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Sharing data improves monitoring of trans-boundary populations: the case of wolverines in central Scandinavia

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Populations of wide-ranging species are likely to extend across multiple jurisdictions, including national and international borders. This requires that local institutions implement data sharing and a standardization of monitoring designs. However, a formal evaluation of the benefits of integrated monitoring systems had not, of yet, been performed. Using the wolverines in central Scandinavia as a study case, we assessed the benefits of data sharing for the monitoring of trans-boundary populations. We also assessed the performance of two demographic monitoring systems, one relying on a count of reproductive units, the other resulting from non-invasive genetic sampling and capture-recapture modeling. Sharing data across the border between Norway and Sweden allowed a strong increase in the precision of population size, population growth rate and vital rates estimates. It also allowed revealing that the probability to emigrate from Sweden to Norway was significantly higher than in the opposite direction, a required condition for the existence of a source–sink dynamics. These findings would have been impossible without trans-boundary data sharing. While the den count monitoring provided an estimated population growth of 138% over the 12-year period, the DNA-based estimate was only 72%. A positive trend likely occurred in the detectability of wolverine dens during the first years of the study, and the index was not able to separate the actual demographic trend from the trend in the system's ability to detect reproductions, thus providing positively biased estimates of population growth rate during the initial phase of the study. Data sharing is a crucial need for the study of the processes occurring in trans-boundary populations. It should be enhanced wherever trans-boundary ecological processes occur. Also, managers should be aware that count-based monitoring has a risk of overestimating population growth during the first years after its implementation.

Large carnivores are wide ranging species, which live at relatively low population densities (Carbone and Gittleman 2002), and usually use large exclusive territories (Nilsen et al. 2005). They also exhibit long dispersal distances, which allow single individuals to colonize areas several hundred kilometers away from their natal range (Santini et al. 2013). Viable large carnivore populations are therefore bound to occupy huge areas, and given the administrative and political fragmentation of the landscape (especially in Europe) they are likely to extend across multiple jurisdictions, including international borders (Chapron et al. 2014).

Although international conventions set a common framework for their conservation and management, in practice large carnivores are managed at the national and regional level, with local institutions being responsible for their demographic monitoring, for implementing actions,

and for evaluating them. Such a tendency has been recently strengthened by the increasing focus on decentralization and devolution of natural resource management to local levels (Linnell 2015). A clear mismatch exists, therefore, between the scale of the ecological processes occurring in large carnivore populations and the scale of their current management and monitoring system.

The existence of populations across national borders requires that different national institutions promote and implement trans-boundary data sharing and a standardization of monitoring designs. Such integration is slowly advancing between several countries sharing large carnivore populations, and it has been advocated on the grounds of allowing harmonization in management, better inter-institutional communication, and an increased awareness about population status and trend (Linnell et al. 2008). Still, a formal evaluation of the relative performance of integrated versus isolated monitoring systems for trans-boundary populations has not, of yet, been performed.

With respect to how the monitoring is conducted, an additional challenge is posed by the fact that large carnivores

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usually exhibit elusive habits. Surveying elusive species is often associated with a low effectiveness of survey methods, as a consequence of the species' behaviour, activity, preferred habitats, and low overall densities (McDonald 2004), which often result in low efficiency and high costs of monitoring. While expensive and time consuming methods are available, like longitudinal individual-based monitoring and non-invasive genetic sampling, demographic monitoring is often performed using simple count-based indices of population trend over time (Landa et al. 1998, Kindberg et al. 2009). Indices offer the advantage of being often easier and cheaper to produce, but they lack any formal treatment of the underlying detection process, and are therefore highly sensitive to temporal variation in sampling effort and/or sampling conditions (Yoccoz et al. 2001). They also do not allow an exploration of the mechanisms behind population performance, for example through the estimation of population vital rates. They are also particularly prone to overestimating population rate of change in the first years of their implementation, due to the risk of confounding population and detection trends (Gervasi et al. 2014). Non-invasive genetic sampling, often coupled with the application of capture–recapture models (Lebreton et al. 1992), requires a higher resource investment, but it enhances the transparency of the monitoring system and places it in a robust probabilistic context. The tradeoff between cost and performance is therefore one of the most important issues when setting up a monitoring program for rare and elusive species.

Using the case of the wolverine *Gulo gulo* in the Scandinavian Peninsula, we explore the two above mentioned questions: 1) we produce an empirical assessment of the benefits deriving from data sharing for the demographic monitoring of trans-boundary populations of elusive species; 2) we assess the relative performance of two demographic monitoring systems, one relying on a simple count-based index of population trend, the other resulting from a long-term non-invasive genetic sampling and the application of capture–recapture models.

Wolverines are solitary large carnivores, distributed in the northern boreal forests of Eurasia and North America, where they usually live at low densities as opportunistic predators and facultative scavengers (Mattisson et al. 2011). The Scandinavian wolverine population declined drastically during the 1900s due to human persecution, and it was considered functionally extinct in southern Norway at the beginning of 1970s (Landa et al. 1997). It then started to recover its former numbers and distribution (Flagstad et al. 2004). Today, around 1000 wolverines live in Scandinavia (Persson and Brøseth 2011), with a distribution which embraces Norway, Sweden and Finland, and has further connections with Russia.

Despite being trans-boundary in nature, the population has been monitored and managed separately and differently on the two sides of the border dividing the Norwegian and the Swedish portions of the population. A process of integration between the two national monitoring programs has been on-going in the last few years, which has led to a progressive standardization of monitoring procedures and to a higher degree of data sharing. Also, since 2002 the southern portion of the population has been monitored in the two countries both by a minimum count of natal dens (Landa

et al. 1998), and by a large-scale collection of scats on snow, followed by DNA extraction and individual identification (Taberlet et al. 1996).

Taking advantage of this analytical framework, we produced population size and growth rate estimates for the period 2003–2013, using both cumulative counts of natal dens and non-invasive genetic sampling. We compared the results in terms of relative consistency, and assessed that the inability of the count-based monitoring to cope with a positive temporal trend in detectability caused a bias in the estimation of population growth rate. We also simulated the scenarios of two national versus one trans-national monitoring program, and empirically document that data sharing provides better insights into the ecological process occurring in trans-boundary populations.

Methods

Den sampling and minimum population size estimation

Wolverine natal dens usually consist of a system of snow tunnels, allowing access to a rock cavity, a talus slope, or simply to a sheltered slope where snow accumulates (May et al. 2012). Adult females start using the den in late January, just before giving birth, and usually abandon it at the latest at the beginning of May, when cubs are able to start accompanying them (Inman et al. 2012). Although the den itself is just a temporary construction, which disappears when the snow melts, females tend to reuse the same area in subsequent years (Landa et al. 1998). Moreover, the same denning area can be inherited for several generations, given that female wolverines are to a large extent philopatric (Chapell et al. 2004).

