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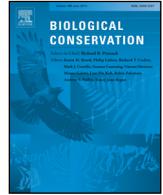


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Compensatory immigration counteracts contrasting conservation strategies of wolverines (*Gulo gulo*) within Scandinavia



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ABSTRACT

In wide ranging species, portions of the same population often fall within different administrative jurisdictions; where different regulations apply. The same species can be fully protected or heavily harvested on different sides of a border. This can generate a source–sink dynamic from the areas with lower to those with higher mortality, a process known as compensatory immigration. We tested this hypothesis on the wolverine (*Gulo gulo*) population of southern Scandinavia, which is shared between two countries: Sweden and Norway. Wolverines are fully protected in Sweden, but subject to intensive population regulation in Norway. Using non-invasive genetic sampling and capture–recapture modeling, we analyzed the dynamics of wolverine survival and emigration patterns between 2002 and 2013. Wolverines in Norway experienced a lower survival than in Sweden. Migration across the national border was directed towards movements from Sweden to Norway. There was a functional relationship between harvest rate in Norway and emigration rates across the national border, both at the individual and population level, thus confirming the compensatory immigration hypothesis. Contrasting management regimes within the same population can generate undesired demographic and spatial dynamics, jeopardize conservation goals on the two sides of a border, and reduce the efficiency of management actions. This calls for the adoption of a coordinate population approach in large carnivore conservation and management. Failing to do so can cause a waste of the already limited resources allocated for large carnivore conservation, and it might hinder effective conflict mitigation.

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1. Introduction

Population properties, such as density or survival rates, are not homogeneously distributed in space, as they frequently vary as a consequence of the uneven spatial distribution of resources and mortality risks (Kareiva, 1990; Thomas and Kunin, 1999). When populations exhibit different local mortality rates this might result in a source–sink dynamic, where individuals emigrating from the areas with lower mortality to those with higher mortality. This process is known as compensatory immigration (Pulliam, 1988; Turgeon and Kramer, 2012).

While it has received much attention in meta-population theory (Hanski, 1996), compensatory immigration can also play a role in continuous populations (McCullough, 1996; Turgeon and Kramer, 2012), with important consequences for their management and conservation. It can jeopardize the effectiveness of alien species control, when more individuals of the undesired species immigrate into a given area after removal (Mack et al., 2000); it can increase disease transmission and prevalence by increasing individual mobility (Donnelly et al., 2006); and it can threaten the persistence of small populations confined to

protected areas, when a gradient in mortality rates exists between the inside and the outside (Gundersen et al., 2001; Woodroffe and Ginsberg, 1998).

In conservation programs aimed at wide ranging species such as large carnivores or marine mammals, there is often a mismatch between the scale of population processes and that at which management actions are implemented (Trouwborst, 2010). This is an additional source of spatial variation in vital rates. Portions of the same population often fall within different administrative units or states, in which different regulations apply, so that the same species can be fully protected or heavily harvested on the two sides of a border. In such a case, different individuals living close in space within the same population can experience different mortality risk patterns, costs associated with reproduction, and local intra-specific competition, depending on where they live with respect to the artificial lines that mark the shift between one conservation regime and the other. Such a sharp gradient can initiate compensatory immigration and other source–sink dynamics between different portions of the same population, so that conservation actions implemented in one administrative unit can generate unintended and undesired consequences on the demography of the species in other administrative units. When contrasting conservation goals exist between bordering geographic areas, compensatory immigration can compromise

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both goals (Cooley et al., 2009; Gundersen et al., 2001; Robinson et al., 2008).

Wolverines (*Gulo gulo*) and their contrasting management regimes in Scandinavia are one such case. They are fully protected in Sweden under the European Union's Habitats Directive 92/43, in which they are listed as strictly protected (annex IV). In contrast, they are subject to intensive lethal control in Norway, which is not part of the European Union and hence not bound to the same set of regulations (Swenson and Andrén, 2005). Sweden has set a national goal of about 550 individuals (Reinfeldt, 2013), which was reached at the end of the 2000s (Fig. 1b). In Norway the national management goal is set at about 250 individuals (Ministry of Environment, 2003), but the population has remained above this goal for the last decade (Flagstad et al., 2013). This happened despite the fact that Norwegian management authorities have steadily increased control pressure during the last 10 years (Fig. 1a). There is no geographic barrier between the two portions of the population, but the consequences of such contrasting management regimes on the demography of the species have not yet been explored.

Here we present an analysis of the spatio-temporal dynamics of wolverine survival and trans-boundary movement patterns in the southern part of the Scandinavian population over a 12 year period between 2002 and 2013. Our aim was to evaluate the consequences of the contrasting management regimes in Norway and Sweden, both on the species demography and on the efficiency of management actions. The study was based on the hypothesis that the contrasting management regimes in the two bordering countries are creating a source-sink dynamic. We also hypothesized that such dynamics are reinforced by the extent of the harvest pressure in Norway, and that compensatory immigration counteracts, at least partially, the effort by the Norwegian management authorities to reduce population size in their country.

