

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

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28 **Abstract**

- 29 1. Large carnivores are expanding in Europe, and their return is associated with conflicts  
30 that often result in policies to regulate their population size through culling. Being wide-  
31 ranging species, their populations are often distributed across several jurisdictions, which  
32 may vary in the extent to which they use lethal control. This creates the conditions for the  
33 establishment of source-sink dynamics across borders, which may frustrate the ability of  
34 countries to reach their respective management objectives.
- 35 2. To explore the consequences of this issue, we constructed a vec-permutation projection  
36 model, applied to the case of wolverines in south-central Scandinavia, shared between  
37 Norway (where they are culled) and Sweden (where they are protected). We evaluated  
38 the effect of compensatory immigration on wolverine population growth rates, and if the  
39 effect was influenced by the distance to the national border. We assessed to what extent  
40 compensatory immigration had an influence on the number of removals needed to keep  
41 the population at a given growth rate.
- 42 3. In Norway the model estimated a stable trend, whereas in Sweden it produced a 10%  
43 annual increase. The effect of compensatory immigration corresponded to a 0.02  
44 reduction in population growth rate in Sweden and to a similar increase in Norway. This  
45 effect was stronger closer to the Norwegian-Swedish border, but weak when moving

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46 away from it. An average of 33 wolverines were shot per year in the Norwegian part of  
47 the study area. If no compensatory immigration from Sweden had occurred, 28  
48 wolverines shot per year would have been sufficient to achieve the same goal. About  
49 15.5% of all the individuals harvested in Norway between 2005-2012 were compensated  
50 for by immigrants, causing a decrease in population growth rate in Sweden.

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

57

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

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65 **INTRODUCTION**

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

75 However, the same type of mechanism can also emerge as an unintended consequence of  
76 contrasting management strategies in transboundary populations, with less predictable  
77 consequences on the overall dynamics of the population. Large carnivores in Europe provide an  
78 example of the latter case. Being wide-ranging species, their populations always span across  
79 several administrative units, which are subject to different legislations, management goals,  
80 conflicts and harvest regimes. At present, 33 functional European large carnivore populations  
81 can be identified, 25 of which are spread over two or more countries, and many more sub-  
82 national borders (Chapron et al., 2014). Out of them, 12 are distributed across a mosaic of  
83 harvested and non-harvested areas, depending on the management policies implemented in the  
84 countries which share portions of their distribution (Kaczensky et al., 2012). This creates the  
85 conditions for the establishment of source-sink dynamics across the national borders, although

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86 no population-level management plan was intended to create them (Reljic et al., 2018). The  
87 consequences of such mechanisms are not easily predicted and could be undesirable for national  
88 management authorities (Bischof, Brøseth, & Gimenez, 2016). However, based on the available  
89 literature on the properties of source-sink systems (Lebreton & Gonzalez-Davila, 1993; Hanski,  
90 1996), we know that contrasting management regimes can induce and maintain an  
91 immigration/emigration process between neighbouring patches. The main effect of such process  
92 is to stabilize population growth rates in the two patches, when compared to a situation with no  
93 migration (Lebreton & Gonzalez-Davila, 1993). Ultimately, we can hypothesize that population  
94 growth rate will lower than expected in the country acting as a source, whereas it will be higher  
95 than expected in the country acting as a sink.

96 Based on this theoretical premise, the goal of the present study is to explore the dynamics of  
97 transboundary harvested populations, in which a spatial structure in harvest is induced by the  
98 existence of contrasting management regimes on the two sides of an administrative border.

99 Within this framework, we assessed how the resulting source-sink dynamics can affect  
100 population performance. We also assessed the resulting effects on the effectiveness of lethal  
101 control as a management tool to limit the growth of each portion of the common population.

102 Lethal control of large carnivores usually implies high economic costs, as finding and killing  
103 large carnivores can be difficult and expensive (Bischof et al. 2012). It also has relevant social  
104 costs, because it is a practice that usually polarizes the debate about coexistence with humans,  
105 has ethical implications, and is legally controversial (Linnell, Trouwborst, & Fleurke, 2017).