Since 1996, the minimum size of the Scandinavian wolverine population has been monitored both in Norway and in Sweden through cumulative counts of reproductive units at natal dens. As part of the National Large Predator Monitoring Programs, wardens from the State Nature Inspectorate in Norway and from the Environmental Protection Agency in Sweden searched for natal dens in the study population each winter and spring, to obtain a minimum count of the number of reproductive females. Then, based on the assumption that the proportion of reproductive females in the population stays constant, the average count in a window of three years was extrapolated to a minimum population size estimate (Landa et al. 1998, Brøseth et al. 2010). Hence, the estimates have been based on no formal treatment of the probability to detect a wolverine den in the study area, and the proportion of undetected dens is unknown.

Throughout the period 1996–2013, each time a wolverine den was found, its coordinates were included in a national database (<www.rovbase.no>, <www.rovbase.se>) and the site was checked for possible new reproductions in subsequent years. Thus, the monitoring system has been each year taking advantage of the information acquired during previous winters, leading to a potential increasing ability to detect the study species. The increasing temporal trend in the number of known wolverine den sites is shown in Fig. 1.

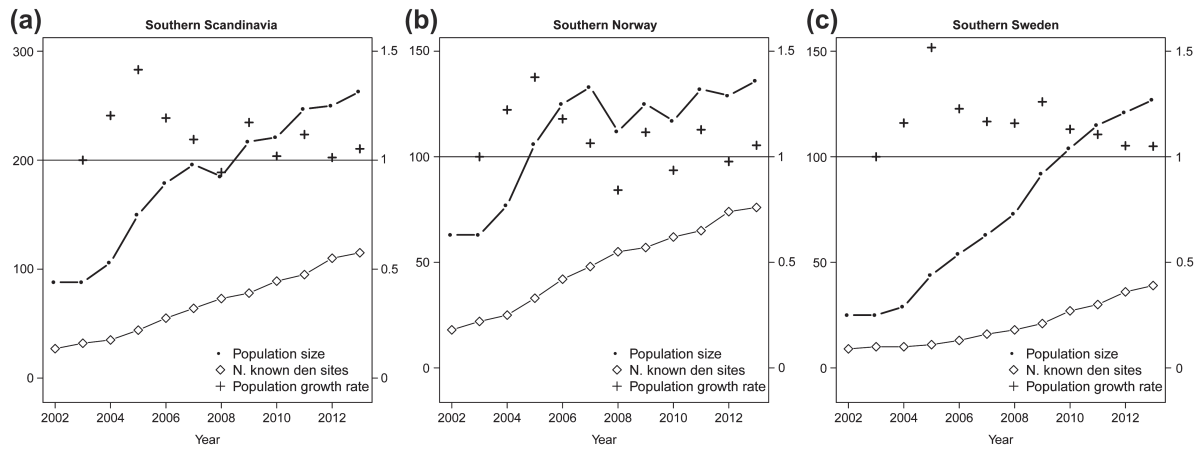


Figure 1. Estimates of population size and growth rate for wolverines in southern Scandinavia, southern Norway and southern Sweden, 2003–2013. Estimates are based on the monitoring of reproductive events. The number of already known den sites for each year is also reported.

DNA sampling and genotyping

Starting in 2002, a protocol of non-invasive genetic sampling, based on scat collection, has been implemented in Norway and Sweden, south of the E14 highway that crosses the whole Scandinavian Peninsula from the North Atlantic Ocean to the Baltic Sea (Fig. 2). A similar protocol has been progressively employed also in the northern part of the peninsula after 2008, but less systematically in Sweden than in Norway. Given the shorter time series available and the spatio-temporal heterogeneity in sampling effort, we decided

not to use data from the northern portion of the study area for this study, but limited it to the wolverines detected south of the E14 highway during the period 2002–2013. This resulted in a dataset of 3652 genetic samples, belonging to 619 individual wolverines.

Scat samples were collected on snow along wolverine tracks, during a three month period from mid-February to mid-May, after the end of the hunting season and before cubs of the year started accompanying their mother away from the den. This ensured that all collected scats were from individuals one year old or older. In Norway, all the sampling

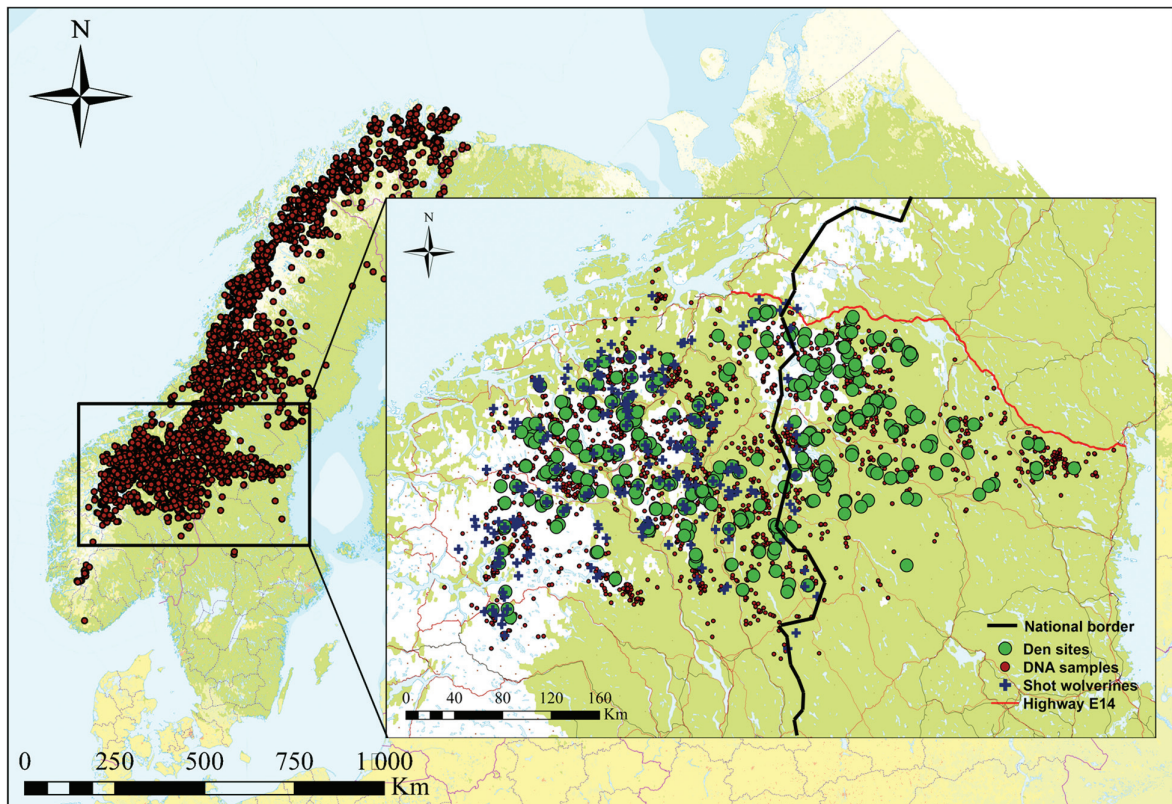


Figure 2. Distribution of wolverine presence signs in Scandinavia 2003–2013.