Under the compensatory immigration hypothesis, we expected the following predictions to be fulfilled:

1. Wolverines experience a higher mortality rate in Norway than in Sweden;
2. Immigration from Sweden to Norway is higher than in the opposite direction;
3. Immigration rates across the Norway–Sweden border are positively correlated with the intensity of the harvest pressure in Norway;

4. A proportion of the wolverines removed in Norway each year is compensated by immigration from Sweden, thus reducing the effective harvest rate.

2. Methods

2.1. Study area and data collection

For our study we used non-invasive genetic sampling data collected between 2002 and 2013 in Southern Scandinavia, south of the E14 highway that separates the northern and the southern portions of the Scandinavian wolverine population (Fig. 2). Such partition is mainly an administrative one, as different sampling regimes have been used north and south of the highway during the study period, but it also marks the main geographic barrier to wolverine movement in this part of the Scandinavian peninsula. Scat samples were collected on snow along wolverine tracks, during a three month period from mid-February to mid-May each year, after the end of the hunting season and before cubs of the year started accompanying their mother away from the den. This resulted in a dataset of 3652 genetic samples, belonging to 619 individual wolverines older than one year, as scats belonging to cubs of the year and found at natal dens were intentionally not collected by field personnel. Additionally, we sampled muscle tissues from the 308 wolverines legally shot in southern Norway during the same time period, and used them to match their identity with those provided by non-invasive genetic samples. About half of the wolverines were shot through a quota-based hunting system, which is allowed from mid-September to mid-February, and which removes on average about 22 individuals each year (Bischof et al., 2012). The remaining portion of the removals were authorized and carried out by national management authorities, in case of intense livestock depredation, or if the estimated regional population size was above the nationally set management goals. The study area covers only a portion of the Scandinavian wolverine population. However, this is the area in which sampling has been more intensive and systematic with a similar sampling effort in both countries during the whole study period (Brøseth and Tovmo, 2013).

After sample collection, we extracted and PCR-amplified DNA using eleven autosomal microsatellite loci to identify individual wolverines.

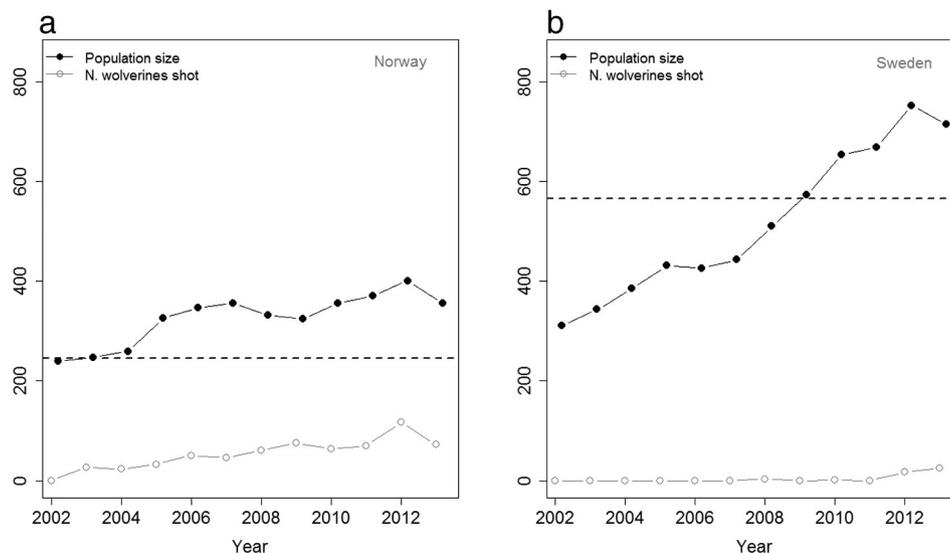


Fig. 1. Population size estimates (based on counts of reproductive units) in Norway (a) and Sweden (b) during the period 2002–2013. The number of wolverines shot each year is also shown for both countries. Dashed lines are the population size goals set by national authorities in each of the two countries.

