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► **To cite this version:**

Malory Randon, Christophe Bonenfant, Jacques Michallet, Thierry Chevrier, Carole Toïgo, et al.. Population responses of roe deer to the recolonization of the French Vercors by wolves. *Population Ecology*, 2020, 62 (2), 10.1002/1438-390X.12043 . hal-02495932

**HAL Id: hal-02495932**

**<https://hal.science/hal-02495932v1>**

Submitted on 19 Nov 2020

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15

16

17 **Abstract**

18 In a context of changing carnivore populations worldwide, it is crucial to understand the  
19 consequences of these changes for prey populations. The recolonization by wolves of the French  
20 Vercors mountain range and the long-term monitoring (2001-2017) of roe deer in this area provided  
21 a unique opportunity to assess the effects of wolves on this prey. Roe deer was the main prey of  
22 wolves in the west Vercors mountain range during this recolonization. We compared roe deer  
23 abundance and fawn body mass in two contrasted areas of a wolf pack territory: a central area (core  
24 of the territory characterized by an intense use by wolves) and a peripheral area (used more  
25 occasionally). Roe deer population growth rates were lower in the central area between 2001 and  
26 2006, resulting in a decline in roe deer abundance. Roe deer abundance substantially dropped in the  
27 two study areas after an extremely severe winter but the abundance of roe deer in the central area  
28 facing with wolves was slower to recover and remained at lower abundance levels for 6 years. Fawn  
29 body mass was consistently lower in the central area, varied similarly as roe deer abundance, and  
30 was not influenced by weather conditions or red deer population abundance. Altogether, the effects  
31 of wolves on roe deer in the central area occurred during a 10-year period following the  
32 establishment of wolves, through the interplay between wolf predation (before wolves started  
33 preying on red deer), harsh winter conditions and possibly naivety of prey to this recolonizing  
34 predator.

35

36 **Key words:** body mass, *Canis lupus*, *Capreolus capreolus*, population abundance, predation.

## 37 **Introduction**

38 For large herbivores, the main drivers of population dynamics have been studied in great detail over  
39 the last few decades (e.g. Coulson et al. 2001; Gaillard et al. 2013 for case studies). The  
40 consequences of density, weather, habitat quality or hunting on age-specific survival and  
41 reproduction are well documented in many species, with increasing empirical evidence of  
42 interactions among these factors (Bonenfant et al. 2009; Hone and Clutton-Brock 2007). Predation is  
43 clearly a major driver of evolution and population dynamics of prey (Reznick et al. 2004; Volterra  
44 1931). Understanding and measuring the consequences of predation on the population dynamics of  
45 large herbivores is, however, much more complex than for most other environmental variables.  
46 Consequently, important ecological questions such as whether large herbivores are undergoing  
47 bottom-up or top-down limitation are still debated (Hopcraft et al. 2010; Laundré et al. 2014).

48 By increasing mortality, predators are strongly expected to limit the population growth rate  
49 of their prey. However, there are several arguments suggesting that prey populations can withstand  
50 strong predation pressure. If predation is compensatory because of density-dependence, prey  
51 population dynamics may remain little affected until attack rates become really high and predation  
52 becomes additive to other sources of mortality (Errington 1946). Similarly, the difference in spatial  
53 scale between the ranging behaviour of large carnivores and herbivores leads to differences in  
54 densities of several orders of magnitude between predators and prey (Skogland 1991). Consequently,  
55 large predators may have limited consequences for population growth rate of prey. This is  
56 particularly the case if predators are generalists and can switch between different prey species  
57 (Murdoch 1969). This is also the case if predators select juvenile or senescent individuals because the  
58 population growth rate of large herbivores is most sensitive to variation in the survival of prime-aged  
59 adults (Gaillard et al. 2000). However, highly specialized predator species or individuals can clearly  
60 reduce population growth rate and the abundance of large herbivores (Bourbeau-Lémieux et al.  
61 2011; Festa-Bianchet et al. 2006). For instance, roe deer *Capreolus capreolus* dynamics are markedly

62 affected by lynx *Lynx lynx* predation (Andrén and Liberg 2015; Heurich et al. 2012) particularly so in  
63 winter when snow depth is thick, which greatly limits roe deer mobility (Heurich et al. 2012).

64 Evidence has also accumulated in the past decades about the numerous anti-predation  
65 behaviours that prey have evolved such as grouping (Fortin et al. 2009), vigilance (Creel et al. 2014),  
66 habitat shift (Courbin et al. 2016), and temporal niche shift (Valeix et al. 2009a) that may affect  
67 foraging behaviour (Barnier et al. 2014). However little is known about the consequences of these  
68 behaviours in large mammals and on the overall non-lethal effects of predators on their prey, that is  
69 the decrease of prey performance generated by the presence of a predator and hence, not involving  
70 killing and prey consumption (Creel et al. 2007, Middleton et al. 2013; review in Say-Sallaz et al.  
71 2019).By

