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Failure to coordinate management in transboundary populations hinders the achievement of national management goals: the case of wolverines in Scandinavia

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Abstract

1. Large carnivores are expanding in Europe, and their return is associated with conflicts that often result in policies to regulate their population size through culling. Being wide-ranging species, their populations are often distributed across several jurisdictions, which may vary in the extent to which they use lethal control. This creates the conditions for the establishment of source-sink dynamics across borders, which may frustrate the ability of countries to reach their respective management objectives.
2. To explore the consequences of this issue, we constructed a vec-permutation projection model, applied to the case of wolverines in south-central Scandinavia, shared between Norway (where they are culled) and Sweden (where they are protected). We evaluated the effect of compensatory immigration on wolverine population growth rates, and if the effect was influenced by the distance to the national border. We assessed to what extent compensatory immigration had an influence on the number of removals needed to keep the population at a given growth rate.
3. In Norway the model estimated a stable trend, whereas in Sweden it produced a 10% annual increase. The effect of compensatory immigration corresponded to a 0.02 reduction in population growth rate in Sweden and to a similar increase in Norway. This effect was stronger closer to the Norwegian-Swedish border, but weak when moving away from it. An average of 33 wolverines were shot per year in the Norwegian part of the study area. If no compensatory immigration from Sweden had

occurred, 28 wolverines shot per year would have been sufficient to achieve the same goal. About 15.5% of all the individuals harvested in Norway between 2005-2012 were compensated for by immigrants, causing a decrease in population growth rate in Sweden.

4. *Synthesis and applications.* When a population is transboundary, the consequences of management decisions are also transboundary, even though the political bodies in charge of those decisions, the stakeholders who influence them, and the taxpayers who finance them are not. It is important that managers and citizens be informed that a difference in management goals can reduce the efficiency, and increase the costs, of wildlife management.

Keywords: compensatory immigration; density-dependent dispersal; vec-permutation matrix model; spatial harvest; source-sink dynamic; transboundary management, policy, transboundary species.

INTRODUCTION

In classic harvest theory, the existence of a spatial structure in the harvest of continuous populations is considered to be a useful strategy to increase the yield of a game species while reducing the risks of overharvesting (McCullough, 1996). This is normally achieved by creating a mosaic of harvested and non-harvested areas within the population distribution. Such a system often generates an internal source-sink dynamic, with individuals emigrating from the non-harvested to the harvested portions of the population, a mechanism known as compensatory immigration (Pulliam, 1988). Spatially-structured harvest has been increasingly employed, especially in fisheries and small game systems, in an attempt to balance high yield and population viability (Kerr, Cadrin, & Secor, 2010).

However, the same type of mechanism can also emerge as an unintended consequence of contrasting management strategies in transboundary populations, with less predictable consequences on the overall dynamics of the population. Large carnivores in Europe provide an example of the latter case. Being wide-ranging species, their populations always span across several administrative units, which are subject to different legislations, management goals, conflicts and harvest regimes. At present, 33 functional European large carnivore populations can be identified, 25 of which are spread over two or more countries, and many more sub-national borders (Chapron et al., 2014). Out of them, 12 are distributed across a mosaic of harvested and non-harvested areas, depending on the management policies implemented in the countries which share portions of their distribution (Kaczensky et al., 2012). This creates the conditions for the establishment of source-sink dynamics across the national borders, although no population-level management plan was intended to create them (Reljic et al., 2018). The consequences of such mechanisms are not easily predicted and could be undesirable for national management authorities (Bischof, Brøseth, & Gimenez, 2016). However, based on the available literature on the properties of source-sink systems (Lebreton & Gonzalez-Davila, 1993; Hanski, 1996), we know that contrasting management regimes can induce and maintain an immigration/emigration process between neighbouring patches. The main effect of such process is to stabilize population growth rates in the two patches, when compared to a situation with no migration (Lebreton & Gonzalez-Davila, 1993). Ultimately, we can hypothesize that population growth rate will lower than expected in the country acting as a source, whereas it will be higher than expected in the country acting as a sink.

Based on this theoretical premise, the goal of the present study is to explore the dynamics of transboundary harvested populations, in which a spatial structure in harvest is induced by the existence of contrasting management regimes on the two sides of an administrative border. Within this framework, we assessed how the resulting source-sink dynamics can affect population performance. We also assessed the resulting effects on the effectiveness of lethal control as a management tool to limit the growth of each portion of the common population. Lethal control of large carnivores usually implies high economic costs, as finding and killing large carnivores can be difficult and expensive (Bischof et al. 2012). It also has relevant social costs, because it is a practice that usually polarizes the debate about coexistence with humans, has ethical implications, and is legally controversial (Linnell, Trouwborst, & Fleurke, 2017). Therefore, once a given management objective is set in relation to the ecological, economic and social carrying capacities, it is usually desirable for managers to reach that objective while minimizing the number of individuals that need to be removed. This marks a fundamental difference with respect to the harvest of game species, in which the objective is often to maximise the resulting yield of a given harvest strategy, while ensuring sustainability (McCullough, 1996).

To illustrate the practical consequences of differential harvest regimes in transboundary large carnivore populations, we present the case of the wolverine (*Gulo gulo*) population in the south-central portion of the Scandinavian peninsula, which is shared between Norway and Sweden. Wolverines are listed on appendix II of the Bern Convention for both countries and are therefore formally "strictly protected". Exceptions can only be given under certain conditions. Due to differences in conflict potential with free-ranging semi-domestic sheep (Ross et al., 2016; Widman & Elofsson, 2018), Sweden has been very restrictive with respect to these exceptions, while Norway has been much more liberal (Swenson & Andrén, 2005). During the period 2005-2012, the Swedish portion of the population increased from about 50 to around 130 individuals (Gervasi et al. 2016), reaching population levels which are in line with the national management goal. In this period, only a few individuals were legally removed from the population, approximating a harvest rate of zero. During the same period, the Norwegian portion of the population was substantially stable at around 130 individuals (Fig. 1), 45% above the management goal of 88 (Persson & Brøseth, 2011). This happened despite the total number of wolverines legally shot each year increasing from 14 in 2005 to 46 in 2012 (+228%; www.rovbase.no). This increase in the number of harvested individuals was justified by the specific culling practice applied in Norway, which sets regional population goals and allows the annual removal of all the individuals exceeding such goals. Moreover, as license hunting only fulfils about 40% of the annual quota (Bischof et al. 2012), rangers from the Nature State Inspectorate are charged with the task of removing an additional portion of the population, with a particular focus on reducing depredation losses of domestic sheep and semi-domestic reindeer (Linnell & Brøseth 2003; Tveraa et al. 2014). Gervasi et al. (2015) showed that the differential harvest regimes between Norway and Sweden induced a compensatory migration process and a source-sink dynamic, with a net immigration from Sweden to Norway throughout the study period. The demographic consequences of this mechanism haven't been explored so far, nor has the effect of such uneven spatial distribution of harvest intensity on the effectiveness of management strategies in the two countries.