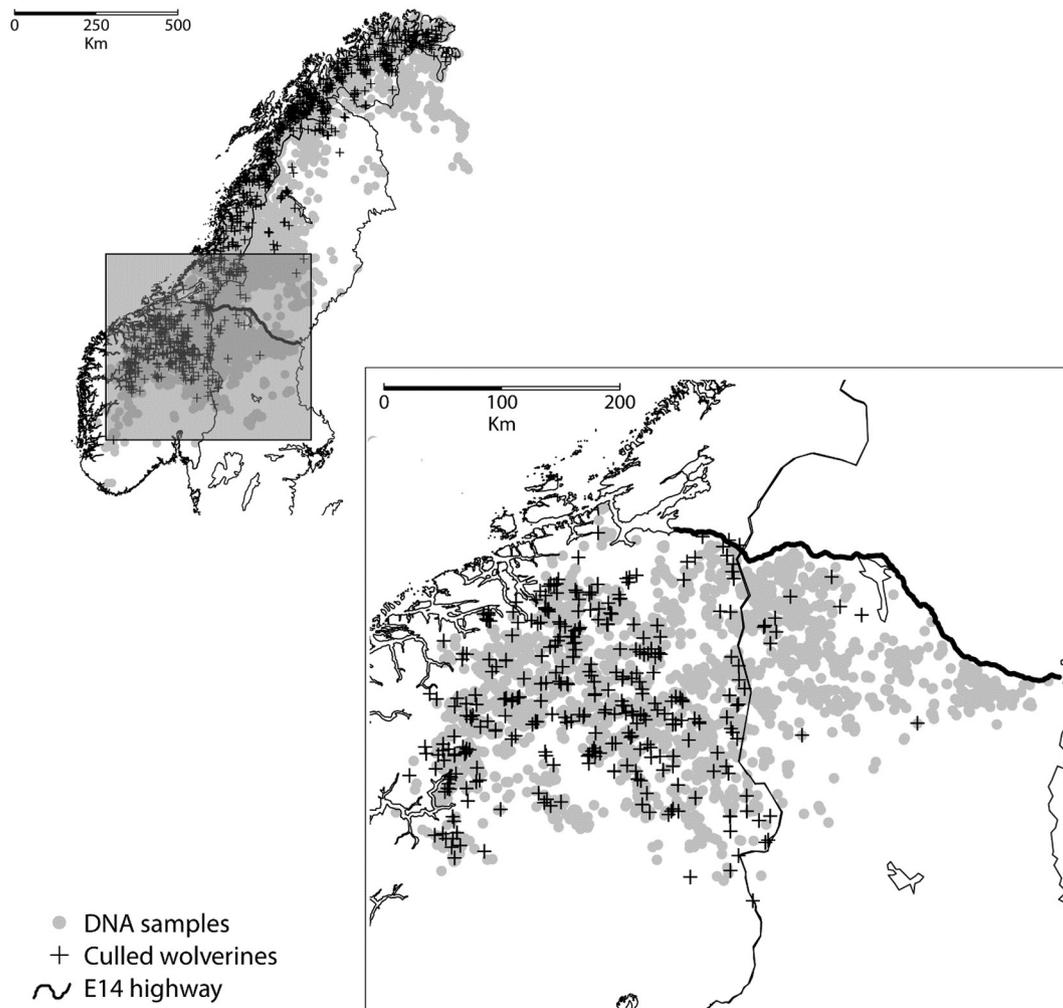


Fig. 2. Spatial distribution of wolverine non-invasive genetic samples (gray dots) and of legally shot wolverines (black crosses) in Scandinavia during the period 2002–2013. DNA samples and wolverines shot south of the E14 highway are shown in the inset.

Assuming a panmictic population across the study area, the probability of identity (pID ; Waits et al. 2001) was $2.9 \cdot 10^{-7}$ for unrelated wolverines, and $9.2 \cdot 10^{-4}$ for siblings. Details about the laboratory procedures including the used set of microsatellite markers are provided in Flagstad et al. (2004) and Brøseth et al. (2010). All the data used is publicly available at www.rovbase.no.

2.2. Multi-state capture–recapture modeling

To model the spatial and temporal variation in wolverine survival and immigration rates we used a two-site multi-state capture–recapture model with live detections and dead recoveries (Burnham, 1993) in the E-SURGE program (Choquet et al., 2005). This resulted in a 5-state analytical design: in any given year wolverines could be alive in Norway (state 1) or alive in Sweden (state 2), die from legal harvest in Norway (state 3) or die from other causes in any of the two countries (state 4). As customary in multi-state capture–recapture modeling, we added an absorbing state for all the individuals that died in previous years (state 5). As some individuals lived across the national border, in a few cases we detected the same individual in both countries in the same year. To comply with the requirements of multi-state CR models, which do not allow detection in multiple states in the same session, we assigned to Norway all the individuals detected on both sides of the national border. Then, we performed all the analyses a second time using Sweden as a country of preferential assignment for bordering

wolverines, and found that this subjective choice had no influence on the results.

Between two successive years, each individual still present in the population was allowed to perform a migration between Norway and Sweden. This process resulted in the following transition matrix T :

$$T = \begin{bmatrix} 1-\psi_{12} & \psi_{12} & 0 & 0 & 0 \\ \psi_{21} & 1-\psi_{21} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

in which ψ_{12} is the probability to immigrate from Norway to Sweden, and ψ_{21} the probability to immigrate from Sweden to Norway.