effort was recorded using a global positioning system (GPS) track-log. The total yearly effort was on average around 25 000 km per year, most of which was driven by wardens on snow scooters. No comparable structured record of sampling effort was available from the Swedish monitoring system.

After data collection, DNA material was extracted and amplified from all collected scats. Over the years, the DNA extraction and microsatellite genotyping protocols have been modified; from manual to automated DNA extraction and by replacing singleplex PCR amplification with multiplex PCR. Earlier protocols are described in Flagstad et al. (2004) and Brøseth et al. (2010). In the most updated protocol automated DNA extraction was used applying a Genemole DNA extraction robot, following the protocol for tissue samples provided by the manufacturer, Mole Genetics, Lysaker, Norway. Microsatellite genotyping to identify individual wolverines included eleven autosomal loci, distributed in two multiplex panels (Table 1). Assuming a panmictic population across the study area, the probability of identity (pID; Waits et al. 2001) was 2.9×10^{-7} for unrelated wolverines, and 9.2×10^{-4} for siblings.

PCR amplifications for autosomal microsatellite loci were performed in 10 μ l reactions containing 3.0 mM MgCl₂, 0.2 mM of each dNTP, 2.0–8.0 pmol of each primer, 0.5 μ g of bovine serum albumine (BSA), 0.9 units of HotStar DNA polymerase (Qiagen) and 2 μ l of undiluted DNA extract. A touchdown PCR program was used with an initial denaturation step of 95°C for 15 min. Six touchdown cycles with 94°C for 30 s, 58°C for 30 s decreasing 1°C each cycle and 72°C for 1 min was followed by 33 cycles of 94°C for 30 s, 52°C for 30 s and 72°C for 1 min, and a final extension at 72°C for 10 min. Genotyping errors caused by amplification of poor quality DNA from scat samples such as allelic dropout and false alleles can severely bias estimates of population parameters by creating ‘false’ individuals (Mills et al. 2000, Waits and Leberg 2000). Therefore, a number of control measures were performed, to ensure the quality of the genetic data. All scat samples were amplified at least three times for each microsatellite marker (the multi-tube approach; Taberlet et al. 1996). A single-locus genotype was not accepted before replicates resulted in at least three identical homozygote profiles or two identical heterozygote profiles. These criteria were based on a pilot study, where we compared genotypes obtained from scats versus blood or

tissue samples (Hedmark et al. 2004). More than 200 single-locus genotypes were tested, and three replicates were always sufficient for deriving the correct genotype. The same rigid use of predefined criteria for accepting single-locus consensus genotypes in this study suggests that most errors – if not all – were eliminated from the data set prior to formal analysis. As an additional quality control, a quality index was calculated for individuals that were only represented with one single sample (Miquel et al. 2006). All samples with $QI < 0.8$ were discarded from the data set. The resulting annual success rate of the genetic identification protocol was of 61% (53–72%), which is comparable to what was obtained in a pilot project on non-invasive genotyping of Scandinavian wolverines (Hedmark et al. 2004).

For sex determination, two Y-chromosome specific markers that had been validated by scat sampling from 16 radio-marked individuals (1 male, 15 females) were used (DBY3Ggu, DBY7Ggu; Hedmark et al. 2004). Each of the Y-linked markers were amplified twice, leading to four replicates for all scat samples with respect to sex determination. Over the years, many samples have been collected from a large proportion of the individuals. This has provided an extensive database of individuals of known sex, offering an additional opportunity to assess the reliability of the sex markers. The error rate for individuals of known sex has been negligible, occurring in $<< 1\%$ of all sex-determined scat samples.

Legal harvest and recovery data

Norway and Sweden apply different management regimes to the portion of the Scandinavian wolverine population that falls within their borders. Being part of the European Union, Sweden is bound by the Habitats Directive 92/43, in which wolverines are listed as strictly protected (annex IV). Hence, very limited legal control of wolverines has occurred in Sweden during the study period, and always under Article 16 derogations of the Directive. Norway is not an EU member and is not bound to the same set of regulations. To limit population size and the extent of depredation on free-ranging sheep and semi-domestic reindeer, wolverines in Norway are therefore subject to intensive culling. A quota-based hunting is allowed from mid-September to mid-February, which removes on average about 20 individuals each year (Bischof et al. 2012). Moreover, regional management authorities can authorize a number of additional removals by SNO officers, in case an intense livestock depredation has been occurring, or if the estimated population size is above the national management goals. As a result, about 300 wolverines have been legally shot in southern Norway and delivered to the authorities between 2002 and 2013. From all of them, we sampled muscle tissue for genetic identification, and extracted an upper premolar to determine the age of the dead individual (Landa and Skogland 1995).

Capture–recapture modeling

To assess if data sharing provides analytical benefits for the demographic monitoring of trans-boundary populations, we set up two alternative capture–recapture scenarios, one resembling two isolated national monitoring programs

Table 1. PCR details of the microsatellite markers applied for the individual identification of wolverines in southern Scandinavia 2002–2013, based on non-invasive genetic sampling (scat collection).

PCR panel	Marker	Primer amount	Reference
Multiplex I	Gg7	6.0 pmol	Davis and Strobeck 1998
	Ggu14	6.0 pmol	Walker et al. 2001
	Ggu42	8.0 pmol	Walker et al. 2001
	Gg234	6.0 pmol	Duffy et al. 1998
	Gg465	6.0 pmol	Walker et al. 2001
	Mvis075	4.0 pmol	Fleming et al. 1999
Multiplex II	Gg216	4.0 pmol	Duffy et al. 1998
	Gg443	3.0 pmol	Walker et al. 2001
	Gg452	2.0 pmol	Walker et al. 2001
	Gg454	8.0 pmol	Walker et al. 2001
	Mvis072	4.0 pmol	Fleming et al. 1999

(hereafter called NOSHARE), the other corresponding to a shared trans-boundary effort (hereafter SHARE). In both cases, we needed to account for the possibility for each individual wolverine to move between two geographic states (Norway and Sweden), and three biological states (alive, dead by legal harvest, dead by other causes). Moreover, we needed to account for the potential presence of individual heterogeneity in detection probability, which can produce biased estimates of abundance when not properly accounted for (Hwang and Huggins 2005, Cubaynes et al. 2010). Therefore, we used the general framework of multi-event models (Pradel 2005) in program E-SURGE (Choquet et al. 2005) to integrate a two-site capture–recapture model with live detections and dead recovery (Burnham 1993), and a mixture model incorporating individual heterogeneity in detection probability (Pledger et al. 2003, Pradel 2009).