Based on the premises illustrated above, we built a population projection model for the wolverine population in central-south Scandinavia. We used vec-permutation matrix models (Hunter & Caswell, 2005) to simultaneously account for both the demographic and spatial processes, with the aim to explore the following research questions:

- What was the effect of the harvest rate difference between the two countries, and of the resulting compensatory immigration process, on wolverine population growth rates in the Norwegian and Swedish portions of the population?
- Was such an effect similar at different distances from the Norwegian-Swedish national border?
- To what extent does the compensatory immigration process influence the ability of the Norwegian management system to regulate the wolverine population growth rate and size in Norway?

We discuss our results and provide recommendations in the light of the widespread mismatch currently existing between the scale of large carnivore populations in Europe and the scale of the administrative authorities in charge of their conservation and management.

MATERIALS AND METHODS

Vec-permutation models allow the demographic and spatial processes occurring each year in each portion of the population to be included separately, but within a holistic model (Hunter & Caswell, 2005). Given the relative complexity of the wolverine study case, we decided to first assess the general properties of a simple system. Then we applied a more realistic version of the same model to the case of the Scandinavian wolverine population.

Accordingly, we initially constructed a 2-patch 2-stage model in R (R Development Core Team, 2008), using a post-breeding Leslie-Usher matrix (Caswell, 2001).

To parameterize the model, we chose a set of simulated vital rates consistent with the case of a long-lived species, with high adult survival and a relatively low intrinsic growth rate. In both patches we set the natural mortality rate to 0.5 and 0.2 for individuals in stage one (“dispersing”) and two (“resident”), respectively. We also fixed fecundity to zero and 0.8 for the two stages, respectively. Harvest rate was absent in patch two, whereas it varied in a range of 0 - 0.2 in patch one. The initial population size was set to 100 individuals in both patches, distributed according to the stable stage distribution (Caswell, 2001).

We also added a density-dependent dispersal function to the model, to link harvest rates and population size with the magnitude of dispersal rates between the two patches. Following Ylikarjula et al. (2000), we assumed that the net dispersal rate at time t was a function of the difference in population size between the two patches, so that

$$\psi_{2,t} = \alpha \frac{(N_{2,t} - N_{1,t})}{(N_{1,t} + N_{2,t})}$$

in which $\psi_{2,t}$ is the net dispersal rate between patch two and patch one at time t (assuming that population size is larger in patch two than in patch one), $N_{1,t}$ and $N_{2,t}$ are population sizes in each of the two patches at time t, and α is the parameter controlling the maximum fraction dispersing. This parameter represented the strength of the compensatory immigration process. We simulated values of 0, 0.2 and 0.4 for this parameter (see Fig. S1 in Supporting Information).

Based on this model structure, harvest rate (h) in patch one was expected to influence population growth rate in two ways: on one hand it reduced it by increasing the annual mortality rate of individuals in patch one; on the other hand, it increased the net dispersal rate from patch two to patch one, thus also increasing the resulting annual population growth rate in patch one. By simulating a range of h and α values, we explored the net effect of these two interacting processes on the demography of the spatially structured population. We ran 1,000 model iterations, each of them parameterized with a different combination of values for the parameters h and α. We ran the model over a period of 25 years and evaluated its outcome in terms of the average population growth rate in patch one (λ_1), in patch two (λ_2) and in the whole population (λ_{tot}). As the population matrix was updated at each time step, we estimated the above mentioned quantities following Tuljapurkar et al. (2003), as the n^{th} root of the ratio between population size in year *n* and population size in year one. For each iteration and year, we also estimated the number of individuals harvested in patch one, as the product between the harvest rate parameter *h* and population size at time *t*. Finally, we performed a sensitivity analysis of population growth rates to variation in the harvest rate *h*, using a life-stage simulation analysis (Wisdom, Mills, & Doak, 2000). A full description of how the vec-permutation model was formulated is provided in Appendix 1.

After exploring the general dynamics of the simple 2-patch 2-stage model, we increased its structural complexity to apply it to the case of the south-central Scandinavian wolverine population. We initially constructed the model considering two patches (Norway and Sweden), two sexes, and 14 age classes. We also included two possible reproductive states (with cubs and without cubs) for the female segment of the population. Overall, the model comprised a total of 42 stages for each country. Stages from 1 to 14 included reproducing females, from 15 to 28 non-reproducing females, and from 29 to 42 they included males. Gervasi et al. (2015) have previously shown that only the individuals within 50 km from the Norwegian-Swedish border had a significant probability to disperse from one country to the other in a given year, so that the demographic effects of the compensatory immigration process were likely to be different at different distances from the national border. Therefore, in an effort to add spatial realism to the model, we sub-divided each of the two patches into five 50 km belts at increasing distances from the Norwegian-Swedish border (Fig 2).

Before using the model for predictive purposes, we first assessed how well it fit with the observed population trends in Norway and Sweden during the period 2005-2012, as estimated by Gervasi et al. (2016). To this aim we resorted to a set of demographic parameters, estimated for the Scandinavian wolverine population during the last 20 years. We derived wolverine reproductive rates from Rauset et al. (2015). The resulting probability distribution is shown in Fig. S2. We used a litter size of 1.38 cubs per female, derived from the same work by Rauset et al. (2015). To describe wolverine mortality patterns, we first included the effect of non-human mortality sources, then accounted for the harvest rates determined in each country by the national management regimes. Gervasi et al. (2015) estimated a 0.11 and 0.18 annual probability for female and male wolverines, respectively, to die from causes other than legal human harvest. We also resorted to the estimates provided by Persson et al. (2003) to parameterize the population model with realistic juvenile survival rates. Harvest rates on adult wolverines of both sexes in Norway were also formally estimated by Gervasi et al. (2015) for the period 2005-2012. We used these estimates to generate overall mortality rates for wolverines older than one year during the study period, assuming full additivity between human-related and other mortality sources. During the same period, legal harvest in south-central Sweden was minimal, to the point that it could be reasonably approximated to zero.

To account for wolverine dispersal across the Swedish-Norwegian national border, and across the five 50-km belts in each country, we used the same density-dependent dispersal function as in the simpler version of the model, setting the slope parameter $\alpha = 0.44$ (see Appendix 2 for details). We applied the function to all neighbouring 50-km belts in the model, using the difference in their local densities to produce a patch-to-patch dispersal rate. Dispersal in wolverines occurs to a different extent in all ages and for both sexes (Aronsson & Persson, 2018; Vangen, Persson, Landa, Andersen, & Segerström, 2001), but females tend to reduce their home range and be more sedentary when raising cubs. The dispersal process was therefore applied to males of all ages and to females without cubs, assuming that females with cubs would not disperse from their residential home range (Aronsson & Persson, 2018).

We used capture-recapture population size estimates for the Norwegian and Swedish portions of the population in year 2005 (Gervasi et al., 2016) to build the initial population vector in the model. The initial population sizes (112 individuals in Norway, 48 in Sweden) were first distributed into the 10 patches using the proportion of reproductions detected in each patch, then among all age and sex classes using the stable stage distribution of each matrix. A synthetic description of all parameter values is shown in Tab. 1.