After the immigration process, we accounted for survival including the probability for each individual to die from different causes, as described in matrix S :

$$S_t = \begin{bmatrix} \phi_{1,t} & 0 & H_{1,t} & 1-\phi_{1,t}-H_{1,t} & 0 \\ 0 & \phi_{2,t} & 0 & 1-\phi_{2,t} & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

in which $\phi_{s,t}$ is the state and time-dependent survival probability, whereas H is the probability to die by legal harvest. We set H to zero

for individuals in state two (Sweden), as minimal legal harvest occurred in Sweden during the study period.

Finally, we considered four possible detection events: detected alive in Norway, detected alive in Sweden, reported as legally shot, and not detected. We fixed the probability to be detected as dead from legal harvest to 1, as all legally shot wolverines in Norway by definition were reported to the authorities either by private citizens or by the State Nature Inspectorate officers.

We performed a goodness-of-fit test for the initial time dependent model, using program U-CARE (Choquet et al., 2009), and found no excess of transients and no significant trap-response. Detection probability was modeled as a function of country (Sweden vs. Norway), year, and sex. For Norway, we also 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. Sex-specific buffer radii correspond to the average estimated home range size of wolverines of the two sexes in Scandinavia (Mattisson et al., 2011). We used this time-dependent individual covariate to explain part of the residual temporal and individual variation in detection probability.

To test if wolverines in Norway had a lower survival than in Sweden (*prediction 1*), we compared models with equal and different survival probabilities in Norway and Sweden, using the Akaike Information Criterion, corrected for overdispersion (QAIC; Burnham and Anderson, 2002). To test if wolverines entered Norway at a higher rate than they left it (*prediction 2*), we estimated two separate probabilities for the two directions (Norway to Sweden and Sweden to Norway). We also modeled immigration probability as a function of the distance of each individual from the national border, under the expectation that wolverines living far away from the border had a lower probability to emigrate. Results showed that immigration probability decreased as a function of the distance from the national border, and that it became close to zero at about 50 km (see Results). Therefore, we limited our further capture–recapture analyses to the sub-sample of wolverines detected in both countries within 50 km from the national border, i.e. those individuals with a non-zero probability to perform a immigration across the national border during the study period.

To test for a functional relationship between the extent of the harvest pressure in Norway and immigration probabilities (*prediction 3*), we used both an individual and a population approach. For each individual in the sample, we estimated if at least one other adult wolverine (older than one year) had been harvested in a buffer of 30 km (to cover neighboring territories) around its home range center after its first DNA detection. We then modeled immigration probability as a function of this factor variable, with the expectation that removal of a neighbor would increase immigration probability from Sweden to Norway and decrease immigration probability from Norway to Sweden. Buffer width was chosen by testing different radii between 5 and 50 km, of which 30 km provided the best fit to the data: a model including a 30 km buffer had a $\Delta AIC = 2.4$ with respect to the second best model (25 km), and $\Delta AIC > 4$ when compared with all the others. At the population level, we tested if the year-to-year immigration probabilities in both directions were correlated with the proportion of wolverines killed in Norway one, two, and three years before. This allowed us to generate a function directly linking the extent of the harvest pressure in Norway with the immigration patterns across the national border, accounting for a possible time lag in the process.

Finally, to evaluate if the feedback between harvest and emigration patterns had the potential to compensate the effort by the Norwegian authorities to reduce wolverine numbers (*prediction 4*), we estimated the absolute number of wolverines who emigrated from southern Norway to southern Sweden and vice-versa. These figures were based on annual estimates of population size (Brøseth and Tovmo, 2013), harvest rates, and immigration rates. Then we calculated how much of the killing in Norway was compensated for by immigration, and plotted a temporal trend in the effective proportion of wolverines removed

each year from the Norwegian portion of the population, accounting for both harvest and immigration. As we did not find any difference in detection probability between wolverines within and outside the 50 km stripe from the national border, we assumed that the proportion of wolverines detected in the two groups was the same as in the actual population.

3. Results

The best supported capture–recapture model included a year, sex, and country effect on the detection probability (model 1 in Table 1). Male wolverines had a higher detection probability than females in both countries. Average detection probability across years, countries, and sexes was 0.60 (95% CIs = 0.57–0.62), and it was similar in the two countries (Norway: $\hat{p} = 0.58$, 95% CIs = 0.54–0.62; Sweden: $\hat{p} = 0.56$, 95% CIs = 0.50–0.62). Males had in average a higher detection probability ($\hat{p} = 0.70$, 95% CIs = 0.64–0.74), than females ($\hat{p} = 0.48$, 95% CIs = 0.44–0.52). Detailed time-dependent detection probability plots for both sexes and countries are shown in the Supporting Information.

