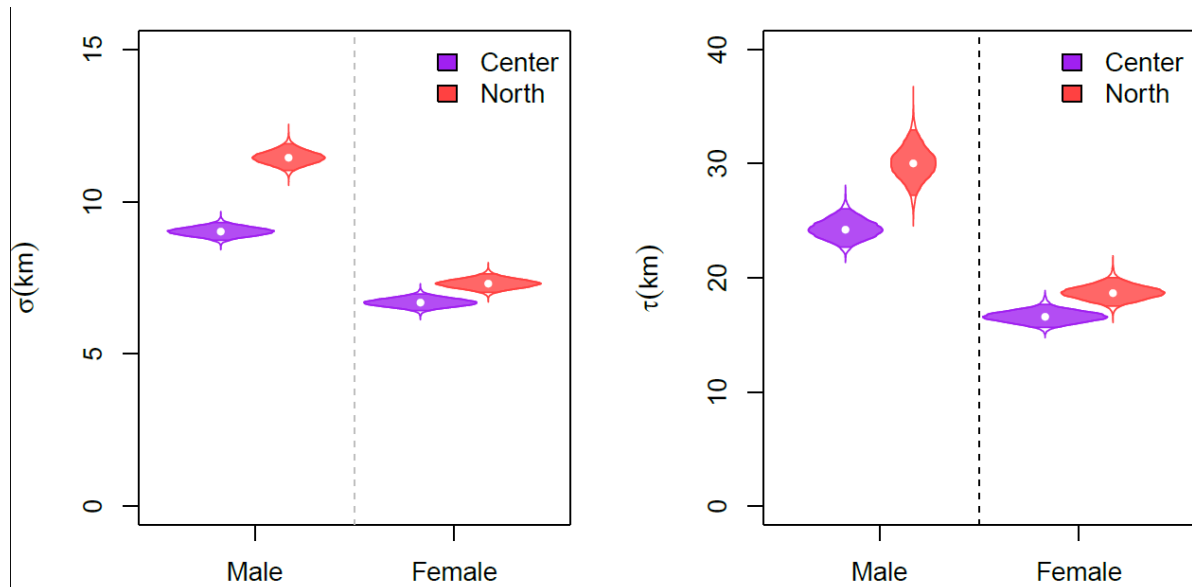
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529 **Figure S4.** Estimates of the scale parameter σ of the detection function representing range of
530 movement of individuals around their activity centers (AC), and scale parameter τ of the
531 bivariate normal representing inter-annual movement of AC locations. Estimates are
532 presented for male and female wolverines for the Central and Northern study areas (Figure
533 1). Violins show the posterior distribution estimates (points: median estimates; solid colors:
534 95% credible interval).