To assess the effect of the compensatory immigration process on population growth rates, we first ran the vec-permutation model including the density-dependent dispersal process, then excluding it. The comparison of the population growth rates resulting from the two models provided the increase/decrease in population growth rate, induced by the compensatory immigration process. We evaluated this effect both at the national level and for all the ten 50-km zones, under the hypothesis that the net effect would be stronger close to the national border than far away from it.

We also evaluated to what extent the source-sink dynamic between Sweden and Norway would affect the number of wolverines that would need to be culled each year in Norway, in order to maintain a given population growth rate. We ran the population model 1,000 times, with randomly generated harvest rate values in Norway (range: 0 – 0.2) and no harvest in Sweden. Then, for each iteration we also ran the alternative model formulation, which excluded the compensatory immigration process. For each iteration we recorded the resulting number of wolverines shot each year. The comparison between the population growth rates obtained with, and without, the source-sink process for a given number of shot wolverines provided the net effect of the compensatory immigration process and also an estimate of the efficiency of the Norwegian harvest system.

RESULTS

Theoretical model

The 2-stage 2-patch model, parameterized with no harvest in both patches, produced the same population growth rate $\lambda_0 = 1.148$ in both portions of the population. When increasing harvest rate values were simulated in patch one, population trajectories in the two patches diverged depending on the strength of the compensatory immigration process. Under the hypothesis of no spatial connection between the two patches ($\alpha = 0$), population growth rate decreased linearly for increasing harvest rate values in patch one, whereas it remained constant at the λ_0 value in patch two (Fig. 3a and b). When dispersal and compensatory immigration were taken into account ($\alpha = 0.2$ and $\alpha = 0.4$), population growth rate in patch one was always higher than in the previous scenario (Fig. 3a), as a consequence of the density differential between the two patches, which generated the compensatory immigration process. Such differences in population growth rates increased for increasing harvest rate values. It was about 3% when the harvest rate was set at 0.05 in patch one, but it increased to 15% for $h = 0.2$. Conversely, population growth rate in patch two was always lower than λ_0, even though no harvest occurred in this portion of the population (Fig. 3b). When looking at the process from the perspective of the total population, the net effect of the compensatory immigration process was to reduce its overall growth rate λ_t, by up to a 44% reduction in the scenario including the highest simulated harvest rate and the strongest density-dependent dispersal ($h = 0.2$, $\alpha = 0.4$; Fig. 3c). The source-sink dynamic initiated by the differential harvest rates in the two patches of the continuous population was not a simple transfer of individuals from one portion of the population to the other. On the contrary, it induced a reduction in the overall population performance, by promoting immigration from an area at lower risk of mortality to one with a higher.

The compensatory immigration process also had an influence on the relationship between the number of individuals harvested each year in patch one and the resulting population growth rate. Under the $\alpha = 0$ scenario, the removal of 15 individuals per year was sufficient to keep the population in patch one substantially stable ($\lambda_1 = 1.01$; Fig. 4). When considering the source-sink dynamic induced by the compensatory immigration process ($\alpha = 0.2$ and $\alpha = 0.4$), the same number of annual removals corresponded to $\lambda_1 = 1.06$ and $\lambda_1 = 1.08$, respectively (Fig. 4). In these two cases, 23 and 26 annual removals were necessary, respectively, in order to keep the population stable, with a 53-73% increase in the effort required to reach the same management goal.

The sensitivity analysis of population growth rates to changes in harvest rate was also influenced by the strength of the compensatory immigration process. In patch one it decreased from -1.41 (no dispersal scenario) to -0.71 (strong density-dependent dispersal scenario; Tab. 2), confirming that the effectiveness of any management action in this part of the population was reduced by the inclusion of compensatory immigration. In patch two the sensitivity of population growth rate to harvest rate in patch one was zero for $\alpha = 0$, but it increased to up to -0.40 in the $\alpha = 0.4$ scenario (Tab. 2), showing that management actions in patch one had an effect on the demography of the population in the neighbouring unharvested patch.

The wolverine case study

When parameterized with the vital rates estimated for the Scandinavian wolverine population (see Tab. 1), the model showed a good fit with the capture-recapture based population trends at the national level in both countries (Fig. 5). In Norway the population model produced an average growth rate of $\lambda = 1.00$, close to the 1.01 previously estimated for the same population and study period (Gervasi et al., 2016). In Sweden the two approaches provided the same estimate of λ = 1.10. In Norway, the population size in 2005 was estimated at 112 individuals (Gervasi et al. 2016). When accounting for the existence of a compensatory immigration process, the model generated a stable population over the 8-year period and a final population size of 113 individuals (Fig. 6a), about 28% higher than the population goal of 88 individuals (14 reproductions; Brøseth, Tovmo, & Andersen, 2012, Anon 2013). The exclusion of the compensatory immigration process generated a λ=0.980 and a final population size of 96 individuals, about 15% lower than in the other scenario and 9% higher than the management goal. In Sweden, the wolverine population grew at the rate of about 11% each year (λ = 1.108). The effect of the compensatory immigration process corresponded to a 0.024 reduction in the annual population growth rate (Fig. 6b). When excluding the dispersal process, the population grew at the rate of about 13% each year (λ = 1.132), with a final population size in 2012 of 115 individuals (16% higher than the observed 99; Fig. 6b).

The influence of compensatory immigration on population growth rate was stronger closer to the Norwegian-Swedish border, but rather weak when moving away from it. In zone N_5, which corresponded to the 50-km belt closest to the border on the Norwegian side, growth rate was 0.04 higher when accounting for dispersal from Sweden than when disregarding it (Fig. 7). Similarly, in zone S_1, which corresponded to the 50-km belt closest to the border in Sweden, dispersal to Norway caused a 0.03 reduction in λ (Fig. 7). At the other extreme, zones N_1 and S_5, which were the most distant from the national border, only exhibited a 0.01 or lower variation in the annual zone-specific growth rate as a consequence of the compensatory immigration process (Fig. 7).

During the 8 years of the study periods, an average of 33.4 wolverines were shot per year in southern Norway, which corresponded to λ = 1.00. If no density-dependent dispersal from Sweden had occurred, removal of 28.2 wolverines per year would have been sufficient to generate the same population growth rate. In other terms, about 15.5% of all the individuals harvested in Norway between 2005-2012 were replaced by immigrants, and also causing an unintended decrease in population growth rate in Sweden.

DISCUSSION

Administrative borders can be seen as a particular kind of ecological edge between two otherwise contiguous landscape patches, whose characteristics are defined by the specific management actions implemented on each side (Minnie et al. 2016). The risks linked to this type of artificial edge have been more often studied in the context of protected areas and their unprotected surroundings, in which the establishment of source-sink dynamics can potentially jeopardize species persistence and even trigger extinction (Woodroffe & Ginsberg, 1998).