72 In a context of rapidly changing abundance and distribution of large carnivore populations  
73 worldwide (Chapron et al. 2014; Ripple et al. 2014), it is important to understand the consequences  
74 of these changes for prey populations and ultimately for ecosystem functioning. Even though studies  
75 on these consequences have accumulated over the past decades, most of our current knowledge  
76 comes from studies in North American National Parks, and particularly from the grey wolf *Canis lupus*  
77 and elk *Cervus canadensis* of the Greater Yellowstone Ecosystem (Kuijper et al. 2016; Say-Sallaz et al.  
78 2019). There is thus a need for studies from different contexts, particularly in Europe where large  
79 carnivores live in or are recolonizing anthropogenic landscapes (Chapron et al. 2014). Further,  
80 whether prey have continuously co-evolved with their predator or have evolved in a predator-free  
81 environment for several generations due to predator extirpation from some ecosystems may  
82 ultimately influence the extent to which prey are vulnerable to predators (Berger et al. 2001; Byers  
83 1997). Indeed, naive prey may fail to recognise the cues of a novel predator (but see Chamaillé-  
84 Jammes et al. 2014) or may fail to respond appropriately and effectively to the risk of predation by  
85 this predator due to the lack of experience (Banks and Dickman 2007; Carthey and Banks 2014). For  
86 instance, along brown bear *Ursus arctos* recolonization fronts, brown bears killed adult moose *Alces*  
87 *alces* at disproportionately high rates compared to sites where brown bears have always been

88 present (Berger et al. 2001). However, very little is known on how naive prey respond to recolonizing  
89 predators and how quickly they become effective at efficiently escaping these predators.

90 In 1992, wolves crossed the Italian border to recolonize eastern France from where this  
91 predator had been missing for ca. 100 years (Valière et al. 2003; Supporting Information 1). In this  
92 work, we preliminarily checked that roe deer is an important prey for wolves during this  
93 recolonization. We then used the long-term monitoring (17 years) of roe deer in the west Vercors  
94 mountain range covering contrasting areas in terms on wolf occupancy to assess the effects of  
95 wolves on roe deer. If predation by wolves and the associated predation risk affect roe deer, we  
96 expect a decrease in the roe deer population abundance and growth rate, and a decrease in roe deer  
97 fawn body mass, following the return of wolves.

98

99

## 100 **Materials and Methods**

101

### 102 ***Study area***

103 The study was carried out between 2001 and 2017 over a study area of 30 776 ha encompassing six  
104 neighbouring counties (Bouvante (8 431 ha), La Chapelle-en-Vercors (4 562 ha), Vassieux-en-Vercors  
105 (4 798 ha), Saint-Julien-en-Vercors (1 867 ha), Saint-Martin-en-Vercors (2 700 ha), Saint-Agnan-en-  
106 Vercors (8418 ha)) in the French department of Drôme, in the west Vercors mountain range (Fig. 1).

107 The west Vercors mountain range is characterized by an Alpine climate (identical to the Northern  
108 Alps) with a forest dominated by beech *Fagus sylvatica* and silver fir *Abies alba*. The large herbivore  
109 community is composed of roe deer, red deer *Cervus elaphus*, chamois *Rupicapra rupicapra*, mouflon  
110 *Ovis gmelini*, and wild boar *Sus scrofa*. The six counties are used by people for agriculture, livestock  
111 breeding, forestry, hunting, and outdoor recreational activities (see Supporting Information 2(a) for  
112 detail on land use type). The mean altitude is 1,110m (range: 305m-1,729m; see Supporting  
113 Information 2(b) for detail by county).

114

115 ***History of wolf presence in the west Vercors mountain range***

116 Wolves were extirpated from the Drôme department in 1901 (Faton and Ladreyt 1982). In 1998, the  
117 first field evidence from prey carcasses, tracks and faeces suggesting the return of wolves from the  
118 Italian Alps to the west Vercors mountain range were found (Valière et al. 2003). The ONCFS (French  
119 National Hunting and Wildlife Agency) network “Grands Prédateurs” later confirmed the permanent  
120 occupancy (3 individuals identified based on DNA analyses) and reproduction of wolves in the west  
121 Vercors mountain range in 2003/2004 (ONCFS 2006). At this early stage of the recolonization, only  
122 lone wolves or single pairs were observed. Since 2007/2008, wolves form packs of a minimum of five  
123 individuals. In this study, we contrasted two main study areas based on the intensity of use by  
124 wolves. The central area is the core of the west Vercors wolf pack territory (central area hereafter),  
125 and encompasses the counties of Bouvante, Vassieux-en-Vercors and the western sector of La  
126 Chapelle-en-Vercors (Fig. 1). The central area is characterized by an intensive use of the area by  
127 wolves where sightings of wolves, wolf tracks, and wild prey carcasses are frequently reported. In  
128 contrast, the peripheral area is used by wolves more occasionally, and encompasses the eastern  
129 sector of La Chapelle-en-Vercors, Saint-Julien-en-Vercors, Saint-Martin-en-Vercors, and Saint-Agnan-  
130 en-Vercors (Fig. 1). We extracted data on land use type from the Corine Land Cover 2006 database  
131 (Table 1 for summarized information for the 2 study areas; Supporting Information 2(a) for detailed  
132 information by county). The central and peripheral areas differ in terms of land use type ( $\chi^2=4711.1$ ;  
133  $p = 0.0005$ ) but the main change is that the central area mostly includes broad-leaved forests,  
134 whereas the peripheral area is dominated by coniferous forests (Table 1). Agricultural lands  
135 represent a low proportion of land use types in both study areas (Table 1).