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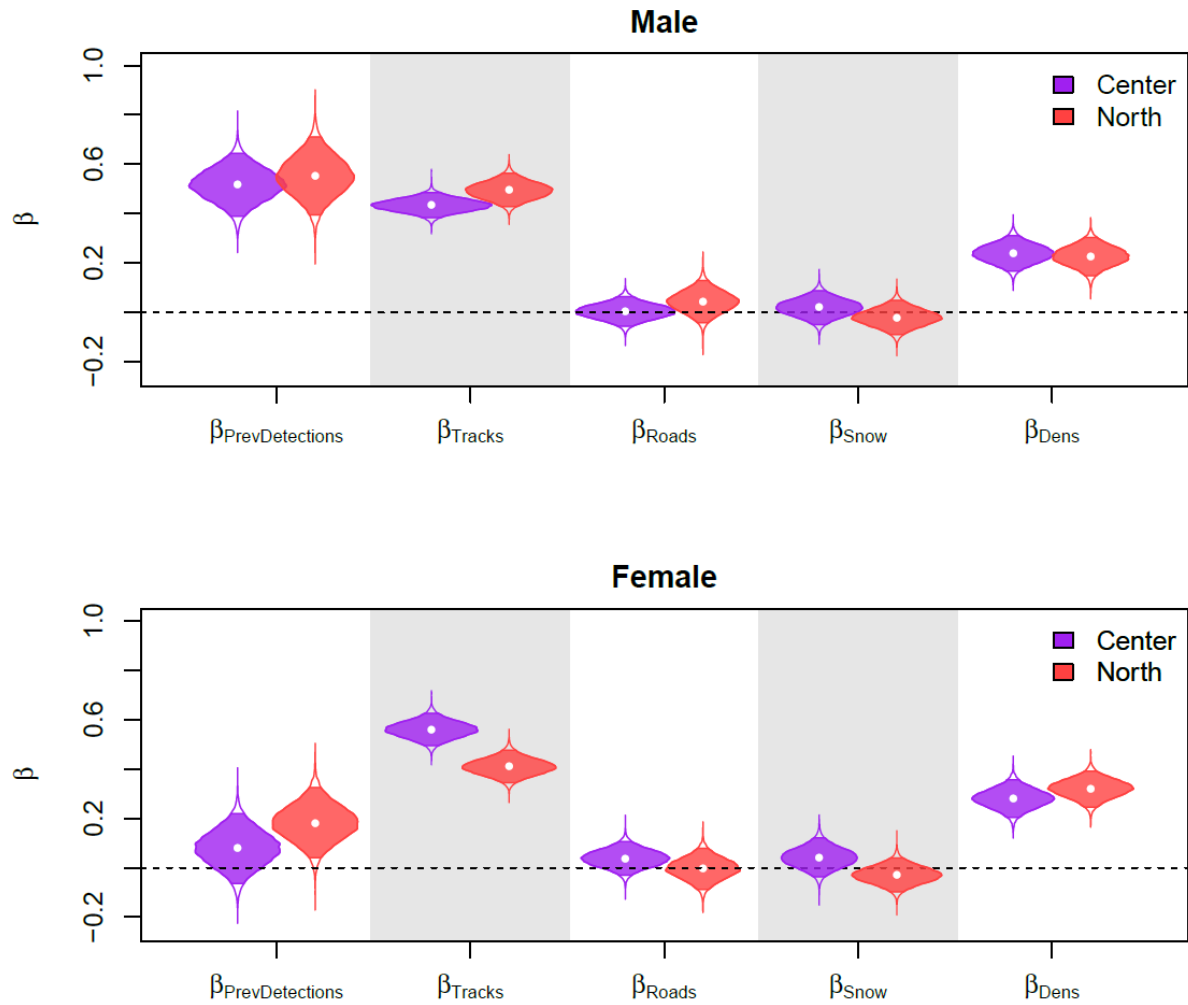
Figure S5. Beta coefficients to model the logit linear effect of spatial covariates on the baseline detection probability (p$_0$; $\beta_{PrevDetections}$, β_{Tracks}, β_{Roads}, β_{Snow}; see OPSCR model section for further details) and density (β_{Dens}). Estimates are presented for male and female wolverines for the Central and Northern study areas (Figure 1). Violins show the posterior distribution estimates (points: median estimates; solid colors: 95% credible interval).