A model with different survival probabilities in Norway and Sweden greatly outcompeted models with identical survival ($\Delta AIC = 16.41$). The most supported model included only a sex effect in Sweden, with males experiencing a lower survival ($\phi = 0.80$, 95% CIs = 0.74–0.86) than females ($\phi = 0.87$, 95% CIs = 0.80–0.91). Consequently, mortality rates in Sweden have remained constant from 2002 until the present (see Fig. 3). The same best supported model included both a sex and a temporal effect in Norway. Males experienced a lower survival probability ($\phi = 0.71$, 95% CIs = 0.66–0.75) than females ($\phi = 0.80$, 95% CIs = 0.76–0.83). The rates of mortality due to other causes than legal harvest in Norway were not significantly different from the ones estimated in Sweden. In both countries, female wolverines had on average an 11% probability to die each year for other reasons than harvest (95% CIs = 0.09–0.14), and males had an 18% (95% CIs = 0.15–0.21) probability. On the contrary, mortality due to human harvest in Norway increased during the study period (Fig. 3). Harvest rate was 0.04 (95% CIs = 0.01–0.15) in 2003, but had risen to 0.16 (95% CIs = 0.10–0.24) by 2012. Males and females did not show a significant difference in the probability to die by legal harvest. Overall, the data supported prediction 1, showing that wolverine survival was lower in Norway than in Sweden, especially during the last years of the study.

In our sample, we observed a higher number of wolverines emigrating from Sweden to Norway ($N = 17$) than in the opposite direction ($N = 9$). The average distance traveled by wolverines dispersing from one country to the other was 93 km (SD = 73 km). Also, based on capture–recapture modeling results (model 1 in Table 1), immigration probability from Sweden to Norway was significantly higher ($\psi = 0.05$, 95% CIs = 0.03–0.08) than in the opposite direction ($\psi = 0.02$, 95% CIs = 0.01–0.03), consistently with the predictions of the compensatory immigration hypothesis (*prediction 2*). Immigration probability decreased with the distance from the border and was zero at about 50 km (Supporting Information). In the area comprised within 50 km from the national border, the probability to emigrate from Sweden to Norway was also significantly higher ($\psi = 0.16$, 95% CIs = 0.10–0.24) than from Norway to Sweden ($\psi = 0.06$, 95% CIs = 0.03–0.10).

After accounting for the effect of the distance from the national border, individuals with at least one other wolverine legally harvested in proximity to their home range had a higher probability to emigrate from Sweden to Norway than the ones who did not have harvested neighbors ($\beta = 3.19$, 95% CIs = 1.71–4.78; Fig. 4b). On the contrary, the probability to emigrate from Norway to Sweden decreased when a neighboring wolverine was shot ($\beta = -1.95$, 95% CIs = -3.28 to -0.62; Fig. 4b). At the population level, a model with a 2-year lag between harvest in Norway and immigration probability was best supported by the data (see Supporting Information S2). In particular, an increase in the harvest rate in Norway was correlated with a decrease

Table 1
Model selection results for the analysis of wolverine survival and trans-boundary movement in southern Scandinavia, 2002–2013.

N.	Model structure				k	Deviance	QAIC	Δ QAIC	
	Mortality		Detection						Immigration
	Other causes	Harvest	Norway	Sweden					
1	Sex	Sex + year	Sex + year + effort ^a	Sex + year	Country ^b + dist. border ^c	33	4439.69	4501.69	0.00
2	Country + sex	Sex + year	Sex + year + effort	Sex + year	Country + dist. border	34	4439.35	4505.35	3.67
3	Sex	Sex	Sex + year + effort	Sex + year	Country + dist. border	23	4467.56	4509.56	7.87
4	Sex	Sex + year	Sex + year + effort	Sex + year	Dist. border	32	4451.12	4511.12	9.43
5	Sex + year	Sex + year	Sex + year + effort	Sex + year	Country + dist. border	43	4430.57	4512.57	10.88
6	Country + sex + year	Sex + year	Sex + year + effort	Sex + year	Country + dist. border + sex	56	4419.74	4527.74	26.05
7	Sex	Sex	Sex + effort	Sex	Country + dist. border	23	4482.79	4524.79	23.10
8	Sex	Sex + year	Year + effort	Year	Country + dist. border	31	4482.75	4540.75	39.06

^a Total number of km of snowmobile surveys driven inside each individual's home range.

^b Indicates a separate effect in Norway and Sweden.

^c Distance between each individual's sampling center and the national border.

in the emigration rate from Norway to Sweden (Fig. 5a). During the first years of the study, when harvest rate was about 5%, the emigration rate was between 10–15% each year, but it had decreased to about 5% in the last years of the study, when harvest rate had risen to almost 20%. The immigration rate from Sweden to Norway was instead not correlated with harvest rate in Norway, and it was about 15% throughout the study (Fig. 5b). Overall, results supported prediction 3, showing that the net immigration of wolverines from Sweden to Norway increased with an increasing harvest rate in Norway.