136

137 ***Weather data***

138 We obtained weather data (daily rainfall and mean daily temperature) from Météo France for the  
139 weather station La Chapelle-en-Vercors. It is the only existing weather station in the two study areas

140 as they are very close geographically (see scale on Fig. 1) and the weather is not likely to differ  
141 between the two study areas. The weather indices calculated below are therefore average weather  
142 indices considered to be representative of the weather of the west Vercors mountain range, and  
143 hence they are the same for the two study areas. We calculated the Gausсен index (i.e. the amount  
144 of precipitation minus twice the mean temperature) to measure the water deficit of plants in spring  
145 (April-June) and summer (July-August) (e.g. Gaillard et al. 1997; Garel et al. 2004) to which roe deer  
146 are particularly susceptible (Pettorelli et al. 2005). The Gausсен index is a proxy of the balance  
147 between rainfall and evapo-transpiration of plants (Gausсен and Bagnouls 1953). High values of the  
148 Gausсен index mean positive water balance, higher plant growth, and hence better foraging  
149 conditions for large herbivores, and conversely (Toïgo et al. 2006). Winter can be very long in the  
150 west Vercors mountain range so this season was defined from October to March. To characterize  
151 winter conditions, we collected information on snow-fall, snow depth, and number of days with  
152 snow cover from the local skiing resorts in Bouvante. Because of the strong correlation existing  
153 among winter variables, we performed a Principal Component Analysis (PCA) on these standardized  
154 variables. The first principal component (PC1) accounted for 62% of the overall variance, so we used  
155 the point projections on PC1 as a winter harshness index. Low values of this index were associated  
156 with severe winters and hence more difficult conditions for roe deer as harsh winters are generally  
157 associated with a lower survival of fawns (Gaillard et al. 1993), especially at high latitude/elevation,  
158 and costly movements for large herbivores (Parker et al. 1984), which, in turn, could increase  
159 predation rates (Mech et al. 2001).

160

### 161 ***Predation by wolves***

162 Large herbivore carcasses due to predation by wolf were recorded in the study areas between 1998,  
163 when the first carcass was attributed to wolf predation, and 2010, when predation by wolf was  
164 common and not reported any more. Carcass report only took place in the winter months (October  
165 to March) when snow allowed easier detection of carcasses. Because the return of the wolf was of



166 high concern to local people (most of them being hunters), any wildlife carcass found during that  
167 period was reported to the “Fédération Départementale des Chasseurs de la Drôme” (local hunting  
168 agency in charge of game management in the study area). Qualified staff then performed autopsy of  
169 the carcasses, identifying species and confirming whether they were due to wolf predation.

170

### 171 ***Roe deer abundance***

172 We monitored the abundance of roe deer after winter, in March-April, when vegetation flush has not  
173 started yet, along roads known to be practicable at that time of the year. This monitoring was carried  
174 out in 5 of the 6 study counties because deep snow cover made most roads in Bouvante county  
175 inaccessible at the time of surveys in all years. We drove along 3 transects located in the central area  
176 (1 transect in the western sector of La Chapelle-en-Vercors and 2 transects in Vassieux-en-Vercors)  
177 and 3 transects in the peripheral area (1 transect in Saint-Agnan-en-Vercors, 1 transect across St-  
178 Julien-en-Vercors and St-Martin-en-Vercors, and 1 transect in the eastern sector of La Chapelle-en-  
179 Vercors – see Fig. 1). Ninety percent of the total transect length included departmental roads, which  
180 were regularly snow-cleared and intensively used by cars. The remaining 10% was forest roads.  
181 Previous works suggest that wolves select trails and low-use roads, but avoid highly used roads  
182 (Fahrig and Rytwinski 2009; Theuerkauf et al. 2003; Whittington et al. 2009). It is thus unlikely that  
183 wolves preferentially used transects we sampled for monitoring roe deer abundance. We carried out  
184 counts at night with a powerful spotlight reflecting animals’ eyes. We drove transects at low speed  
185 (10-15 km/h) with one driver, two observers who spotted and identified all animals seen, and one  
186 person who recorded the observations. Spatial information was not available for the observations for  
187 the whole study period so habitat covariates could not be taken into account in the subsequent  
188 analyses. However, transects sampled similar habitats in the two study areas (central area: 80% of  
189 forests, 15% of pastures or agricultural lands, and 5% of natural open areas; peripheral area: 84% of  
190 forests, 15% of pastures or agricultural lands, and 1% of natural open areas). We repeated counts  
191 twice a year between 2001 and 2004, three times a year between 2005 and 2012, and four times a

192 year since 2013. For the central and peripheral areas, we obtained an abundance index of roe deer  
193 population (AI) by calculating the mean number of roe deer seen per kilometre (see Pellerin et al.  
194 2017 for a similar approach applied to diurnal car counts). Although spotlight counts do not allow  
195 accurate assessment of roe deer population size and are unlikely to detect small changes in  
196 population abundance (Cederlund et al. 1998), this method can still be used to detect marked  
197 changes in population abundance.