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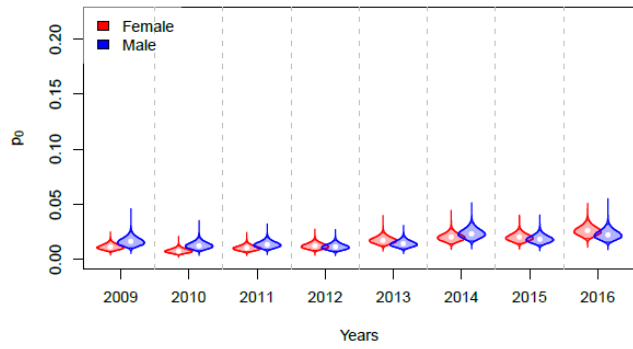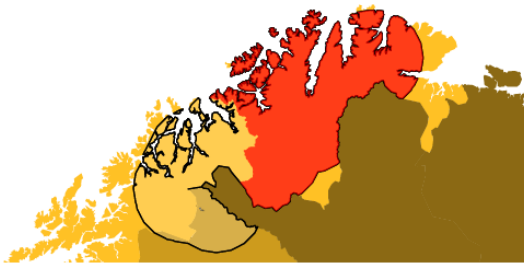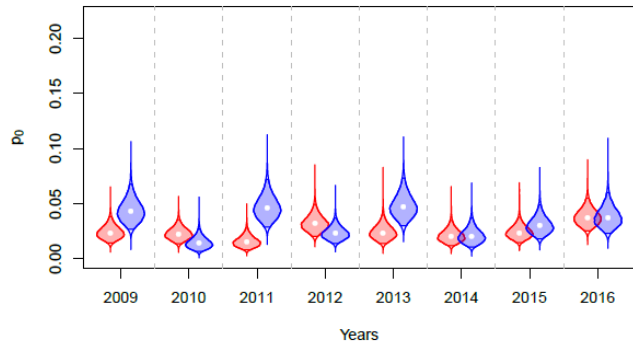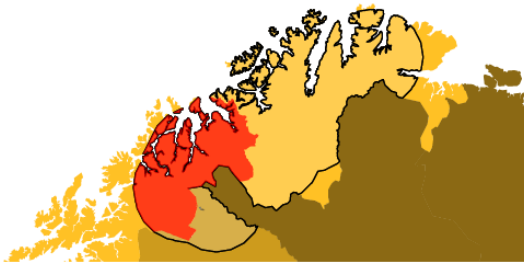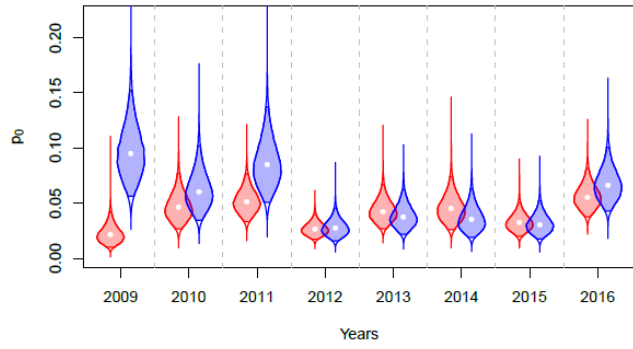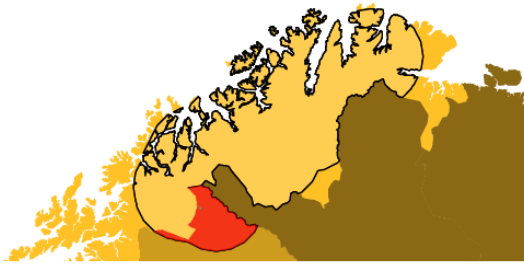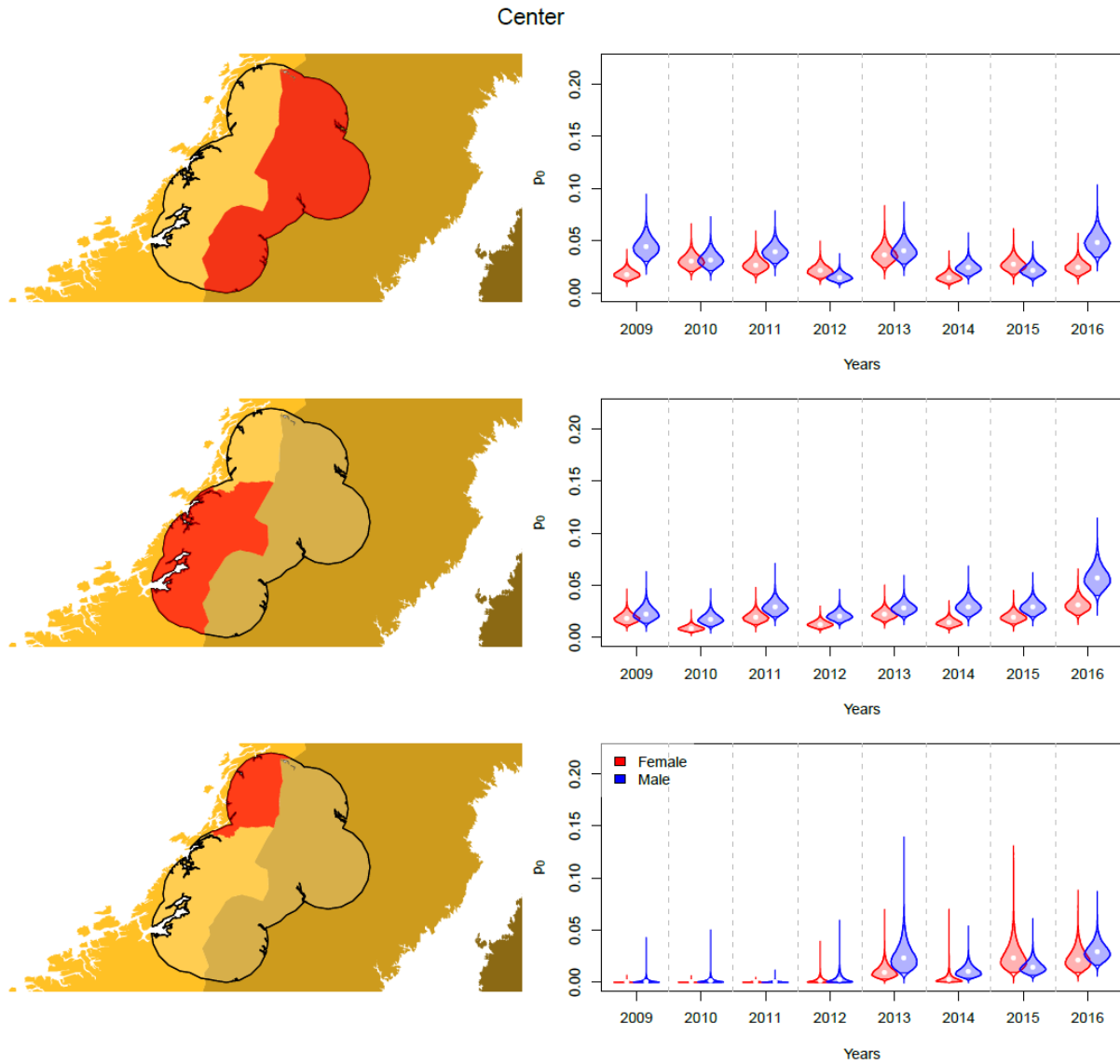
Figure S6. Estimates of the baseline detection probability (p_0) presented for male and female wolverines for the central and northern study areas (Figure 1). p_0 was estimated separately for each year and for every region (three for the Central and Northern study areas, colored red in the map from the left panel plot). Violins show the posterior distribution estimates (points: median estimates; solid colors: 95% credible interval).