When estimating the functional relationship between wolverine removals and immigration, we found that compensatory immigration was minimal or zero until 2007 (Fig. 5c). After 2007, an increasing proportion of the harvest in Norway has been compensated by the net immigration across the national border (Fig. 5c). Even though total harvest has increased by about 60% between 2009 and 2013, the effective increase was only 35%, as a consistent proportion of the additional wolverine removals were compensated by new immigrants from Sweden at the same time as emigration from Norway decreased (Fig. 5d). During the last years, compensatory immigration neutralizes the killing of one of every three wolverines shot in southern Norway.

4. Discussion

In the southern portion of the Scandinavian wolverine population Sweden acts as a source and Norway as a sink. This has not been taken into account so far when planning and evaluating conservation and management strategies in the two countries. All the conditions expected under the compensatory immigration hypothesis were confirmed.

First, wolverines living in Norway experienced a higher mortality than the ones living in Sweden, and this difference in survival has been increasing over the last decade. Secondly, immigration/emigration patterns across the national border exhibited a preferential direction from Sweden to Norway.

While multiple causes can initiate and maintain source–sink dynamics, such as differences in habitat quality (Kristan, 2003) or in naturally occurring mortality risks (Pulliam, 1988), in this case we present strong evidence that the extent of the harvest pressure in Norway is likely to be the main factor causing and reinforcing the compensatory immigration process. As survival rates were similar for the two countries at the beginning of the study when lethal control in Norway was low, (Fig. 3), it is unlikely that habitat quality and natural mortality rates differ markedly between the two countries. Furthermore, in the absence of hunting, immigration rates in the two directions were estimated to be equal (Fig. 5a, b), so that no net transfer of individuals would occur between the two countries, without the existing difference in harvest pressure. The emerging pattern shows that management actions implemented in a given country on a species of conservation concern can generate direct consequences on the spatial, and potentially demographic, dynamics in the neighboring countries.

The existence of a potential compensation between lethal control and immigration, which can counteract the effort of lowering carnivore densities, is not a new finding. Hunting of cougars (*Puma concolor*) in Washington State (USA) has failed to reduce population size, due to a post-harvest increase in immigration rates from the neighboring areas (Robinson et al., 2008). Similarly, densities of culpeo foxes (*Pseudalopex culpaeus*) in the Argentinean Patagonia did not change significantly

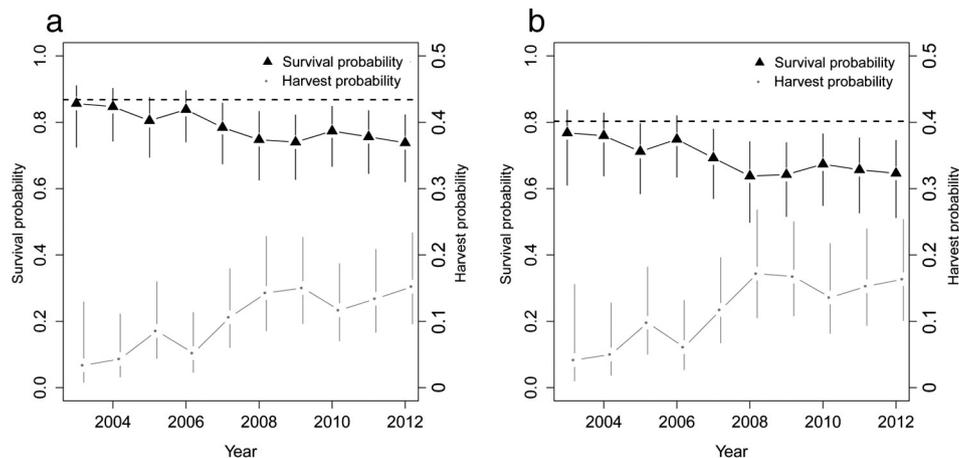


Fig. 3. Year-specific estimates of survival and harvest probability for female (a) and male (b) wolverines in southern Norway during the period 2003–2012, as estimated from non-invasive genetic sampling and capture–recapture modeling (model 1 in Table 1). The dashed line is the constant estimate of survival in southern Sweden during the same period (females 0.87, males 0.80).