198

### 199 ***Red deer abundance***

200 Roe deer suffer competition from red deer (Richard et al. 2010). Red deer observations were also  
201 recorded during the roe deer spotlight counts described above. Hence, for the central and peripheral  
202 areas, we were able to obtain an abundance index of red deer population (AI) by calculating the  
203 mean number of red deer seen per kilometre. Contrary to the roe deer case, spotlight counts have  
204 been shown to be a reliable method to monitor population abundance of red deer (Garel et al. 2010).

205

### 206 ***Roe deer fawn body mass***

207 Twenty local hunting associations (which encompass 500 hunters) contributed to this study and were  
208 equipped with a digital scale with an accuracy of 100 grams to weigh hunted roe deer. Between 2002  
209 and 2007, hunters measured the full body mass of harvested roe deer, but have switched to dressed  
210 body mass (i.e. guts, liver, heart and lungs removed) since 2007. Between 2007 and 2009, 43 local  
211 hunting associations in the whole Drôme department were asked to measure both full and dressed  
212 body masses. From a sample of 170 roe deer with the two measurements, we checked that a close  
213 relationship existed between dressed and full body masses (dressed body mass =  $(0.837 \times \text{full body mass}) - 1.054$ ;  $R^2 = 0.92$ ) and used this relationship to estimate dressed body mass of roe deer  
214 harvested during 2002-2007. We used dressed body mass in all subsequent analyses. Because roe  
215 deer are income breeders with limited fat reserves (Andersen et al. 2000), and variation in adult body  
216 mass is mainly caused by early-life conditions (Pettorelli et al. 2002), we analyzed body mass of roe  
217

218 deer fawns (individuals < 1 year when shot). We excluded body mass data from la Chapelle-en-  
219 Vercors because the exact locations of where animals were shot were not recorded, which prevented  
220 us from assigning the hunted roe deer of this county to the central vs. peripheral area.

221

222

## 223 **Analyses**

### 224 ***Predation by wolves***

225 We calculated the percentage that roe deer represented in the large herbivore carcasses attributed  
226 to predation by wolves. We then compared if the distribution of the carcasses differed in terms of  
227 large herbivore species between the early stage of the recolonization, when only lone wolves or  
228 single pairs were observed, and the later stage of the recolonization, when wolves formed a pack of a  
229 minimum of five individuals, using a  $\chi^2$  test with bootstrap p-value calculation.

230

### 231 ***Roe deer population abundance and growth rate***

232 We analysed variation in roe deer abundance (assessed using the AI) in time with a state-space  
233 model to tease apart sampling from process variances (also known as Kalman filter; de Valpine and  
234 Hastings 2002) in its Bayesian formulation (Kéry and Schaub 2011). We built a Generalised Linear  
235 Models (GLMs) setting a logarithmic link function and a negative binomial distribution. We opted for  
236 a negative binomial distribution because the model with a Poisson distribution did not fit the data  
237 well (goodness-of-fit test:  $\chi^2 = 1\,451.71$ ,  $df = 287$ ,  $P < 0.001$ ) resulting from over-dispersed count data  
238 (ver Hoef and Boveng 2007). Even if we did our best not to change the road count protocol, transect  
239 length did vary among years and across transects. We included an offset variable (log-transformed  
240 number of kilometres) to account for this heterogeneity in the length of the driven transects. Our  
241 observation process equation hence was:

$$\ln(AI_{z,t}) = \mu + \ln(km) + B_t \times year + B_z \times wolf\ area + B_i \times year \times wolf\ area,$$

242 where  $AI_{z,t}$  is the number of observed roe deer in each transect per year,  $\mu$  is the intercept,  $B_t$  are the  
243  $t-1$  coefficients of the variable ‘year’ (a categorical variable with 16 levels),  $B_z$  is the effect of the  
244 variable ‘wolf area’ (a 2-level categorical variable: “central area” vs. “peripheral area”), and  $B_i$  are the  
245 coefficients for the interaction between ‘time’ and ‘wolf area’. Corresponding to the state process of  
246 our model, the predicted number of roe deer seen per km  $\hat{AI}_{z,t}$  was then linked to the unobserved  
247 variable  $D_{z,t}$  by the following equation:

$$\ln(D_{z,t}) \sim N(\ln(\hat{AI}_{z,t}), \sigma_{proc}^2)$$

248 where  $D_{z,t}$  is a normally distributed random variable of mean  $\hat{AI}_{z,t}$  and variance  $\sigma_{proc}^2$ . This baseline  
249 state-space model hence returns  $D_{z,t}$  the predicted roe deer abundance per km, accounting for the  
250 sampling variance of the counts.