Appendix S2 : Instrumented individuals are not representative of the population. Survival of wolverines with and without GPS collars

Cyril Milleret, Richard Bischof, Pierre Dupont, Henrik Brøseth, John Odden, Jenny Mattisson

To account for individual, spatial, and temporal heterogeneity in detection probability we included several linear effects on a logistic scale on the baseline detection probability (p_0):

1) Length of GPS search tracks logged by searchers within each detector grid cell in each monitoring period (*Tracks*).

2) Average distance from the nearest road (*Roads*): the distance from each detector to the closest road (1:100,000, the Swedish mapping, cadastral and land registration authority; N50 kartdata, the Norwegian Mapping Authority,). This variable represents accessibility, which we predicted to facilitate detectability.

3) Yearly 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) between December 1– June 31 (*Snow*). As wolverine NGS during winter relies heavily on the presence of snow, we predicted that greater snow cover increases detectability.

4) Indicator of whether an individual was detected or not during the previous monitoring season (*PrevDetection*). Previous detection could be expected to positively influence the probability of being detected at subsequent occasions (Gervasi et al. 2014).

5) Whether the individual was GPS collared (*GPS*) or not to account for different detection probabilities. Furthermore, we estimated independent baseline detection probabilities ($p_{0Intercept}$) for each year (*t*):

577 $$logit\left(p_{0_{i,j,t}}\right) = p_{0Intercept_t} + \beta_{Tracks} * Tracks_{j,t} + \beta_{Snow} * Snow_{j,t} + \beta_{Roads} *$$

578 $$Roads_{j,t} + \beta_{PrevDetections} * PrevDetection_{i,t} + \beta p_{0_{GPS}} * GPS_{i,t}$$ eqn 2

579 Note that we estimated separate β parameters for each region and sex.

580