Our study shows that the dynamics occurring across administrative borders can also influence, and sometimes frustrate, the achievement of management goals and the effective use of the available economic resources. In this sense, the theoretical and applied approach provided complementary insights into the effect of compensatory immigration. The simpler and more general version of the vec-permutation model provided three main results : 1) the source-sink dynamics induced by different harvest regimes on the two sides of a border can reduce the overall population growth rate; 2) such a difference in harvest intensity can increase the number of removals necessary to achieve a certain population goal; and 3) the overall effect of this type of process is to reduce harvest efficiency in the country with the highest harvest intensity, as part of the effort in lethal control produces demographic effects in the neighbouring country, and not locally. From a demographic point of view, the patterns emerging from the theoretical vec-permutation model are in line with the previously demonstrated general stabilizing effect of migration in subdivided populations (Lebreton & Gonzalez-Davila, 1993). When two portions of a population have different intrinsic growth rates, because of a difference in the underlying demographic parameters, density-dependent migration has the effect of reducing both the overall population growth and the difference in patch-specific growth rates (Lebreton, 1996). However, the sensitivity analysis (Tab. 2) shows that this effect is strongly dependent on the strength (and likely on the shape) of the density-dependent dispersal process. Therefore, while our approach provides a flexible framework for a wide variety of wide-ranging species, particular care should be used in identifying an appropriate mathematical description of the link between density and dispersal rates. No generalizations can be easily made, as dispersal has been shown to be sometimes directly positively (Herzig, 1995) and sometimes inversely (Woodroffe, Macdonald, & Da Silva, 1993) related to population density, but also highly affected by other factors not related to density or competition (Waser, 1985).

By promoting dispersal from an area with low mortality to an area with high mortality, without reaching an equilibrium point between additions and subtractions, compensatory immigration creates the conditions for the establishment of an ecological trap *sensu* Dwernychuk & Boag (1972). Ecological traps, also defined as attractive sinks, are areas in a species' distribution in which high suitability and high mortality risks overlap (Battin, 2004). These areas usually attract individuals from the surroundings, thanks to the availability of food, cover, mating opportunities, and other crucial resources. At the same time, they reduce individual survival because of a localized mortality risk which is not correlated with the otherwise high suitability of the area. Attractive sinks can threaten the conservation of small endangered populations (Nielsen, Stenhouse, & Boyce, 2006), in particular in those ecosystems where human-related mortality risks have become predominant (Battin, 2004).

In our case, the attractive sink was initiated and maintained by the local density gradient across the Norwegian-Swedish national border, resulting from the differential harvest regimes in the two countries. This situation attracted wolverines to the area in which competition for resources was likely lower, which was also the area in which mortality risks were higher (Gervasi et al., 2015). Our results show that, besides having consequences on population persistence and extinction risk, attractive sinks can also affect the costs and benefits of a given management strategy, when lethal control is used as a tool to limit population size and growth. On average, one in every six wolverines shot in Norway during the study period was replaced by another wolverine immigrating from the Swedish side of the border. Given the high costs associated with lethal control of large carnivores, and the polarized debate about its ethical and legal aspects, this type of practice should be carefully evaluated before setting national harvest rates to levels that could initiate and maintain a transboundary source sink-dynamic, especially when a neighbouring country exerts a lower harvest pressure on its portion of the shared population. This is a rather common and widespread situation in European large carnivore populations, as about 40% of them are shared between countries that apply contrasting management regimes when it comes to lethal control (Kaczensky et al., 2012). The Alpine wolf population, shared between France and Italy is a well-known example of such a case, as the French legislation allows a yearly quota-based culling, whereas the Italian one does not (Kaczensky et al., 2012). Similar examples of contrasting management regimes are provided by the Dinaric-Balkan and North-Western Iberian wolf populations, or by the Scandinavian lynx (*Lynx lynx*) population, which are either protected or harvested in specific national portions of their distribution (Kaczensky et al., 2012). From an international perspective, one of the consequences of the Swedish-Norwegian compensatory immigration process was also that part of the effort performed by the Norwegian management system in reducing wolverine population growth rate in Norway actually produced a reduction on the Swedish side of the border (33% reduction in the overall population growth over the study period; see Fig. 6b). This highlights that, when a population is shared among two or more countries, the consequences of management decisions are also transboundary, even though the political bodies which are in charge of those decisions, the stakeholders who influenced them, and the taxpayers who financed them are not. However, some differences in management goals between neighbouring countries are unavoidable, for multiple reasons: *i)* the material conflict between humans and large carnivores is sometimes different between neighbouring countries, depending for example on the different importance of farming and livestock herding in the national economic system. Sheep farming, for example, has a higher economic and social importance in Norway than in Sweden, creating the conditions for different levels of potential material conflict (Swenson & Andrén, 2005); *ii)* even when the material conflict is similar, people from different countries often have a different perception of the potential threat that large carnivores represent to their property or values, depending on their social, cultural and historical context. People living in larger communities have been shown to be in general more positive towards large carnivores than those from small rural communities (Røskaft et al., 2007). This is the case when comparing the Swedish and Norwegian contexts, with the first exhibiting a higher level of urbanization than the second (United Nations, 2015); *iii)* Governments of different political orientation can generate contrasting management policies in neighbouring countries, in order to achieve different political goals. Therefore, while agreeing on a common management policy at the population level would be desirable from the point of view of management efficiency, it might not always be easy to implement in practice. It’s important, though, that managers and citizens be informed about the ecological and economic consequences of a difference in management goals with a neighbouring country and take these effects into account (Reljic et al. 2018), especially when limited resources are available to promote coexistence between humans and large carnivores. In practical and applied terms, we recommend that policy integration and transboundary communication be promoted between countries sharing portions of the same large carnivore population. Such integration should include population monitoring, through the standardization of methods and data sharing (Gervasi et al. 2016), and also the political processes that lead to the establishment of national population goals and management strategies. Such integration is already going on for the Scandinavian wolverine population, which is now monitored through a shared and standardized monitoring program in Norway and Sweden, which makes use of a common field methodology and of a shared database of all DNA-sampled individuals which facilitated our analysis (Brøseth et al., 2012). This model should be further extended to other similar cases and large carnivore populations in other parts of the continent.

On the other hand, the effort to match the scale of ecological processes with that of management decisions should not overshadow the idea that the consequences of national and international management decisions can be substantially different at smaller spatial scales and in more local contexts. In our case, the eastern part of southern Norway (the area closest to the national border) was highly affected by the compensatory immigration process, as it received most of the wolverines immigrating from Sweden. As a consequence, the efficiency of the Norwegian lethal control on wolverines was rather low in this part of the country. On the other extreme, the western part of the country (the most distant from the national border) was minimally affected by the transboundary source-sink dynamic, and the trajectory of wolverine abundance in that area, with and without the compensatory immigration process, would have been rather similar (Fig. 7). This suggests the positive value of combining national and regional population goals in a way that allows monitoring the overall population trend in the country, while taking into account the local dynamics occurring in the different portions of the species distribution. Regions and sub-national administrative units closer to national borders should explicitly incorporate the evaluation of transboundary dynamics in their decision-making process, under the risk of otherwise generating unrealistic expectations and ineffective management actions.