106 Therefore, once a given management objective is set in relation to the ecological, economic and

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107 social carrying capacities, it is usually desirable for managers to reach that objective while  
108 minimizing the number of individuals that need to be removed. This marks a fundamental  
109 difference with respect to the harvest of game species, in which the objective is often to  
110 maximise the resulting yield of a given harvest strategy, while ensuring sustainability  
111 (McCullough, 1996).

112 To illustrate the practical consequences of differential harvest regimes in transboundary large  
113 carnivore populations, we present the case of the wolverine (*Gulo gulo*) population in the south-  
114 central portion of the Scandinavian peninsula, which is shared between Norway and Sweden.  
115 Wolverines are listed on appendix II of the Bern Convention for both countries and are therefore  
116 formally “strictly protected”. Exceptions can only be given under certain conditions. Due to  
117 differences in conflict potential with free-ranging semi-domestic sheep (Ross et al., 2016;  
118 Widman & Elofsson, 2018), Sweden has been very restrictive with respect to these exceptions,  
119 while Norway has been much more liberal (Swenson & Andrén, 2005). During the period 2005-  
120 2012, the Swedish portion of the population increased from about 50 to around 130 individuals  
121 (Gervasi et al. 2016), reaching population levels which are in line with the national management  
122 goal. In this period, only a few individuals were legally removed from the population,  
123 approximating a harvest rate of zero. During the same period, the Norwegian portion of the  
124 population was substantially stable at around 130 individuals (Fig. 1), 45% above the  
125 management goal of 88 (Persson & Brøseth, 2011). This happened despite the total number of  
126 wolverines legally shot each year increasing from 14 in 2005 to 46 in 2012 (+228%;  
127 [www.rovbase.no](http://www.rovbase.no)). This increase in the number of harvested individuals was justified by the

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128 specific culling practice applied in Norway, which sets regional population goals and allows the  
129 annual removal of all the individuals exceeding such goals. Moreover, as license hunting only  
130 fulfils about 40% of the annual quota (Bischof et al. 2012), rangers from the Nature State  
131 Inspectorate are charged with the task of removing an additional portion of the population, with a  
132 particular focus on reducing depredation losses of domestic sheep and semi-domestic reindeer  
133 (Linnell & Brøseth 2003; Tveraa et al. 2014). Gervasi et al. (2015) showed that the differential  
134 harvest regimes between Norway and Sweden induced a compensatory migration process and a  
135 source-sink dynamic, with a net immigration from Sweden to Norway throughout the study  
136 period. The demographic consequences of this mechanism haven't been explored so far, nor has  
137 the effect of such uneven spatial distribution of harvest intensity on the effectiveness of  
138 management strategies in the two countries.

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

- 143 - What was the effect of the harvest rate difference between the two countries, and of the  
144 resulting compensatory immigration process, on wolverine population growth rates in the  
145 Norwegian and Swedish portions of the population?
- 146 - Was such an effect similar at different distances from the Norwegian-Swedish national  
147 border?

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148 - To what extent does the compensatory immigration process influence the ability of the  
149 Norwegian management system to regulate the wolverine population growth rate and size  
150 in Norway?

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

154

155

## 156 **MATERIALS AND METHODS**

157 Vec-permutation models allow the demographic and spatial processes occurring each year in  
158 each portion of the population to be included separately, but within a holistic model (Hunter &  
159 Caswell, 2005). Given the relative complexity of the wolverine study case, we decided to first  
160 assess the general properties of a simple system. Then we applied a more realistic version of the  
161 same model to the case of the Scandinavian wolverine population. Accordingly, we initially  
162 constructed a 2-patch 2-stage model in R (R Development Core Team, 2008), using a post-  
163 breeding Leslie-Usher matrix (Caswell, 2001).