In the case of the SHARE design, all wolverines were potentially observable while alive, irrespective of their transition across the Norway–Sweden border, as a result of the data-sharing between the two monitoring programs. Therefore, the resulting model structure comprised seven possible states. Individuals alive in Norway could have either high or low detectability, and the same classification was used for wolverines in Sweden. Additionally, we included a specific state for wolverines legally harvested in Norway, one for the individuals dying from other causes, and one absorbing state containing all individuals dead in previous years. We did not include in the model the probability of emigration outside the study area across the E14 highway, as our data showed that such probability could be reasonably disregarded. Out of the 683 wolverines detected within 200 km north and south from the E14, only about 1% was detected on both sides of the highway during the whole 12-year monitoring period. Detection probability for legally shot wolverines was set to one, as all of them were reported to the authorities. We performed a goodness of fit test in program U-CARE (Choquet et al. 2009), which revealed no excess of transients and no trap-dependence.

For the NOSHARE design, the detection matrix was modified to take into account that Norwegian wolverines moving to Sweden became unobservable and vice versa. This corresponded to the temporary-emigration model of Kendall and Nichols (2002), which allows the production of unbiased estimates of survival and transition probabilities, under Markovian (i.e. non-random) temporary emigration (Schaub et al. 2004). We used the test 2C.t in program U-CARE (Choquet et al. 2009) to reveal such a possible non-random temporary emigration (Schaub et al. 2004), which was indeed confirmed ($z = -2.343$, $p = 0.019$). This indicated that estimating population size, survival, and transition probabilities from a design with no trans-boundary data sharing required the addition of an unobservable state, as biased parameter estimates would have been likely otherwise (Schaub et al. 2004). A detailed description of the multi-event parameterization is provided in the Supplementary material Appendix 1.

For both designs, we modeled transition probability as a function of gender, and of the distance between the geometric center of all individual sampling locations and the national Norway–Sweden border. For survival, we considered models with time and gender effects, and we tested

for a country effect. Detection probability was modeled as a function of both a common and separate time effect in the two countries. We also tested for a gender effect, and we checked if one or two classes of detectability were more supported by the data. Finally, and only for Norway, we estimated the yearly sampling effort in a circle of 8 km radius for females and 15 km for males, centered on the geometric mean of all sampling location of each individual, and used it to explain part of the temporal and individual variation in detection probability. Buffer values correspond to the average estimated home range size of wolverines of the two sexes in Scandinavia (Mattisson et al. 2011).

Estimating population size accounting for violation of the closure assumption

One of the assumptions of the multi-state approach is that individuals cannot be in more than one state during the same session. This created a conflict with our sampling design, as a few of the wolverines living close to the national border were sometimes detected both in Norway and in Sweden during the same sampling session. This issue also constituted a violation of the assumption of geographic closure, a rather common problem in the estimation of population size (Kendall 1999). Several approaches have been developed to correct population size and density estimates when the study area is not geographically closed (Gardner et al. 2010, Bischof and Swenson 2012), most of them based on the idea of estimating the proportion of time each individual is expected to spend inside and outside the study area during the sampling period.

We used a similar approach for our case study. We compiled a dataset of about 12 000 locations from 26 wolverines, captured and fitted with GPS-collars in the regions of Finnmark, Troms and Trøndelag in central–northern Norway, between 2010 and 2013. We selected locations referring to the period February–May, and calculated the average GPS location for each individual. Then we calculated the distance between this center point and all the other locations, and produced a probability distribution, estimating the proportion of time each individual was expected to spend farther than a given distance from its home range center (Fig. 3a, c). As the probability distribution function was significantly different for males and females, we produced a different curve for the two sexes. This allowed us to estimate the proportion of time each individual wolverine sampled by DNA was expected to spend in Norway and Sweden, based on the distance between the geometric center of its DNA sampling locations and the national border (Fig. 3b, d).

Then, to comply with the requirements of the multi-state analytical design, we first assigned to Norway all the individuals detected on both sides of the national border, and produced a closure-corrected population size estimate for each of the two countries, using the following equation:

$$\widehat{N}_{t,x} = \sum_{i=1}^{n_{t,x}} \frac{\widehat{F}_{i,x}}{\widehat{P}_{(i,t,x)}}$$

in which $\widehat{N}_{t,x}$ is population size for year t in state x , $n_{t,x}$ is the number of individuals sampled at time t in state x , $\widehat{P}_{(i,t,x)}$ is the estimate of detection probability for the