Ultimately, the results of our study underline the need to consider both sides of large carnivore population management: on one hand, it would be advisable that the general goals of large carnivore management be set at the population (and therefore often international) level, to avoid a waste of economic resources and to maintain a balance between the investment in each country and the resulting demographic trends. On the other hand, local factors should also be considered when dealing with the consequences of the general management strategies, accounting for the fact that citizens inhabiting different local contexts will be affected to a different extent by the consequences of larger scale management decisions. This reflects the great challenge at the heart of large carnivore management: the need to develop institutional structures and procedures that can simultaneously coordinate actions at international scales while remaining flexible enough to deal with local level considerations (Linnell, 2015; Linnell & Kaltenborn, 2019).

AUTHORS’ CONTRIBUTIONS

All authors conceived the research questions and designed the methodology; V. Gervasi and O. Gimenez analysed the data; V. Gervasi led the writing of the manuscript. J. Linnell provided details of the management and policy contexts and implications. All authors contributed critically to the drafts and gave final approval for publication.

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DATA ACCESSIBILITY

Data used for the analyses present in this article was previously published on peer-reviewed journals. Input parameters for the wolverine population model were derived from Gervasi et al. (2015) and Rauset et al. (2015). R code to build and run the vec-permutation matrix model is stored in the Dryad Digital Repository, doi:10.5061/dryad.rd300kf. Gervasi, Linnell, Brøseth ,Gimenez (2019).

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Parameter	Value / Interval		Source
	Norway	Sweden	
Reproduction probability	0 – 0.7	0 – 0.7	Rauset et al. 2015
Litter size[a]	1.38	1.38	Rauset et al. 2015
Adult female mortality for other causes than harvest (> one year old)	0.11	0.11	Gervasi et al. 2015
Adult male mortality for other causes than harvest (> one year old)	0.18	0.18	Gervasi et al. 2015
Juvenile mortality for other causes than harvest (< one year old)[b]	0.29	0.29	Persson et al. 2003
Harvest rate on adult females (> one year old)	0.05 – 0.15	0	Gervasi et al. 2015
Harvest rate on males (> one year old)	0.06 – 0.17	0	Gervasi et al. 2015
Harvest rate on juveniles of both sexes (< one year old)	0.09 – 0.36	0	www.rovdata.no
Initial Population size	112	48	Gervasi et al. 2016
Strength of the density-dependent dispersal (α)	0.44	0.44	Gervasi et al. 2015

[a] Refers to the number of cubs still alive in the first week of June.

[b] Refers to the period between 3 and 12 months of age.

Tab. 1 - Input parameters for the population projection model of wolverines (*Gulo gulo*) in south-central Scandinavia.

	$\alpha = 0$	$\alpha = 0.2$	$\alpha = 0.4$
λ_1	-1.41	-0.75	-0.71
λ_2	0.00	-0.27	-0.40
λ_{tot}	-0.24	-0.43	-0.52

Tab. 2 - Sensitivity analysis of population growth rate to changes in harvest rate for a 2-patch 2-stage vec-permutation model including density-dependent dispersal. Sensitivity values are provided for the harvested patch (λ_1), in the non-harvested patch (λ_2) and for the whole population (λ_{tot}) under three scenarios of incrasing strenght in the density-dependent dispersal function, controlled by the parameter α.

Fig. 1 - Population size estimates (based on counts of reproductive units) in southern Norway and southern Sweden during the period 2005–2017. The number of wolverines harvested each year in southern Norway is also shown.

Fig. 2 – Distribution of wolverine (*Gulo gulo)* DNA samples collected in south-central Scandinavia during the period 2005-2012 (black dots), divided into 10 x 50-km belts around the Norwegian-Swedish border (continuous grey line). The E14 highway marking the northern border of the study area is also shown (grey dotted line).

Fig. 3 – Relationship between harvest rate and population growth rate in a 2-patch 2-stage vec-permutation model including density-dependent dispersal. Harvest was simulated only in patch one in a range of 0-0.2. The resulting population growth rate is shown for patch one (a), patch two (b) and for the whole population (c) under three scenarios of incrasing strenght in the density-dependent dispersal function, controlled by the parameter α.

Fig. 4 - Relationship between the number of individuals harvested and population growth rate in a 2-patch 2-stage vec-permutation model including density-dependent dispersal. The relationship is shown under three scenarios of incrasing strength in the density-dependent dispersal function, controlled by the parameter α.

Fig. 5 – Comparison between the population trajectories of wolverines (*Gulo gulo*) in southern Norway (a) and Sweden (b), obtained through DNA-sampling and capture-recapture modelling (Gervasi et al. 2016) and by applying the vec-permutation population projection model.

Fig. 6 – Population trajectories of wolverines in southern Norway (a) and Sweden (b) between 2005-2012, obtained by running the vec-permutation projection model with and without the effect of the compensatory immigration process.

Fig. 7 – Variation in annual population growth rate induced by compensatory immigration (from Sweden to Norway) in each of the ten 50-km zones identified for the wolverine (*Gulo gulo*) population in south-central Scandinavia, during the period 2005-2012. Zones N_1-N_5 refer to the Norwegian portion of the population (see Fig. 2), S_1-S_5 to the Swedish portion.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