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

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169 one. The initial population size was set to 100 individuals in both patches, distributed according  
170 to the stable stage distribution (Caswell, 2001).

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

$$175 \quad \psi_{2,t} = \alpha \frac{(N_{2,t} - N_{1,t})}{(N_{1,t} + N_{2,t})}$$

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

181 Based on this model structure, harvest rate ( $h$ ) in patch one was expected to influence population  
182 growth rate in two ways: on one hand it reduced it by increasing the annual mortality rate of  
183 individuals in patch one; on the other hand, it increased the net dispersal rate from patch two to  
184 patch one, thus also increasing the resulting annual population growth rate in patch one. By  
185 simulating a range of  $h$  and  $\alpha$  values, we explored the net effect of these two interacting  
186 processes on the demography of the spatially structured population. We ran 1,000 model  
187 iterations, each of them parameterized with a different combination of values for the parameters  
188  $h$  and  $\alpha$ . We ran the model over a period of 25 years and evaluated its outcome in terms of the

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189 average population growth rate in patch one ( $\lambda_1$ ), in patch two ( $\lambda_2$ ) and in the whole population  
190 ( $\lambda_{tot}$ ). As the population matrix was updated at each time step, we estimated the above mentioned  
191 quantities following Tuljapurkar et al. (2003), as the  $n^{\text{th}}$  root of the ratio between population size  
192 in year  $n$  and population size in year one. For each iteration and year, we also estimated the  
193 number of individuals harvested in patch one, as the product between the harvest rate parameter  
194  $h$  and population size at time  $t$ . Finally, we performed a sensitivity analysis of population growth  
195 rates to variation in the harvest rate  $h$ , using a life-stage simulation analysis (Wisdom, Mills, &  
196 Doak, 2000). A full description of how the vec-permutation model was formulated is provided in  
197 Appendix 1.

198 After exploring the general dynamics of the simple 2-patch 2-stage model, we increased its  
199 structural complexity to apply it to the case of the south-central Scandinavian wolverine  
200 population. We initially constructed the model considering two patches (Norway and Sweden),  
201 two sexes, and 14 age classes. We also included two possible reproductive states (with cubs and  
202 without cubs) for the female segment of the population. Overall, the model comprised a total of  
203 42 stages for each country. Stages from 1 to 14 included reproducing females, from 15 to 28  
204 non-reproducing females, and from 29 to 42 they included males. Gervasi et al. (2015) have  
205 previously shown that only the individuals within 50 km from the Norwegian-Swedish border  
206 had a significant probability to disperse from one country to the other in a given year, so that the  
207 demographic effects of the compensatory immigration process were likely to be different at  
208 different distances from the national border. Therefore, in an effort to add spatial realism to the

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209 model, we sub-divided each of the two patches into five 50 km belts at increasing distances from  
210 the Norwegian-Swedish border (Fig 2).

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

228 To account for wolverine dispersal across the Swedish-Norwegian national border, and across  
229 the five 50-km belts in each country, we used the same density-dependent dispersal function as

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230 in the simpler version of the model, setting the slope parameter  $\alpha = 0.44$  (see Appendix 2 for  
231 details). We applied the function to all neighbouring 50-km belts in the model, using the  
232 difference in their local densities to produce a patch-to-patch dispersal rate. Dispersal in  
233 wolverines occurs to a different extent in all ages and for both sexes (Aronsson & Persson, 2018;  
234 Vangen, Persson, Landa, Andersen, & Segerström, 2001), but females tend to reduce their home  
235 range and be more sedentary when raising cubs. The dispersal process was therefore applied to  
236 males of all ages and to females without cubs, assuming that females with cubs would not  
237 disperse from their residential home range (Aronsson & Persson, 2018).