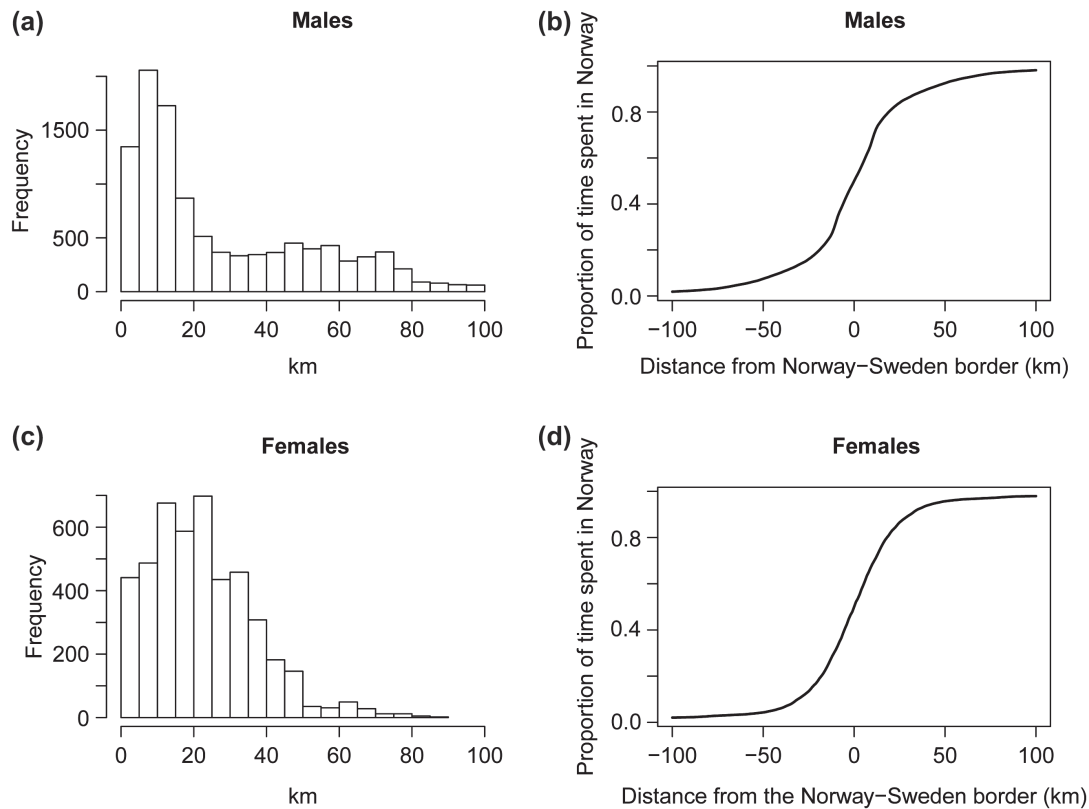


Figure 3. Proportion of wolverine GPS locations falling within a given distance from the home range geometric center for male (a) and female (c) wolverines in Scandinavia. The predicted proportion of time spent by each individual in Norway is also shown for both sexes (b, d).

individual i at time t in state x , and $\hat{F}_{i,x}$ is the estimated proportion of time the individual i is expected to spend in state x . We performed all the analyses using also Sweden as a country of first assignment for bordering wolverines, and found that this subjective choice had no influence on the results.

Results

Population size and growth rate estimates based on den counts

Based on extrapolation from the annual counts of reproductive units, the wolverine population of southern Scandinavia was estimated to have grown from 104 to 248 individuals in 10 years, corresponding to an overall 138% increase between 2002 and 2013 (Fig. 1a). The annual growth rate was particularly high during the first years of the study, when estimates of up to a 40% increase in population size in a single year were produced by the monitoring system (Fig. 1a). When examining the Swedish and Norwegian portions of the population separately, two different patterns emerged. On the Norwegian side, the population was estimated to grow rapidly between 2003 and 2006, with an 80% increase in population size in three years, and to remain more or less stable around 120 individuals afterwards (Fig. 1b). On the Swedish side the den monitoring estimates showed a strong increase in abundance over the whole monitoring period,

with peaks of 50% increase in population size in a single year, and an overall 417% population growth over the 10 years of monitoring (Fig. 1c).

DNA-based estimates of population size

For the NOSHARE design, model selection procedures revealed that in both countries a model with a single class of detectability was better supported than a two-mixture model. Also, detection probability was higher for males than for females in both countries, but both sexes exhibited a relatively high detection over the whole sampling period. Average detection probability for females was 0.48 in Norway (95% CIs = 0.44–0.53) and 0.49 in Sweden (95% CIs = 0.41–0.57), whereas males exhibited a 0.72 detection in Norway (95% CIs = 0.66–0.77) and 0.67 in Sweden (95% CIs = 0.58–0.75). In both countries, detection also showed a significant temporal variation. Model ranking for both countries and time-dependent detection probability estimates are shown in the Supplementary material Appendix 1 Table A1–A2 and Fig. A1. When analyzing the SHARE design, model selection supported the same main effects on detection probability, but revealed that a common time effect for the two countries was more supported than two independent temporal variations in detection (see model 1 and 3 in Table 2).

Resulting from the models with the highest rank (models 1 in Table 1, Supplementary material Appendix 1 Table A1–A2), point estimates of population size from the two

Table 2. Model selection for the analysis of wolverine population size in southern Scandinavia 2002–2013. The analysis is based on the SHARE design: π_1 and π_2 are models with one or two classes of heterogeneity, respectively; t is a country-specific time effect; t* is a common time effect in the two countries; effort is the total number of km driven inside each individual's home range; border dist. is the distance between each individual's sampling center and the national border.

Model N.	Survival			Detection		k	Deviance	QAIC	Δ QAIC
	Norway	Sweden	Transition	Norway	Sweden				
1	sex	sex	border dist.	$\pi_1 + \text{sex} + \text{effort} + t^*$	$\pi_1 + \text{sex} + t^*$	25	4380.90	4431.76	0
2	sex	sex	border dist. + sex	$\pi_1 + \text{sex} + \text{effort} + t^*$	$\pi_1 + \text{sex} + t^*$	26	4379.87	4431.87	0.11
3	sex	sex	border dist.	$\pi_1 + \text{sex} + \text{effort} + t$	$\pi_1 + \text{sex} + t$	35	4359.53	4434.20	2.44
4	sex	sex	border dist.	$\pi_1 + \text{sex} + \text{effort} + t^*$	$\pi_2 + \text{sex} + t^*$	29	4373.41	4434.41	2.65
5	sex	sex	border dist.	$\pi_2 + \text{sex} + \text{effort} + t^*$	$\pi_1 + \text{sex} + t^*$	29	4377.93	4435.93	4.17
6	sex	sex	border dist.	$\pi_1 + \text{effort} + t^*$	$\pi_1 + t^*$	23	4438.91	4484.91	53.15
7	sex	sex	border dist.	$\pi_1 + \text{sex} + t^*$	$\pi_1 + \text{sex} + t^*$	24	4439.47	4487.47	55.71
8	sex+t	sex+t	border dist.	$\pi_1 + \text{sex} + \text{effort} + t^*$	$\pi_1 + \text{sex} + t^*$	55	4336.92	4446.92	115.16

monitoring scenarios were rather similar, but the ones based on trans-boundary data sharing were more precise (Fig. 4). The average coefficients of variation (CV) of population size estimates were 0.24 and 0.17 for the NOSHARE and SHARE design, respectively, indicating a 30% increase in precision. Also for the two national estimates, the SHARE design provided more precise estimates. Such reduction of uncertainty was about 16% in Norway (from 0.21 to 0.18 CV) and about 48% in Sweden (from 0.31 to 0.16), showing that Sweden benefitted the most from the sharing of wolverine DNA data.