251 We first investigated differences in roe deer abundance in time and between the central and  
252 peripheral areas by modelling  $D_{z,t}$  as a function of ‘year’, ‘wolf area’, and the interaction term  
253 between the effects of ‘year’ and ‘wolf area’. We selected the best model describing the spatio-  
254 temporal variation of  $D_{z,t}$  with the Widely Applicable Information Criterion (WAIC; Vehtari et al. 2017;  
255 Watanabe 2010). The lower the WAIC is, the better the compromise between the relative fit of the  
256 model and the number of parameters entered to describe the data is. We calculated 95% credible  
257 intervals for predicted abundance without any attempt to model spatial autocorrelation of  
258 observations because the exact location of seen roe deer was not recorded during the protocol. We  
259 then assessed whether there were contrasted periods in terms of roe deer population abundance by  
260 modelling and  $D_{z,t}$  as a function of ‘year’, ‘wolf area’, and the interaction term between ‘wolf area’  
261 and ‘period’, with ‘period’ (a three-level categorical variable with ‘period 2001-2005’ the beginning of  
262 wolf settlement when they were either alone or in pairs and preyed mainly on roe deer (see results),  
263 ‘period 2006-2010’ the establishment of wolf packs and the increase in red deer consumption (see  
264 results), and ‘period 2011-2016’ the period with wolf packs of a minimum of 5 individuals clearly  
265 established and preying mainly on red deer).

266 We derived the annual population growth rate in each wolf area ( $r_{z,t}$ ) from our baseline state-  
 267 space model with a simple exponential demographic model linking roe deer abundance at  $t$  and  $t+1$   
 268 (see Knappe et al. 2011 for a similar approach). This was achieved by adding the following constraints  
 269 on  $D_{z,t}$ :

$$D_{z,t+1} = r_{z,t} + D_{z,t},$$

$$r_{z,t} \sim N(\bar{r}, \sigma_r^2)$$

270 where the annual growth rate  $r_{z,t}$  is a normally distributed random variable with mean  $\bar{r}$  and variance  
 271  $\sigma_r^2$ . Note that we ended up with  $t-1$  estimates of annual growth rates in each area. We first tested  
 272 whether roe deer population growth rates differed among periods, once the yearly variation was  
 273 accounted for, by fitting the following model:

$$r_{z,t} = B_t \times year + B_z \times wolf\ area + B_i \times wolf\ area \times period$$

274 whereby  $B_t$  are the coefficients of the variable 'year',  $B_z$  the coefficients of the variable 'wolf area',  
 275 and  $B_i$  the coefficients for the interaction between 'wolf area' and 'period'. We then tested the  
 276 association between an ecological variable and  $r_{z,t}$  with an additional level of analysis in the state-  
 277 space model:

$$r_{z,t} = \gamma_0 + \gamma_1 \times E_{z,t} + \epsilon_{z,t}$$

278 where  $\gamma_0$  and  $\gamma_1$  are the intercept and slope of the effect of variable  $E$  on the annual  
 279 population growth rate, respectively. The four different ecological variables  $E$  we considered were  
 280 winter harshness index, spring and summer Gaussens indices, and the red deer abundance. We  
 281 concluded to the statistical significance of the different ecological variables on  $r_{z,t}$  if the 95% credible  
 282 interval of the posterior MCMC (Monte Carlo Markov Chains) distribution of the  
 283 corresponding  $\gamma_1$  excluded 0. Modelling the interaction between 'wolf area' and the environmental  
 284 variable is straightforward and we proceeded the same way to test its statistical significance.

285 We implemented the Bayesian state-space model on roe deer abundance using JAGS  
 286 (Plummer 2003). We ran all models with 50 000 iterations, 3 MCMC, and a burn-in stage of 30 000  
 287 iterations. With a thinning factor of 5, we estimated the posterior distributions of model parameters

288 from a 5 000 MCMC samples and report the mean and its associated 95% credible intervals. We  
289 checked model convergence graphically, looking for a good mixing of MCMC chains, in combination  
290 with the Rhat statistic (Brooks and Gelman 1998), which should read 1 at convergence for all  
291 estimated parameters. All distributions for priors were flat and non-informative. The JAGS code of  
292 our baseline model is provided in Supporting Information (Supporting Information 3).

293

294

### 295 ***Fawn body mass***

296 We analysed fawn body mass of roe deer using Gaussian linear models. All models consistently  
297 included both sex (a 2-level categorical variable) and date of harvest (the number of days elapsed  
298 since June 1<sup>st</sup> of the year of birth) as explanatory variables to account for sex differences and fawn  
299 body growth over the hunting season. In a first model, we tested for temporal variation in average  
300 body mass of fawns and whether the temporal dynamics of roe deer fawn body mass differed  
301 between the central and peripheral areas by modelling fawn body mass depending on 'year' (a  
302 categorical variable with 16 levels), wolf area (a 2-level categorical variable: "central area" vs.  
303 "peripheral area"), and the interaction term between the effects of 'year' and 'wolf area'. We then  
304 quantified and tested for the effects of five environmental variables: spring Gausse index at year  $t$ ,  
305 summer Gausse index at year  $t$ , winter harshness index for the winter season covering years  $t$  and  
306  $t+1$ , roe deer population abundance at year  $t$  (to test for density-dependence) and red deer  
307 population at year  $t$  (to test for interspecific competition) on fawn body mass from the hunting  
308 season covering years  $t$  and  $t+1$  by replacing 'year' in the model described above with the  
309 corresponding environmental variable, one at a time (i.e. 5 different models for the 5 environmental  
310 covariates). For example, to test for the effect of the spring Gausse index, we modelled fawn body  
311 mass depending on 'spring Gausse index', 'wolf area', and the interaction term between the effects  
312 of 'spring Gausse index' and 'wolf area'. For our model selection, we sequentially removed non-  
313 statistically significant variables starting from the most complex model. We tested for the effect of