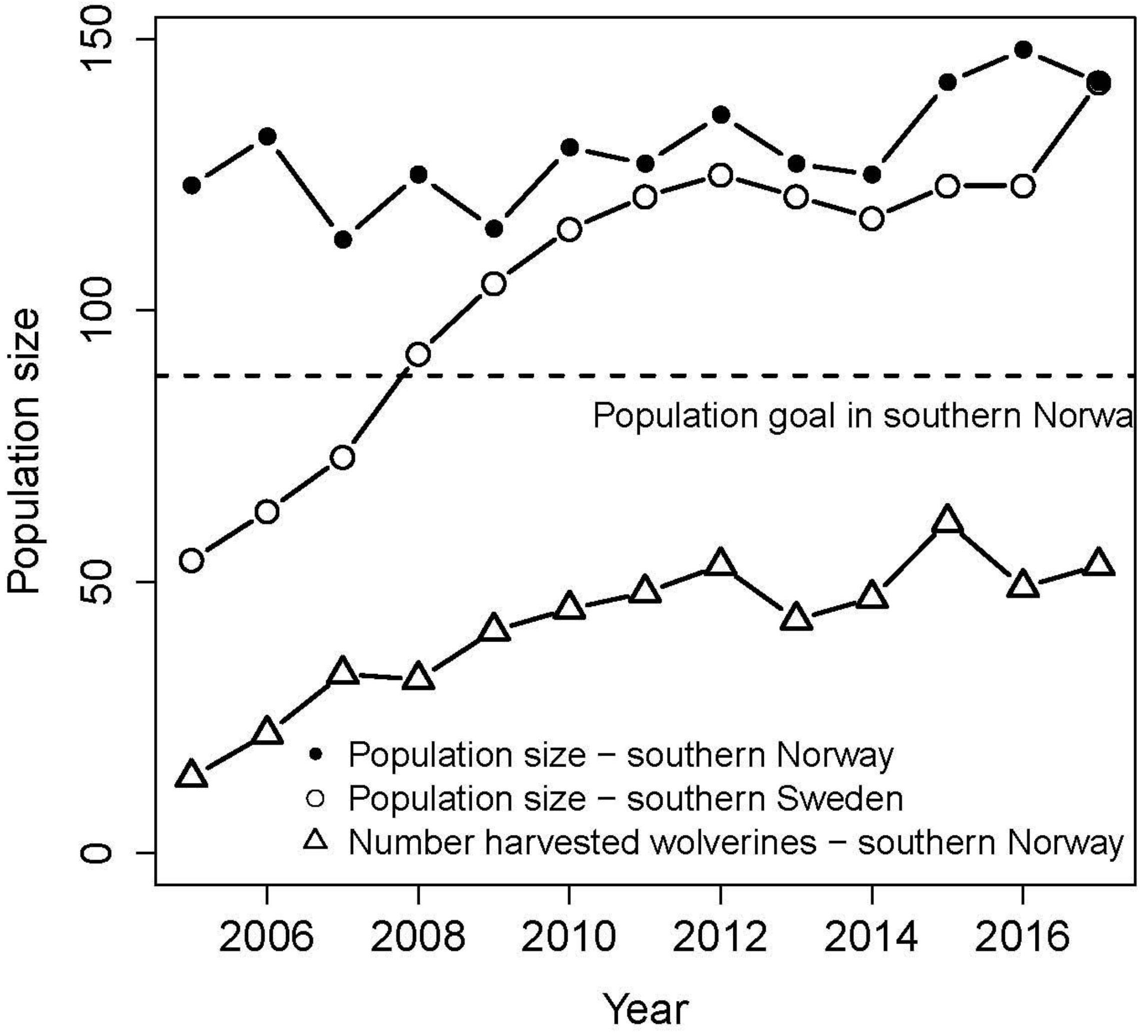
Fig. S1 – Relationship between density differential and dispersal rate in the vec-permutation matrix model.

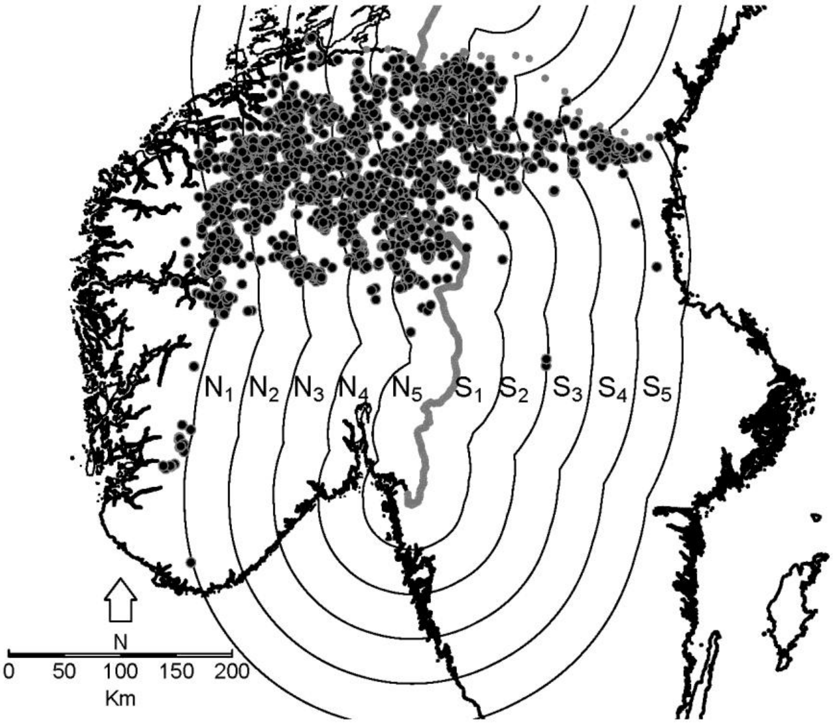
Fig. S2 – Age specific reproduction probability of female wolverines in Scandinavia (from Rauset et al. 2015).

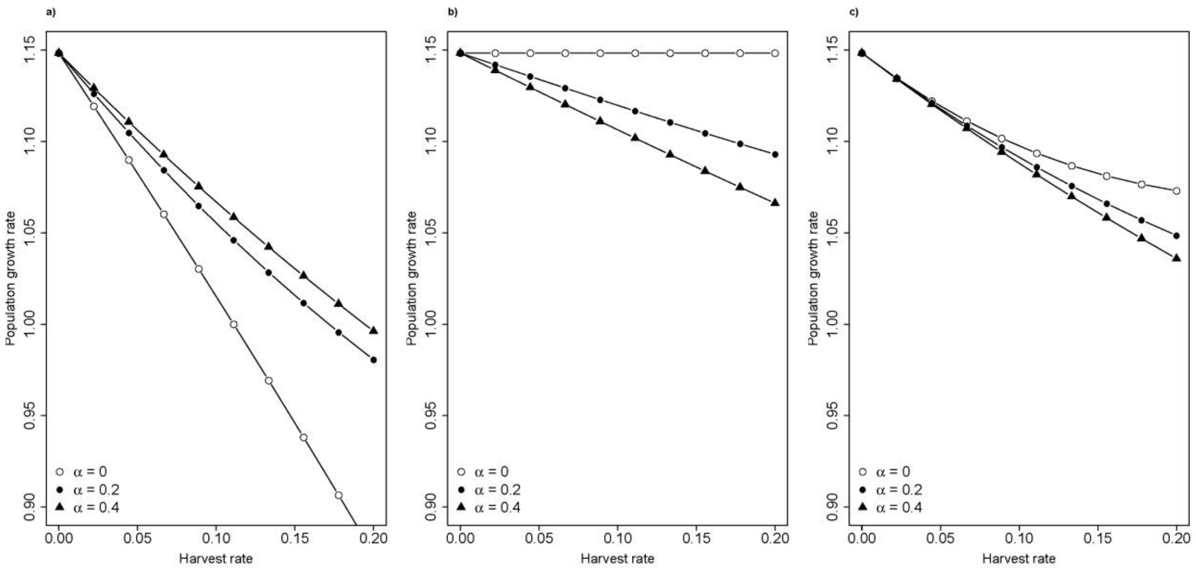
Appendix 1 - Formulation of the 2-patch 2-stage vec-permutation model.