Comparison of estimates from the two methods

When evaluated at the scale of the whole of the southern Scandinavian wolverine population, abundance estimates derived from the two monitoring methods exhibited a good consistency. A 20% negative bias in the den-count estimates

emerged in the first years, which disappeared in the subsequent years of monitoring (Fig. 5a). A similar pattern was revealed when comparing the estimates for the Norwegian portion of the population alone: the den-count based estimates of population size got closer to the DNA-based ones with time, stabilizing on an asymptotic 10% negative bias (Fig. 5b). A different pattern emerged for Sweden with population size estimates derived from den-counts consistently 15–20% higher than the estimates resulting from the DNA monitoring (Fig. 5c).

When comparing the estimates of population growth rate, the two methods produced different estimates for the whole population and for its national portions. While the den-count monitoring provided an estimated population growth of 138% over the 12-year period, the DNA-based monitoring estimated such growth to be only 72% during the same period. Also, as shown in Fig. 6, the den-count monitoring produced the image of a population growing at a

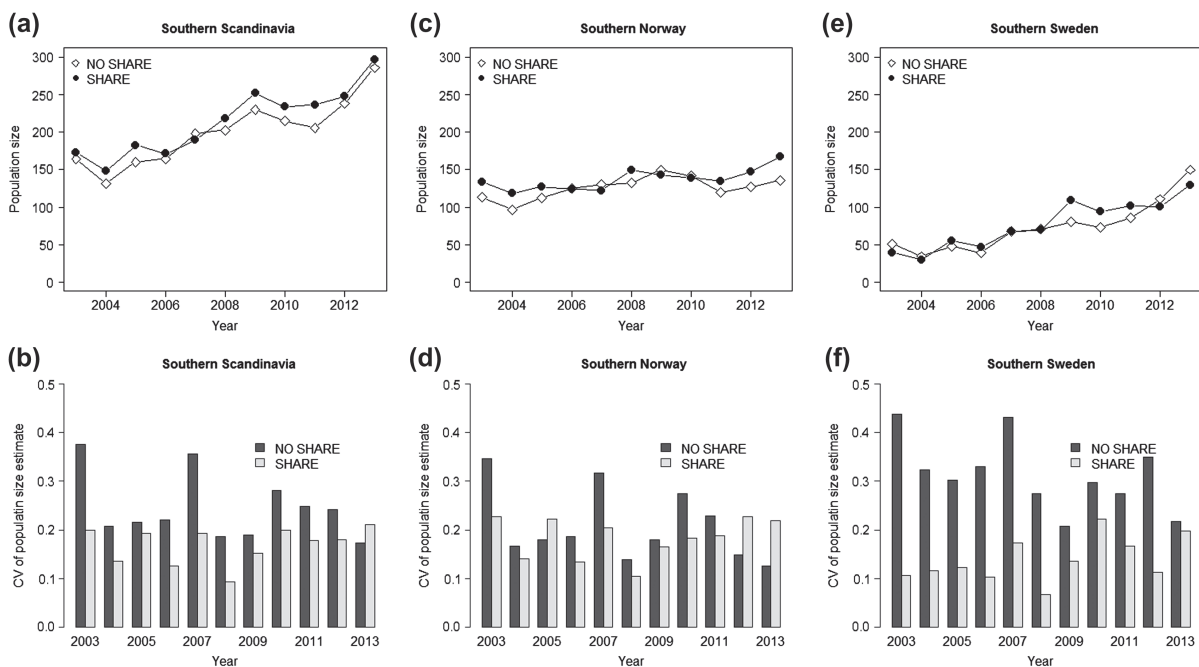


Figure 4. Estimates of population size for wolverines in southern Scandinavia, southern Norway and southern Sweden 2003–2013, based on DNA sampling and capture–recapture modeling. Point estimates (a, b, c) and the coefficient of variation (d, e, f) are shown for the NO SHARE and SHARE designs.

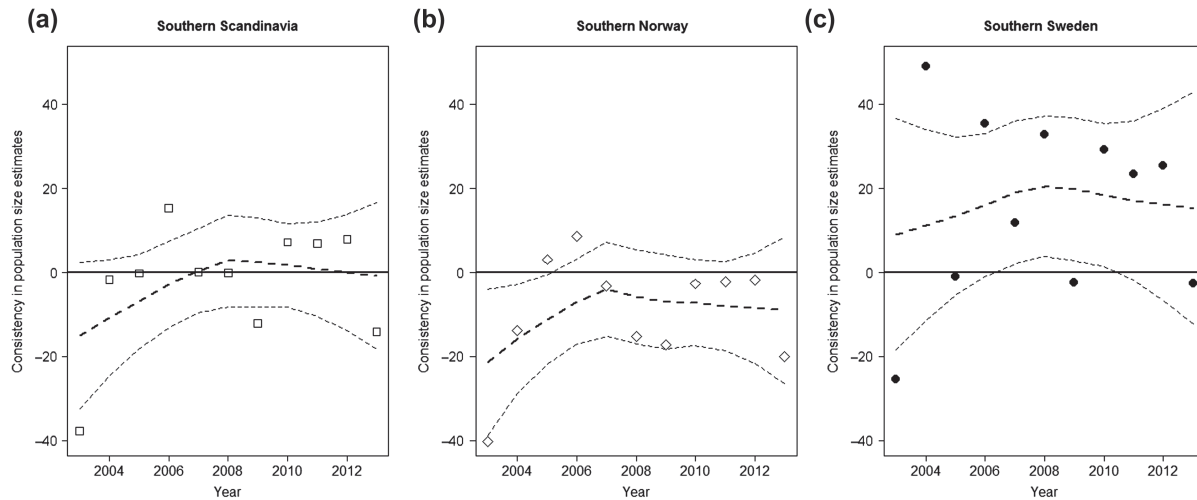


Figure 5. Relative consistency between den-based and DNA-based estimates of population size in southern Scandinavia, southern Norway and southern Sweden 2003–2013. DNA-based estimates are used as reference (horizontal continuous line).

fast rate (about 27% per year) during the first years of monitoring, but significantly slowing down its rate of increase during subsequent year ($\beta = -3.186$, $p < 0.01$; Fig. 6a). DNA monitoring and capture–recapture modeling showed that population growth rate was instead rather constant throughout the study period ($\beta = 0.9645$, $p = 0.51$), and on average about 5% per year (Fig. 6b). Therefore, taking the DNA-based estimates as a reference, the monitoring system based on den counts seems to have overestimated population growth rate at least until the years 2007–2008.

The same pattern emerged when considering population growth rate estimates for Norway and Sweden separately. Population growth based on DNA sampling and capture–recapture modeling was 25% in Norway and 230% in Sweden, respectively, over the 12-year period, much lower than the 69% and 317% resulting from den-counts. The overestimation of population growth rate was concentrated during the first 5–6 years of monitoring (Supplementary material Appendix 1 Fig. A2–A3).