314 sex, date of harvest and year using LRT. For the effect of environmental covariates, we tested their  
315 significance using an analysis of deviance (ANODEV) (Grosbois et al. 2008; Skalski 1996).  
316 We performed the analyses with the statistical software R 3.4 (R Core Team 2018) extended with the  
317 MASS package (Venables and Ripley 2002). We set the significance level to  $\alpha = 0.05$  and reported  
318 estimates as mean  $\pm$  95% confidence interval unless otherwise stated.

319

320

## 321 **Results**

322

323 Weather variables (i.e. winter harshness index, spring and summer Gausson indices) during the study  
324 period are provided in Supporting Information (Supporting Information 4). Winter 2004/2005 was  
325 the harshest of the time series, with a record of snow-fall (total snow-fall = 498 mm, max snow depth  
326 = 140 mm) and snow duration (number of days with snow cover = 110).

327

### 328 ***Predation by wolves***

329 Overall, we recorded 178 large herbivore carcasses attributed to predation by wolves during the  
330 period 1998-2010 in the west Vercors mountain range. Roe deer represented the main prey of  
331 wolves (37% of these carcasses), together with red deer (36 % of the carcasses). Additionally, the  
332 contribution of the different prey species changed between the early stage of the recolonization  
333 (1998-2005), when only lone wolves or single pairs were observed, and the later stage of the  
334 recolonization (2006-2010), when wolves formed a pack of a minimum of five individuals ( $\chi^2=10.56$ ;  
335  $p = 0.019$ ). This change is mainly characterized by a decrease of the contribution of roe deer and an  
336 increase in the contribution of red deer (Fig. 2).

337

### 338 ***Roe deer population abundance and growth rate***

339 The negative binomial model fitted the data satisfactorily (goodness-of-fit test:  $\chi^2 = 292.55$ ,  $df = 287$ ,  
340  $P = 0.40$ ). According WAIC, the roe deer population abundance varied between years, with different  
341 patterns between the central and peripheral areas (Table 2; Fig. 3A). Roe deer AI decreased  
342 continuously between 2001 and 2006 in the central area (Fig. 3A), and roe deer AI decreased  
343 dramatically in both areas in 2005 (Fig. 3A), coinciding with the most severe winter of the study  
344 period (2004-2005). Between 2005 and 2010, roe deer AI remained low in the central area while it  
345 increased in the peripheral area (Fig. 3A). Since 2011, the annual variation in roe deer AI was  
346 synchronous in the two areas (Fig. 3A). Overall, roe deer AIs were significantly lower in the central  
347 area in the period 2005-2010 only (mean difference in AI = - 0.400 [CI: - 0.677; -0.119]; see the  
348 horizontal grey bar in Fig. 3A).

349

350 Roe deer population growth rates were lower in the central area in the period 2001-2005 only (mean  
351 difference in growth rates = - 0.124 [CI: -0.327; 0.070]; see the horizontal grey bar in Fig. 3B). This  
352 explains the decline in AIs in the central area during that period. It further shows that the difference  
353 in roe deer AI between the two areas for the period 2005-2010 did not result from lower growth  
354 rates in the central area these years but resulted from the combined lower growth rates in the  
355 central area between 2001 and 2005. After 2006, the annual growth rates were rather similar in the  
356 two study areas (Fig. 3B). Despite the lowest growth rate occurring between 2004 and 2005  
357 henceforth including the harshest winter, we did not detect an effect of the winter harshness index  
358 on roe deer population growth rate (Table 3). Only the Gausse index in spring at year  $t$  had a  
359 significant positive effect on the population growth between year  $t$  and  $t+1$  (Table 3).