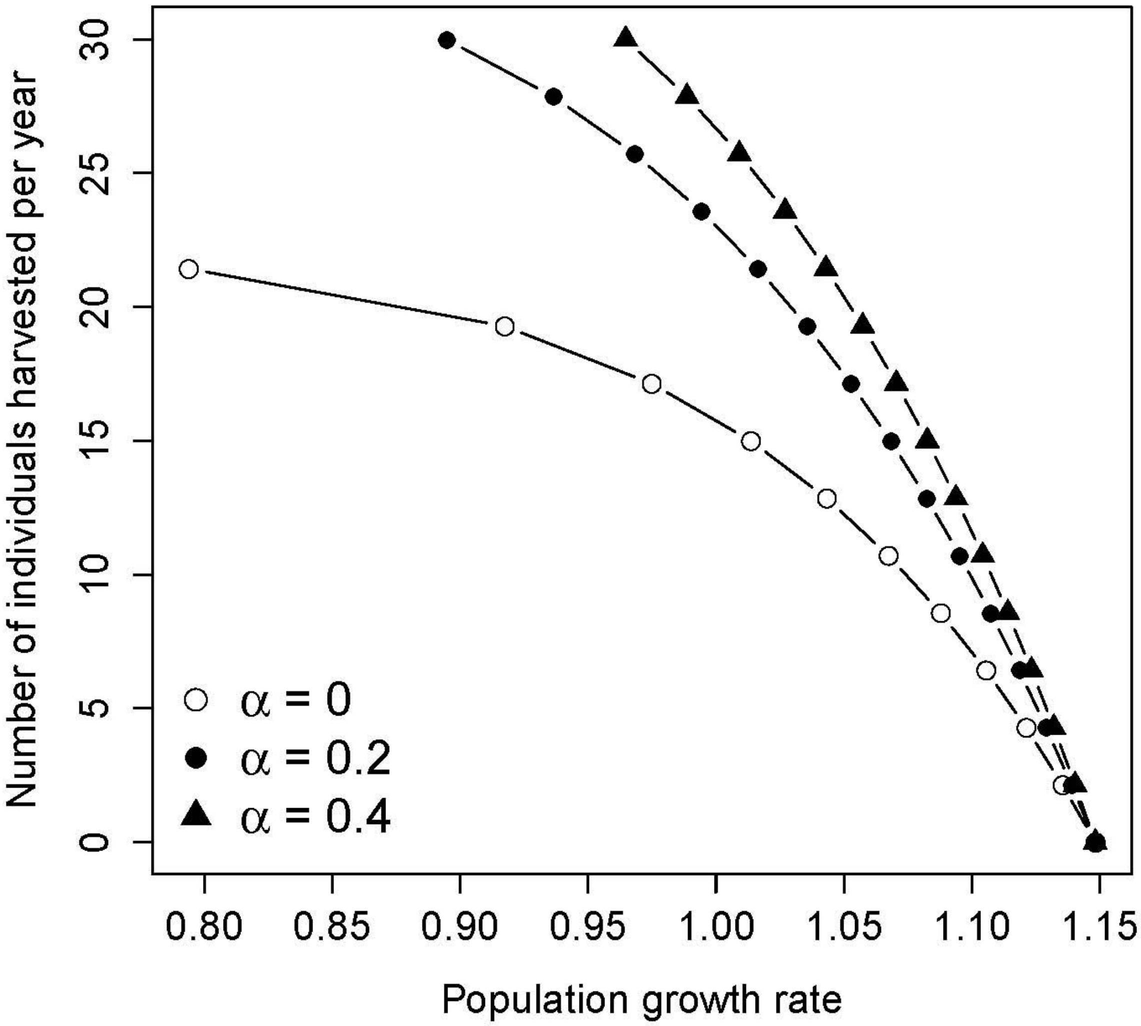
Appendix 2 - Derivation of the appropriate value for the strength of the density dependent dispersal process in Scandinavian wolverines.

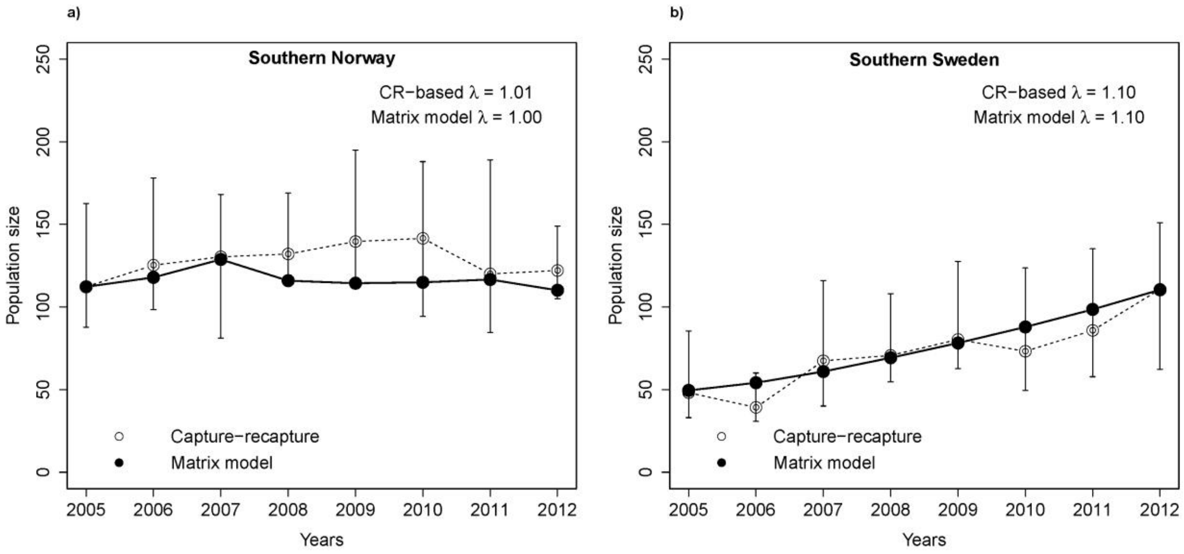
Appendix 3 - R-code used to run the 2-patch 2-stage vec-permutation model.