Estimates of population vital rates

The plot in Fig. 7 shows that sharing data across the national border between Norway and Sweden allowed a strong increase in the precision of vital rates estimates. While the point estimates of sex-specific survival probabilities were similar between the two analytical scenarios, precision was three times higher for the SHARE design. This permitted the documentation of male wolverines having a significantly lower survival rate than females in Norway, which would not have been detectable without the increased precision resulting from data-sharing (Fig. 7a). Similarly, the estimates of the transition probabilities in the two directions across the national border have large and overlapping confidence intervals, when obtained from the NO SHARE design, but they exhibit a five times higher precision and non-overlapping confidence intervals in the SHARE scenario (Fig. 7b). This was due to the lower ability of the model to distinguish between survival and temporary

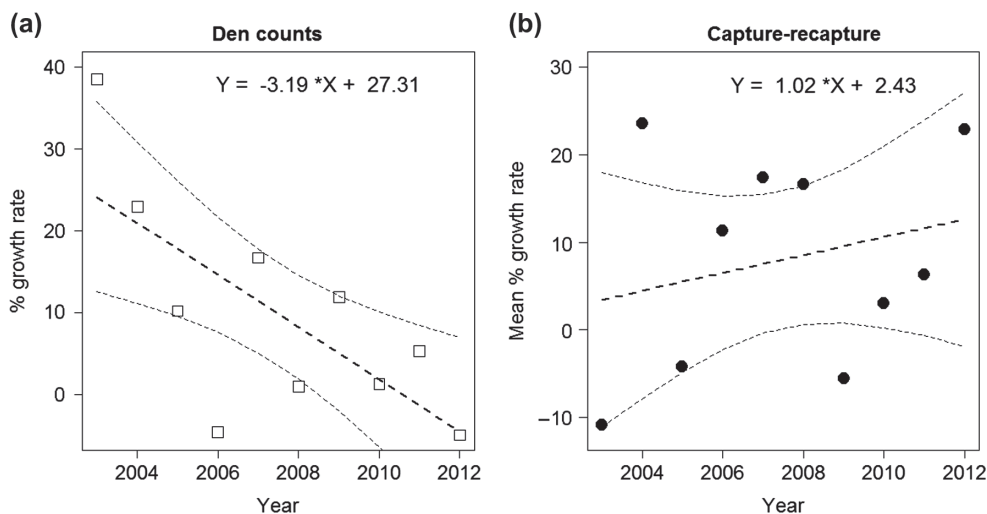


Figure 6. Annual estimates of population growth rate in southern Scandinavia (2003–2012) derived from den counts (a) and DNA-based capture–recapture modeling (b).

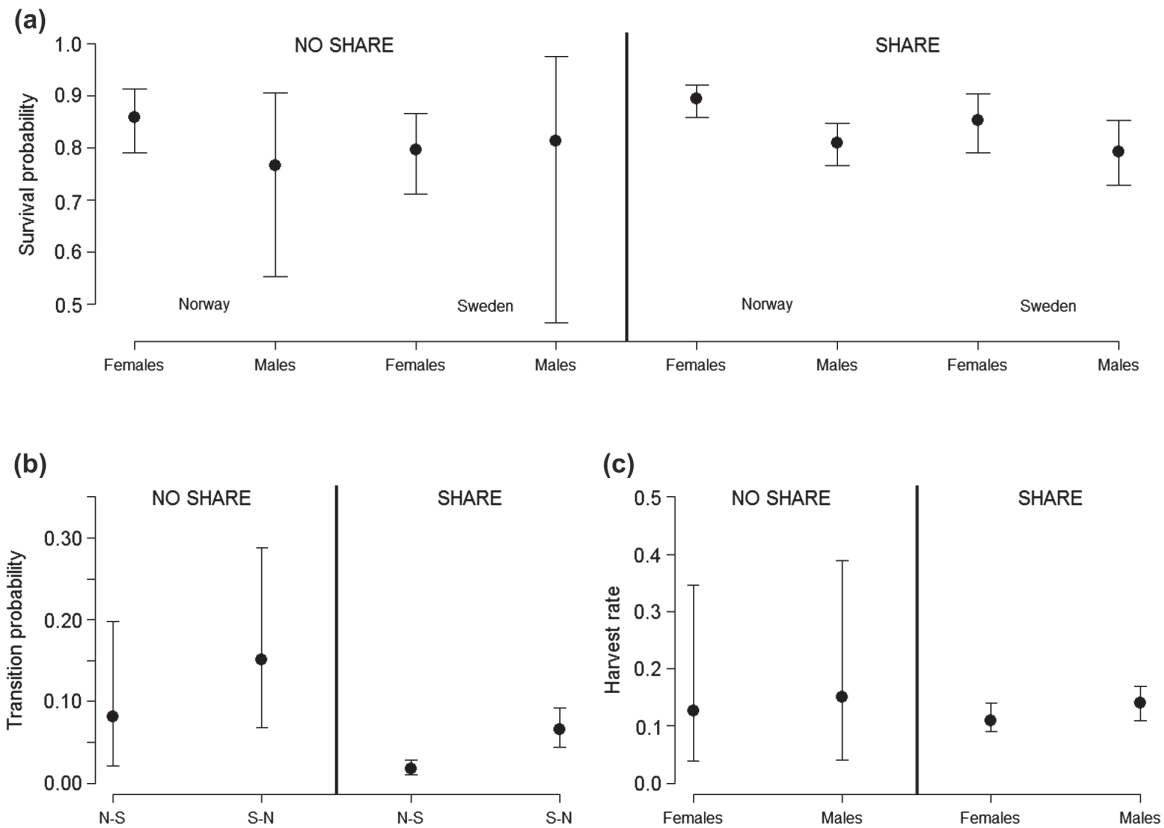


Figure 7. Estimates of survival rate, transition probability, and harvest rate in southern Norway and Sweden (2003–2013), resulting from the NO SHARE and SHARE designs. Estimates are derived from the most supported models in Table 2, Supplementary material Appendix 1 Table A1–A2.

emigration, when one of the states was associated with zero detection probability. Consequently, the SHARE monitoring system was able to reveal that the probability to perform a transition from Sweden to Norway ($\psi_{SN} = 0.07$, $SE = 0.013$, $95\% \text{ CIs} = 0.04\text{--}0.09$) was significantly higher than in the opposite direction ($\psi_{NS} = 0.017$, $SE = 0.005$, $95\% \text{ CIs} = 0.01\text{--}0.03$). Finally, the harvest rate estimates in Norway also exhibited higher precision when data was shared, with CV being 50% smaller than in the case of two isolated monitoring systems (Fig. 7c).