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

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

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

261

## 262 **RESULTS**

### 263 **Theoretical model**

264 The 2-stage 2-patch model, parameterized with no harvest in both patches, produced the same  
265 population growth rate  $\lambda_0 = 1.148$  in both portions of the population. When increasing harvest  
266 rate values were simulated in patch one, population trajectories in the two patches diverged  
267 depending on the strength of the compensatory immigration process. Under the hypothesis of no  
268 spatial connection between the two patches ( $\alpha = 0$ ), population growth rate decreased linearly for  
269 increasing harvest rate values in patch one, whereas it remained constant at the  $\lambda_0$  value in patch  
270 two (Fig. 3a and b). When dispersal and compensatory immigration were taken into account ( $\alpha =$   
271 0.2 and  $\alpha = 0.4$ ), population growth rate in patch one was always higher than in the previous  
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272 scenario (Fig. 3a), as a consequence of the density differential between the two patches, which  
273 generated the compensatory immigration process. Such differences in population growth rates  
274 increased for increasing harvest rate values. It was about 3% when the harvest rate was set at  
275 0.05 in patch one, but it increased to 15% for  $h = 0.2$ . Conversely, population growth rate in  
276 patch two was always lower than  $\lambda_0$ , even though no harvest occurred in this portion of the  
277 population (Fig. 3b). When looking at the process from the perspective of the total population,  
278 the net effect of the compensatory immigration process was to reduce its overall growth rate  $\lambda_t$ ,  
279 by up to a 44% reduction in the scenario including the highest simulated harvest rate and the  
280 strongest density-dependent dispersal ( $h = 0.2$ ,  $\alpha = 0.4$ ; Fig. 3c). The source-sink dynamic  
281 initiated by the differential harvest rates in the two patches of the continuous population was not  
282 a simple transfer of individuals from one portion of the population to the other. On the contrary,  
283 it induced a reduction in the overall population performance, by promoting immigration from an  
284 area at lower risk of mortality to one with a higher.

285 The compensatory immigration process also had an influence on the relationship between the  
286 number of individuals harvested each year in patch one and the resulting population growth rate.  
287 Under the  $\alpha = 0$  scenario, the removal of 15 individuals per year was sufficient to keep the  
288 population in patch one substantially stable ( $\lambda_I = 1.01$ ; Fig. 4). When considering the source-sink  
289 dynamic induced by the compensatory immigration process ( $\alpha = 0.2$  and  $\alpha = 0.4$ ), the same  
290 number of annual removals corresponded to  $\lambda_I = 1.06$  and  $\lambda_I = 1.08$ , respectively (Fig. 4). In  
291 these two cases, 23 and 26 annual removals were necessary, respectively, in order to keep the

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292 population stable, with a 53-73% increase in the effort required to reach the same management  
293 goal.

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

302

### 303 **The wolverine case study**

304 When parameterized with the vital rates estimated for the Scandinavian wolverine population  
305 (see Tab. 1), the model showed a good fit with the capture-recapture based population trends at  
306 the national level in both countries (Fig. 5). In Norway the population model produced an  
307 average growth rate of  $\lambda = 1.00$ , close to the 1.01 previously estimated for the same population  
308 and study period (Gervasi et al., 2016). In Sweden the two approaches provided the same  
309 estimate of  $\lambda = 1.10$ . In Norway, the population size in 2005 was estimated at 112 individuals  
310 (Gervasi et al. 2016). When accounting for the existence of a compensatory immigration process,  
311 the model generated a stable population over the 8-year period and a final population size of 113  
312 individuals (Fig. 6a), about 28% higher than the population goal of 88 individuals (14

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313 reproductions; Brøseth, Tovmo, & Andersen, 2012, Anon 2013). The exclusion of the  
314 compensatory immigration process generated a  $\lambda=0.980$  and a final population size of 96  
315 individuals, about 15% lower than in the other scenario and 9% higher than the management  
316 goal. In Sweden, the wolverine population grew at the rate of about 11% each year ( $\lambda = 1.108$ ).  
317 The effect of the compensatory immigration process corresponded to a 0.024 reduction in the  
318 annual population growth rate (Fig. 6b). When excluding the dispersal process, the population  
319 grew at the rate of about 13% each year ( $\lambda = 1.132$ ), with a final population size in 2012 of 115  
320 individuals (16% higher than the observed 99; Fig. 6b).