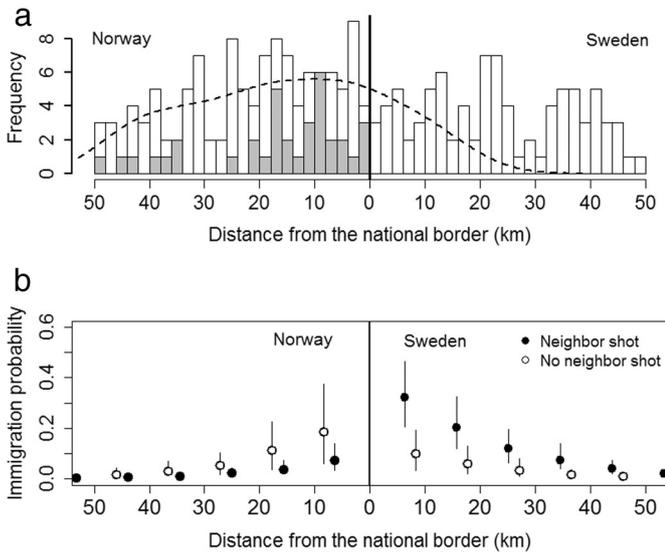


Fig. 4. a) Frequency distribution of the distances between each wolverine's sampling center and the national border (white bars), and of the distances between killing locations and the national border (gray bars). The histogram is plotted for the area comprised within 50 km from the border. The dashed line is the density function of the probability to have at least one neighbor shot in a range of 30 km; b) effect of a neighboring wolverine shot on the probability to immigrate from Norway to Sweden (left side of the figure) and from Sweden to Norway (right side of the figure). The effect is shown for increasing distances from the national border.

after hunting, as compensatory immigration led new foxes to re-colonize hunted areas from the neighboring un-hunted ranches (Novaro et al., 2005). Ecologists have therefore long recognized that contrasting management regimes can generate source–sink dynamics, and that these can frustrate local management goals. Still, such awareness has not been transferred into most management and conservation practices, as

the authorities in charge of their implementation have jurisdiction on smaller areas than the ones on which carnivore population dynamics usually operate.

The wolverine case study in Scandinavia is therefore another example of the mismatch existing between the scale of the ecological processes occurring in most large carnivore populations, and the scale at which their populations are managed (Linnell et al., 2008). One of the main consequences of such a mismatch is that the sustainability of conservation actions implemented in a given country may depend on which policy the neighboring countries will adopt during the same period. In the case of Scandinavian wolverines, the sustainability of the Norwegian harvest regime might be related to what conservation actions are implemented in Sweden, and vice-versa. The current harvest pressure allowed in Norway, which removes 15–20% of the whole population each year (Fig. 3), has so far been considered as sustainable by the management authorities, since the population has been mostly stable or slightly increasing despite such intense control pressure (Fig. 1). This occurred in a period during which Sweden has implemented a protective policy with no hunting and very limited control, which has generated a net transfer of individuals from Sweden to Norway (Fig. 5). As this policy has already changed, with progressively more wolverines legally harvested in Sweden in recent years, a careful evaluation of the potential consequences on the dynamics of the Norwegian portion of the population will be necessary. Without accounting for the feedback existing between the two countries, a sharp increase in the effective harvest rate and a consequential population decline might occur.

The functional relationship between lethal control of wolverines in Norway and the immigration/emigration rates emerging both at the local and at the population level (Figs. 4 and 5) reveals the need to evaluate the consequences of this process at both scales. While long-term population goals for wolverines (and most other large carnivore species) are set by national authorities to ensure species persistence and minimize conflicts with humans, the actual distribution of individual