Discussion

The results of this study contain two main messages for the demographic monitoring of wide ranging, elusive species. Firstly, the blind use of simple count-based indices, when they fail to account for temporal variation in detectability, can cause serious bias in the estimation of population trend. Secondly, data sharing is a crucial need for the study of the ecological processes occurring in trans-boundary populations.

Regarding the first outcome of our study, the use of non-invasive genetic sampling and capture–recapture modeling drew a more nuanced picture of the demographic changes occurring in the Scandinavian wolverine population, than the one depicted by the count-based monitoring. While the DNA based picture should not be regarded as the truth, as it was derived from just another type of estimation process,

it is based on fewer assumptions and on a formal statistical treatment of the underlying detection process. It is therefore suitable to be used as a reference for the evaluation of the less robust methodology.

All count-based monitoring systems are highly sensitive to temporal variation in detection probability (Yoccoz et al. 2001), and those that learn from the accumulation of previous knowledge are especially likely to overestimate population trend during the first years of monitoring (Gervasi et al. 2014). In our specific case, the patterns observed were consistent with the hypothesis that a positive trend occurred in the detectability of wolverine dens during the first years of the study. As the count-based index of population trend was not able to separate the actual demographic trend of the wolverine population from the trend in the system's ability to detect reproductions, it provided the management system with positively biased estimates of population growth rate during the initial phase of the study. The social and economic costs of this bias are not easy to quantify, but they may have been high. Overestimating population growth rate may have contributed to overemphasize the perception of the conflict resulting from wolverine presence in Scandinavia, where carnivore acceptance is generally low, and where the level of perceived conflict between human interests and carnivore presence is high (Røskaft et al. 2007).

Although the overestimation of population growth rate was highly influenced by the first 2–3 years of monitoring (Fig. 6), it should be noted that the time series between 2002–2013 probably only captures the tail of the learning

phase in the monitoring process. A structured count of wolverine reproductive units started in Scandinavia in 1996, so that 25% of known denning sites had already been discovered before the beginning of the DNA sampling in 2002, while an additional 40% were first found and included in the national databases during the first three years after 2002. Accordingly, it is likely that most of the positive trend in the detection probability of wolverine denning sites also occurred during that initial period. On the other hand, results show that the performance of the count-based monitoring system improved after this initial phase, exhibiting a substantial consistency with population size and trend estimates provided by the DNA-based capture–recapture approach.

Counts of natal dens, nests, and more generally of fixed structures that persist in time, is a standard tool to monitor abundance and trend of elusive species. Mammals such as badgers *Meles meles* (Wilson et al. 2003), Eurasian lynx *Lynx lynx* (Linnell et al. 2007a), Eurasian otters *Lutra lutra* (Hájková et al. 2008), and brown bears *Ursus arctos* (Bischof et al. 2016) are still mainly monitored through naïve count-based indices in most of their distribution range. Birds like spotted owls *Strix occidentalis* (Seamans et al. 2001), bald eagles *Haliaeetus leucocephalus* (Hatfield et al. 1996) and several other species of raptors share the same sampling limitations. Even though the use of systematic sampling and of an explicit inclusion of detection probability in the estimation process have long been recognized as a requirement for any monitoring effort (Yoccoz et al. 2001), it is still likely that indices of population trend will be heavily used in the future, especially when more structured and robust forms of sampling are associated with prohibitive costs. A typical case of the current trends in the large-scale monitoring of elusive species is provided by the increasing involvement of lay people in the opportunistic collection and reporting of demographic monitoring data (i.e. citizen science; Dickinson et al. 2010), which has led to an increase in the quantity of information available, and to a potential decrease in its quality. Based on the evidence provided by the wolverine case, we recommend that caution should be used whenever using naïve indices to monitor population trend. In particular, alternative sampling methods should also be employed whenever feasible, to serve as a tool for the evaluation of the performance of the monitoring system. Managers should also be aware that count-based monitoring has a risk of overestimating population growth during the first years after its implementation. Conservation and management decisions should be made and evaluated on long time series, as short monitoring programs are more likely to produce flawed information. This being said, monitoring programs have multiple goals and need to consider multiple issues, including social acceptance. The den based monitoring provides a metric that the public can easily relate to, at least in part because it has been in use for almost 20 years. It also provides spatially explicit data on reproduction and reproductive sites, which can be important when considering land use planning and conflict mitigation. Finally, the data collection protocols for the two methods are linked, such that the fieldwork associated with den monitoring is also used to find tracks and search for the scats that are the foundation of the DNA based estimate.

Regarding the second objective of our study, the performance of the SHARE design clearly showed the benefits of matching the scale of monitoring to the scale of the population processes. By reducing the uncertainty around the estimates of transition probabilities, the SHARE design showed that the flow of individuals from one country to the other is not balanced overall. More individuals enter Norway from Sweden than the opposite, thus creating the potential for source-sink dynamics across the national border. The possibility of a source–sink system is especially likely, given that the high hunting pressure in Norway contrasts with the protectionist policy on the other side of the border. Based on our model results, the net flow of individuals from southern Sweden to southern Norway should be about 7–9 individuals per year, whereas the annual number of adult wolverines shot in southern Norway in the last five years is 23.2. This means that about one third of the wolverines removed in Norway each year might be immediately replaced by immigrant wolverines from Sweden, with clear potential consequences on the efficacy and efficiency of the current management system. It will be crucial to evaluate if such unbalanced transition probabilities are indeed caused by the different management policies implemented in the two countries, and especially if there is a positive feedback between the extent of hunting pressure in Norway and the patterns of wolverine movements across the national border (Gervasi et al. 2015). Other cases, such as the culling of cougars in the USA (Robinson et al. 2008), have shown that culling of territorial species can disrupt the stability of the territory arrangement and increase immigration, in a way that undermines the initial management objectives of the removal.

From a strictly modeling point of view, it is not surprising that the inclusion of an unobservable state in a multi-state capture–recapture design was associated with a reduction of precision in the estimates. It was less obvious that the effort by different national monitoring institutions to set up and maintain a common monitoring program on a trans-boundary population, with shared protocols and database, could produce large benefits on the amount and quality of the monitoring output. While 88% of European large carnivore populations are trans-boundary in nature (Linnell et al. 2007b), most of them are still monitored and managed at a strictly national scale, with poor communication between the bordering monitoring institutions (Linnell et al. 2007b). The results of our study indicate the potential benefits deriving from a trans-boundary integration of large carnivore monitoring systems and the risks of failing to do so.

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Supplementary material (available online as Appendix wlb-00142 at <www.wildlifebiology.org/appendix/wlb-00142>). Appendix 1.