321 The influence of compensatory immigration on population growth rate was stronger closer to the  
322 Norwegian-Swedish border, but rather weak when moving away from it. In zone N<sub>5</sub>, which  
323 corresponded to the 50-km belt closest to the border on the Norwegian side, growth rate was 0.04  
324 higher when accounting for dispersal from Sweden than when disregarding it (Fig. 7). Similarly,  
325 in zone S<sub>1</sub>, which corresponded to the 50-km belt closest to the border in Sweden, dispersal to  
326 Norway caused a 0.03 reduction in  $\lambda$  (Fig. 7). At the other extreme, zones N<sub>1</sub> and S<sub>5</sub>, which were  
327 the most distant from the national border, only exhibited a 0.01 or lower variation in the annual  
328 zone-specific growth rate as a consequence of the compensatory immigration process (Fig. 7).

329 During the 8 years of the study periods, an average of 33.4 wolverines were shot per year in  
330 southern Norway, which corresponded to  $\lambda = 1.00$ . If no density-dependent dispersal from  
331 Sweden had occurred, removal of 28.2 wolverines per year would have been sufficient to  
332 generate the same population growth rate. In other terms, about 15.5% of all the individuals

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333 harvested in Norway between 2005-2012 were replaced by immigrants, and also causing an  
334 unintended decrease in population growth rate in Sweden.

335

## 336 **DISCUSSION**

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

343 Our study shows that the dynamics occurring across administrative borders can also influence,  
344 and sometimes frustrate, the achievement of management goals and the effective use of the  
345 available economic resources. In this sense, the theoretical and applied approach provided  
346 complementary insights into the effect of compensatory immigration. The simpler and more  
347 general version of the vec-permutation model provided three main results : 1) the source-sink  
348 dynamics induced by different harvest regimes on the two sides of a border can reduce the  
349 overall population growth rate; 2) such a difference in harvest intensity can increase the number  
350 of removals necessary to achieve a certain population goal; and 3) the overall effect of this type  
351 of process is to reduce harvest efficiency in the country with the highest harvest intensity, as part  
352 of the effort in lethal control produces demographic effects in the neighbouring country, and not  
353 locally. From a demographic point of view, the patterns emerging from the theoretical vec-

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354 permutation model are in line with the previously demonstrated general stabilizing effect of  
355 migration in subdivided populations (Lebreton & Gonzalez-Davila, 1993). When two portions of  
356 a population have different intrinsic growth rates, because of a difference in the underlying  
357 demographic parameters, density-dependent migration has the effect of reducing both the overall  
358 population growth and the difference in patch-specific growth rates (Lebreton, 1996). However,  
359 the sensitivity analysis (Tab. 2) shows that this effect is strongly dependent on the strength (and  
360 likely on the shape) of the density-dependent dispersal process. Therefore, while our approach  
361 provides a flexible framework for a wide variety of wide-ranging species, particular care should  
362 be used in identifying an appropriate mathematical description of the link between density and  
363 dispersal rates. No generalizations can be easily made, as dispersal has been shown to be  
364 sometimes directly positively (Herzig, 1995) and sometimes inversely (Woodroffe, Macdonald,  
365 & Da Silva, 1993) related to population density, but also highly affected by other factors not  
366 related to density or competition (Waser, 1985).

367 By promoting dispersal from an area with low mortality to an area with high mortality, without  
368 reaching an equilibrium point between additions and subtractions, compensatory immigration  
369 creates the conditions for the establishment of an ecological trap *sensu* Dwernychuk & Boag  
370 (1972). Ecological traps, also defined as attractive sinks, are areas in a species' distribution in  
371 which high suitability and high mortality risks overlap (Battin, 2004). These areas usually attract  
372 individuals from the surroundings, thanks to the availability of food, cover, mating opportunities,  
373 and other crucial resources. At the same time, they reduce individual survival because of a  
374 localized mortality risk which is not correlated with the otherwise high suitability of the area.