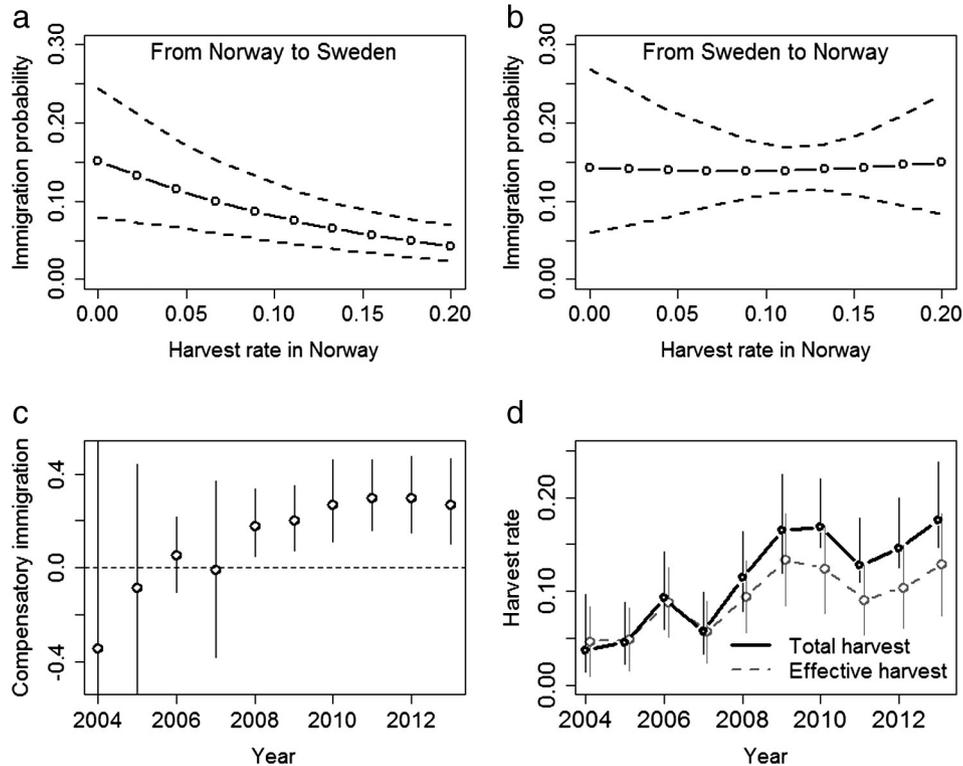


Fig. 5. Relationship between wolverine harvest rate in Norway and the individual probability to immigrate from Norway to Sweden (a) and from Sweden to Norway (b). The extent of compensatory immigration (c) is the ratio between the number of wolverines shot in Norway and the estimated number of wolverines immigrating in Norway each year. The relationship between total and effective harvest (d) is also shown.

removals are more often decided by local authorities as a responsive and preventive tool for damage control. Wolverine harvest in Norway often has the aim to remove specific individuals in areas where the levels of conflict with sheep farmers and semi-domestic reindeer (*Rangifer tarandus*) herders are particularly high (Swenson and Andrén, 2005). As individual removals can reduce the likelihood of resident wolverines emigrating from the area, hunting might have no effect or even a negative effect on the extent of the conflict. Lynx (*Lynx lynx*) hunting in Norway has been shown to provide only a minimal benefit in reducing the magnitude of the local conflict with sheep farmers (Herfindal et al., 2005). Similar evidence has been provided for the same species in the Jura mountains of France (Stahl et al., 2002). Also, as shown for badgers (*Meles meles*) in the United Kingdom (Donnelly et al., 2006), culling can increase local disease transmission and prevalence by disrupting the stability of the territorial arrangement and favoring contacts among individuals. Seen from the opposite perspective, compensation between harvest and trans-boundary movements can also depress the effort by neighboring countries to increase population numbers and density. Even though wolverines did not leave Sweden at a higher rate in response to increased harvest in Norway, the net balance between wolverine emigration and immigration across the border became progressively more negative for Sweden during the last decade. This underlines the need to include the spatial component of harvest and its potential forms of compensation, when evaluating the effectiveness and the consequences of a given management regime both for the country of interest and for the neighboring ones (Bischof et al., in press). Thinking of harvest as a simply numerical removal of individuals can be misleading and counterproductive.

It should be noted, though, that both the local and population effects of compensatory immigration might involve more complex mechanisms other than the one revealed by our model. Disruption of territorial stability through local immigration/emigration can also be associated with an increase in infanticide rates in several carnivore species (Swenson, 2003). While wolverine harvest in Norway is partially compensated for by trans-boundary immigration, it might also increase cub mortality through infanticide, by favoring territorial occupation by young males.

Our results describe the wolverine management system in Norway and Sweden as a potential case of inefficient resource allocation, due to contrasting conservation goals between neighboring countries. Between 2010 and 2013, an average of 45 wolverines older than one year have been killed each year in Norway by management authorities for damage control in addition to the ca. 20 wolverines removed annually through license hunting (Bischof et al., 2012). Since about 20–30% of the removals are compensated by new immigrants (Fig. 5c), a relevant portion of the economic investment in damage control is at risk of producing no long term effects both at the local and at the population level (Fig. 1). The increase in wolverine population size in Norway during the last decade also seems to suggest this (Fig. 1b).

The wolverine case in Scandinavia, with its contrasting management regimes between two neighboring countries, is not an exception in large carnivore conservation. Twenty-nine out of 33 large carnivore populations in Europe are trans-boundary in nature (Linnell et al., 2008), and several of them exhibit different, often contrasting management regimes within neighboring countries. The brown bears (*Ursus arctos*) of north-eastern Europe are protected in Latvia, but considered as de facto game species in neighboring Estonia and Russia (Linnell et al., 2008). The Carpathian lynx population is hunted in Romania, but not in the Czech Republic, Slovakia, Poland, or Ukraine, which all host neighboring portions of the same population (Linnell et al., 2008). Wolves (*Canis lupus*) are fully protected in Portugal, and south of the Duoro river in Spain, but considered as a game species north of the same river, under various autonomous regional legislations in Spain (Linnell et al., 2008). This situation is not limited to large carnivore populations, but it affects all migratory and wide-ranging species, whose distributions

are likely to span over several administrative units. As contrasting management regimes within the same population can generate undesired demographic and spatial dynamics, jeopardize conservation goals on the two sides of a border, reduce the efficiency of management actions, and cause a waste of economic resources for conservation, this calls for the adoption of a coordinated population approach in large carnivore conservation and management. Failing to match the scale of population processes and that of conservation can cause a waste of the already limited resources allocated for large carnivore conservation. Countries that aim to increase their large carnivore populations might see their animals emigrate abroad, whereas countries that want to reduce population numbers might see newcomers replace the ones they have just removed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.07.024>.

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