360

### 361 ***Roe deer fawn body mass***

362 Overall, we collected dressed body mass measurements for  $n = 422$  roe deer fawns in the study area  
363 from 2002 to 2016, both in the central (Vassieux-en-Vercors, Bouvante;  $n = 243$ ) and the peripheral  
364 (Saint-Julien-en-Vercors, Saint-Martin-en-Vercors, Saint-Agnan-en-Vercors;  $n = 179$ ) areas. The mean



365 difference in fawn body mass between sexes was  $0.30 \pm 0.24$  kg (males heavier, as expected;  
366 Douhard et al. 2017), and fawns gained on average  $0.29 \pm 0.09$  kg per month over the hunting season  
367 from September to the following March. Mean body mass of fawns varied among years ( $F = 1.80$ ,  $df =$   
368  $(14, 404)$ ,  $P = 0.03$ ; see Supporting Information 5 for detailed coefficients per year) but not differently  
369 between the central and peripheral wolf areas (interaction term between 'year' and 'wolf area' ( $F =$   
370  $1.51$ ,  $df = (14, 390)$ ,  $P = 0.10$ )). Fawn body mass was on average lower in the central than in the  
371 peripheral wolf area ( $F = 9.19$ ,  $df = (1, 404)$ ,  $P = 0.02$ ;  $0.79 \pm 0.26$  kg; Fig. 4). The first years of the  
372 study were characterized by a high variability due to lower sample sizes in those years. Between  
373 2006 and 2008, roe deer fawn body mass decreased in the two areas and has increased since 2008.  
374 The differences in mean fawn body mass among years and between areas were, however, rather low  
375 ( $\leq 1$  kg). Of the five environmental covariates (i.e. the 3 weather indices, the roe deer population  
376 abundance index, and the red deer population index), none accounted for annual variation in fawn  
377 body mass (Table 4), but the positive relationship between roe deer abundance and roe deer fawn  
378 body mass approached significance.

379

380

## 381 **Discussion**

382 At the early stage of the recolonization of the west Vercors mountain range by wolves (before 2005),  
383 roe deer was one of the main prey killed by wolves (with red deer). This result is in line with a  
384 previous analysis of wolf diet from 41 wolf scats carried out during the same period in the same area,  
385 which showed that roe deer represented 43.8% of the scats found and was the main prey of wolves  
386 (ONCFS network "Grands Prédateurs", unpublished data; Fluhr 2011). In parallel, roe deer abundance  
387 dropped in the central area, which corresponds to the core of a wolf pack territory and is  
388 characterized by an intense use of the area by wolves, with lower population growth rates in the  
389 central area than in the peripheral area between 2001 and 2005. The abundance of roe deer strongly  
390 dropped between 2004 and 2005 in both the central and the peripheral areas most likely because of

391 the extreme severity of the winter 2004-2005, which was the harshest winter throughout the 17-year  
392 study period. This is consistent with several previous studies that showed that severe winters  
393 decrease survival of young and old individuals in populations of large herbivores (e.g. Gaillard et al.  
394 2000; Saether 1997 for reviews). Wolf predation is expected to increase with snow depth. For  
395 instance, on the Isle Royale, wolves hunted in larger packs and tripled the number of moose they  
396 killed per day in the snowiest years (Post et al. 1999). Likewise, the relative importance of wolf  
397 predation on white-tailed deer *Odocoileus virginianus* mortality increased with winter severity in  
398 Minnesota (DelGiudice et al. 2002). Such higher susceptibility of ungulates to wolf predation during  
399 severe winters is associated with costlier and less efficient movements of ungulates in deep snow  
400 (Parker et al. 1984). Between 2006 and 2010, roe deer abundance remained lower in the central  
401 area. This difference in population abundance results from the consistent lower growth rates  
402 reported in the AI between 2001 and 2005. Additionally, our findings are in line with previous studies  
403 that showed that the presence of established wolves suppress the recovery of prey populations after  
404 a stochastic density-independent event, such as a severe winter (Hebblewhite et al. 2002).

405         The decrease of roe deer AI in the central area between 2001 and 2005 combined with the  
406 slower recovery of the roe deer population in the central area after the severe winter reveals that  
407 something different occurred between the two study areas during the period 2001-2010. When  
408 studying the effect of a carnivore on a prey, it is important to consider alternative hypotheses that  
409 could underline the patterns observed in prey (see fig. 2 in Ford and Goheen 2015): (i) alternative  
410 predator species, (ii) resource limitation, and (iii) disease. Regarding (i), no other large carnivore is  
411 present in the study areas. Since roe deer are hunted in both study areas, it is important to note that  
412 the yearly variation in roe deer harvest bags was similar in the two areas (Supporting Information 6).  
413 Regarding (ii), differences in forest species composition obviously affect the resource availability in  
414 the two areas and differences in resource availability between the two areas may exist and affect roe  
415 deer population abundance. However, no change in forest management occurred, so we can discard  
416 big changes in resource availability within an area to account for the difference observed. Likewise,

417 possible competition with red deer (Richard et al. 2010) seems unlikely because we did not find any  
418 effect of red deer population abundance on roe deer population growth rate and fawn body mass  
419 (supported by the lack of increase of the browsing index – see Supporting Information 7). The two  
420 wolf areas being very close geographically, differences in local weather conditions can also be  
421 excluded. Regarding (iii), no disease outbreak was reported over the study period. Predation by  
422 wolves is thus the most likely factor to explain the difference we reported in population dynamics  
423 between the central and peripheral areas. However, the changes in the roe deer abundance we  
424 detected based on spotlight counts correspond to local changes in the areas close to the transects  
425 sampled and can thus arise from either true changes in the study areas' roe deer population  
426 abundance or changes in roe deer space use and habitat selection that would affect the detection  
427 probability of roe deer on the driven transects. A change in the foraging behaviour of roe deer with  
428 an increased use of suboptimal habitats may have occurred (as shown in other systems, e.g. Creel et  
429 al. 2005; Valeix et al. 2009b). However, future studies involving detailed GPS monitoring of individual  
430 roe deer are needed to investigate whether roe deer alter their habitat use and selection as a  
431 response to predation risk by wolves. Unfortunately our data did not allow us to disentangle  
432 between the lethal and non-lethal effects of wolves. Wolves clearly killed roe deer but we cannot  
433 assess whether this mortality was additive or compensatory.