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375 Attractive sinks can threaten the conservation of small endangered populations (Nielsen,  
376 Stenhouse, & Boyce, 2006), in particular in those ecosystems where human-related mortality  
377 risks have become predominant (Battin, 2004).

378 In our case, the attractive sink was initiated and maintained by the local density gradient across  
379 the Norwegian-Swedish national border, resulting from the differential harvest regimes in the  
380 two countries. This situation attracted wolverines to the area in which competition for resources  
381 was likely lower, which was also the area in which mortality risks were higher (Gervasi et al.,  
382 2015). Our results show that, besides having consequences on population persistence and  
383 extinction risk, attractive sinks can also affect the costs and benefits of a given management  
384 strategy, when lethal control is used as a tool to limit population size and growth. On average,  
385 one in every six wolverines shot in Norway during the study period was replaced by another  
386 wolverine immigrating from the Swedish side of the border. Given the high costs associated with  
387 lethal control of large carnivores, and the polarized debate about its ethical and legal aspects, this  
388 type of practice should be carefully evaluated before setting national harvest rates to levels that  
389 could initiate and maintain a transboundary source sink-dynamic, especially when a  
390 neighbouring country exerts a lower harvest pressure on its portion of the shared population.

391 This is a rather common and widespread situation in European large carnivore populations, as  
392 about 40% of them are shared between countries that apply contrasting management regimes  
393 when it comes to lethal control (Kaczensky et al., 2012). The Alpine wolf population, shared  
394 between France and Italy is a well-known example of such a case, as the French legislation  
395 allows a yearly quota-based culling, whereas the Italian one does not (Kaczensky et al., 2012).

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396 Similar examples of contrasting management regimes are provided by the Dinaric-Balkan and  
397 North-Western Iberian wolf populations, or by the Scandinavian lynx (*Lynx lynx*) population,  
398 which are either protected or harvested in specific national portions of their distribution  
399 (Kaczensky et al., 2012). From an international perspective, one of the consequences of the  
400 Swedish-Norwegian compensatory immigration process was also that part of the effort  
401 performed by the Norwegian management system in reducing wolverine population growth rate  
402 in Norway actually produced a reduction on the Swedish side of the border (33% reduction in the  
403 overall population growth over the study period; see Fig. 6b). This highlights that, when a  
404 population is shared among two or more countries, the consequences of management decisions  
405 are also transboundary, even though the political bodies which are in charge of those decisions,  
406 the stakeholders who influenced them, and the taxpayers who financed them are not. However,  
407 some differences in management goals between neighbouring countries are unavoidable, for  
408 multiple reasons: *i*) the material conflict between humans and large carnivores is sometimes  
409 different between neighbouring countries, depending for example on the different importance of  
410 farming and livestock herding in the national economic system. Sheep farming, for example, has  
411 a higher economic and social importance in Norway than in Sweden, creating the conditions for  
412 different levels of potential material conflict (Swenson & Andrén, 2005); *ii*) even when the  
413 material conflict is similar, people from different countries often have a different perception of  
414 the potential threat that large carnivores represent to their property or values, depending on their  
415 social, cultural and historical context. People living in larger communities have been shown to be  
416 in general more positive towards large carnivores than those from small rural communities