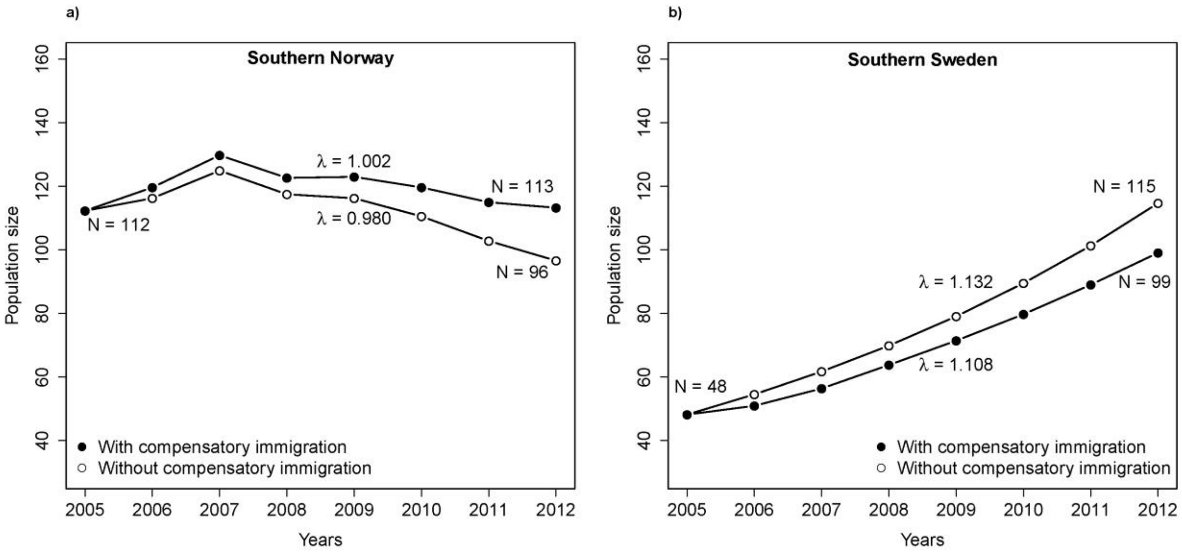

150
100
50
0
Population size
2006
2008
2010
2012
2014
2016
Year
Population goal in southern Norwa
● Population size − southern Norway
○ Population size − southern Sweden
△ Number harvested wolverines − southern Norway

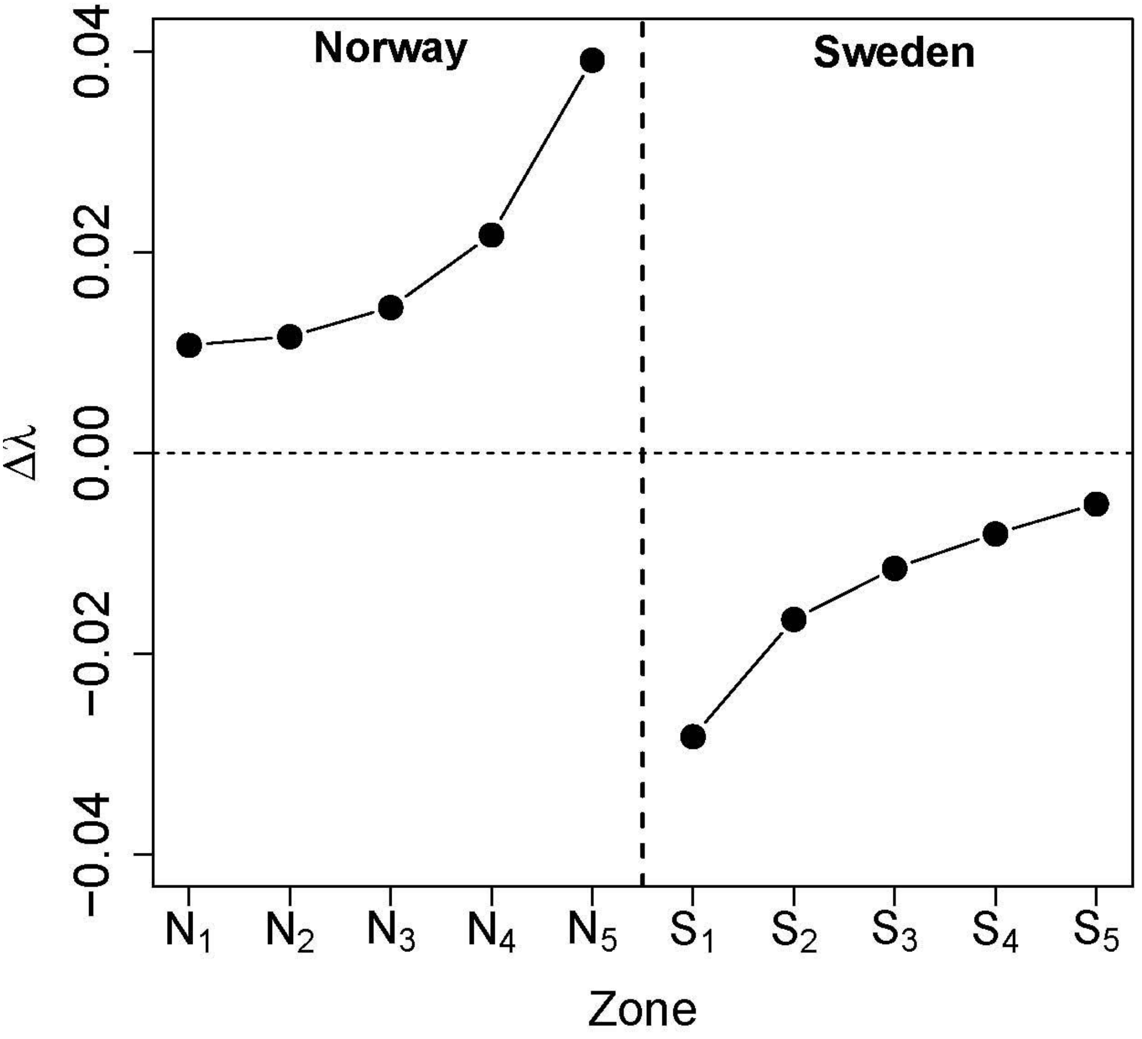

N$_1$
N$_2$
N$_3$
N$_4$
N$_5$
S$_1$
S$_2$
S$_3$
S$_4$
S$_5$
N
0
50
100
150
200
Km


a)
b)
c)
Population growth rate
0.90
0.95
1.00
1.05
1.10
1.15
Harvest rate
0.00
0.05
0.10
0.15
0.20
○ α = 0
● α = 0.2
▲ α = 0.4


Number of individuals harvested per year
0
5
10
15
20
25
30
0.80
0.85
0.90
0.95
1.00
1.05
1.10
1.15
Population growth rate
○ α = 0
● α = 0.2
▲ α = 0.4


a)
Southern Norway
CR−based λ = 1.01
Matrix model λ = 1.00
Population size
0
50
100
150
200
250
Capture−recapture
Matrix model
2005
2006
2007
2008
2009
2010
2011
2012
Years
b)
Southern Sweden
CR−based λ = 1.10
Matrix model λ = 1.10
Population size
0
50
100
150
200
250
Capture−recapture
Matrix model
2005
2006
2007
2008
2009
2010
2011
2012
Years


a)
Southern Norway
Population size
Years
160
140
120
100
80
60
40
2005
2006
2007
2008
2009
2010
2011
2012
λ = 1.002
λ = 0.980
N = 112
N = 113
N = 96
● With compensatory immigration
○ Without compensatory immigration
b)
Southern Sweden
Population size
Years
160
140
120
100
80
60
40
2005
2006
2007
2008
2009
2010
2011
2012
N = 48
λ = 1.132
λ = 1.108
N = 115
N = 99
● With compensatory immigration
○ Without compensatory immigration


Norway
Sweden
Δλ
0.04
0.02
0.00
−0.02
−0.04
N_1
N_2
N_3
N_4
N_5
S_1
S_2
S_3
S_4
S_5
Zone