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417 (Røskaft et al., 2007). This is the case when comparing the Swedish and Norwegian contexts,  
418 with the first exhibiting a higher level of urbanization than the second (United Nations, 2015);  
419 *iii*) Governments of different political orientation can generate contrasting management policies  
420 in neighbouring countries, in order to achieve different political goals. Therefore, while agreeing  
421 on a common management policy at the population level would be desirable from the point of  
422 view of management efficiency, it might not always be easy to implement in practice. It's  
423 important, though, that managers and citizens be informed about the ecological and economic  
424 consequences of a difference in management goals with a neighbouring country and take these  
425 effects into account (Reljic et al. 2018), especially when limited resources are available to  
426 promote coexistence between humans and large carnivores. In practical and applied terms, we  
427 recommend that policy integration and transboundary communication be promoted between  
428 countries sharing portions of the same large carnivore population. Such integration should  
429 include population monitoring, through the standardization of methods and data sharing (Gervasi  
430 et al. 2016), and also the political processes that lead to the establishment of national population  
431 goals and management strategies. Such integration is already going on for the Scandinavian  
432 wolverine population, which is now monitored through a shared and standardized monitoring  
433 program in Norway and Sweden, which makes use of a common field methodology and of a  
434 shared database of all DNA-sampled individuals which facilitated our analysis (Brøseth et al.,  
435 2012). This model should be further extended to other similar cases and large carnivore  
436 populations in other parts of the continent.

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

453 Ultimately, the results of our study underline the need to consider both sides of large carnivore  
454 population management: on one hand, it would be advisable that the general goals of large  
455 carnivore management be set at the population (and therefore often international) level, to avoid  
456 a waste of economic resources and to maintain a balance between the investment in each country  
457 and the resulting demographic trends. On the other hand, local factors should also be considered

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458 when dealing with the consequences of the general management strategies, accounting for the  
459 fact that citizens inhabiting different local contexts will be affected to a different extent by the  
460 consequences of larger scale management decisions. This reflects the great challenge at the heart  
461 of large carnivore management: the need to develop institutional structures and procedures that  
462 can simultaneously coordinate actions at international scales while remaining flexible enough to  
463 deal with local level considerations (Linnell, 2015; Linnell & Kaltenborn, 2019).

464

#### 465 **AUTHORS' CONTRIBUTIONS**

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

470

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477

#### 478 **DATA ACCESSIBILITY**

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479 All the data used for the analyses present in this article was previously published on peer-  
480 reviewed journals. In particular, most input parameters for the wolverine population model were  
481 derived from Gervasi et al. (2015) and Rauset et al. (2015). The R code to build and run the vec-  
482 permutation matrix model is stored in Gervasi V., Linnell J.D.C, Brøseth H., Gimenez O. (2019)  
483 Data from: Failure to coordinate management in transboundary populations hinders the  
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Parameter	Value / Interval		Source
	Norway	Sweden	
Reproduction probability	0 – 0.7	0 – 0.7	Rauset et al. 2015
Litter size <sup>a</sup>	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) <sup>b</sup>	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	<a href="http://www.rovdata.no">www.rovdata.no</a>
Initial Population size	112	48	Gervasi et al. 2016
Strength of the density-dependent dispersal ( $\alpha$ )	0.44	0.44	Gervasi et al. 2015

<sup>a</sup> Refers to the number of cubs still alive in the first week of June.

<sup>b</sup> Refers to the period between 3 and 12 months of age.

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

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	$\alpha = 0$	$\alpha = 0.2$	$\alpha = 0.4$
$\lambda_1$	-1.41	-0.75	-0.71
$\lambda_2$	0.00	-0.27	-0.40
$\lambda_{tot}$	-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 ( $\lambda_1$ ), in the non-harvested patch ( $\lambda_2$ ) and for the whole population ( $\lambda_{tot}$ ) under three scenarios of increasing strenght in the density-dependent dispersal function, controlled by the parameter  $\alpha$ .

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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.

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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

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Norwegian-Swedish border (continuous grey line). The E14 highway marking the northern border of the study area is also shown (grey dotted line).

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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 increasing strength in the density-dependent dispersal function, controlled by the parameter  $\alpha$ .

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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 increasing strength in the density-dependent dispersal function, controlled by the parameter  $\alpha$ .

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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.

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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.

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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*)

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population in south-central Scandinavia, during the period 2005-2012. Zones N<sub>1</sub>-N<sub>5</sub> refer to the Norwegian portion of the population (see Fig. 2), S<sub>1</sub>-S<sub>5</sub> to the Swedish portion.

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## 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.

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