434         The sample sizes of roe deer fawn body mass were rather low but still allowed us to depict  
435 that body mass was lower in the central area than in the peripheral area. It is noteworthy that the  
436 difference in fawn body mass between the two areas was low (~1kg) compared to differences  
437 previously reported in roe deer in response to changes in density (about 2 kg in response to spatial  
438 variation in resources, Pettorelli et al. 2003; > 3kg in response to population density, Douhard et al.  
439 2013). This difference could arise from non-lethal effects of predation risk through stress-mediated  
440 and food-mediated costs, which occur even at a low density of predators (Ramler et al. 2014; Creel  
441 2018; MacLeod et al. 2018), but because the temporal dynamics of changes in roe deer fawn body  
442 mass were similar in the two study areas, it is more likely that an unmeasured/unknown variable

443 explains this body mass difference. The positive relationship between roe deer fawn body mass and  
444 roe deer AI we reported is opposite to what was expected in presence of density-dependence  
445 (Bonenfant et al. 2009). Indeed, fawn body masses were lower in 2006-2010 when roe deer AI was  
446 low abundance in the central area. Such positive relationship has already been demonstrated in a  
447 study whereby bighorn sheep *Ovis canadensis* lambs suffered mortality through reduced growth  
448 during years of high predation by cougars *Puma concolor*, contributing a third of the total impact of  
449 predation on lamb survival (Bourbeau-Lémieux et al. 2011); a study that illustrated a case of non-  
450 consumptive effects of predation on a prey population. While our results may suggest such a  
451 mechanism, the alternative of a delayed effect of the extremely rigorous winter 2004/2005 that led  
452 several consecutive cohorts to be light, and hence prevented any relationship between average fawn  
453 body mass and population AI cannot be discarded. Overall, our results do not provide strong support  
454 for non-lethal effects of wolves on roe deer fawn body mass. This result aligns with some existing  
455 evidence in the literature about weak to non-existent non-lethal effects of wolf predation on prey  
456 because behavioural responses of prey are not strong or frequent enough to lead to major changes  
457 in individual performance (White et al. 2011, Middleton et al. 2013). However, the two study areas  
458 were characterized by wolf presence with different levels of utilization by wolves. Because non-lethal  
459 effects may occur even at a low density of predators, it is also possible that they have occurred in  
460 both study areas and future studies will need to focus on areas with strictly no wolf before firm  
461 conclusions on the existence of non-lethal effects can be drawn.

462 Roe deer populations in the central and peripheral areas had similar patterns of temporal  
463 variation of AI and growth rates after 2011. This suggests that the effects of wolves on the roe deer  
464 population in the central area occurred mainly during a 10-year period following the establishment  
465 of the pack, with effects at the population level detected during a 6-year period only (2005-2010).  
466 The little difference we reported between the central and peripheral areas after 2011 may be  
467 explained by (i) a learning process to recognize wolf cues allowing roe deer to escape from wolf  
468 predation (end of naive period), and/or (ii) a predation shift by wolves, which targeted their

469 predation on red deer instead of roe deer (Fig. 2) with increasing pack size. This second explanation is  
470 supported by the fact that the attack success of wolves on red deer increases with larger pack size  
471 between 1 and 5 wolves (MacNulty et al. 2012).

472 Altogether, our findings suggest that the settlement of a wolf pack in an area from where the  
473 predator was absent for a very long time leads to a 10-year period of impact of the predator on the  
474 naive prey living in this area. Our study highlights the importance of long-term studies as different  
475 phases were detected in this work after the arrival of wolves. Indeed, after a first period when  
476 differences in roe population growth rates between the two study areas were detected, we detected  
477 a 6-year period when differences in roe deer abundance between the two areas were detected, and  
478 after no long-lasting detectable effect of wolves on roe deer populations could be detected. Our  
479 study further shows the difficulty of disentangling the lethal versus non-lethal effects of predators on  
480 their prey and encourage future studies to study (i) the spatial distribution of prey before and after  
481 the settlement of the predator, and (ii) the population dynamics of prey using capture-mark-  
482 recapture monitoring whenever possible. Finally, from a management or conservation perspective,  
483 our results suggest that a new equilibrium has been reached between wolves and the roe deer in the  
484 west Vercors mountain range.

485

#### 486 **Acknowledgements**

487 We sincerely thank the successive Presidents of the “Fédération Départementale des Chasseurs de la  
488 Drôme” (Alain Golin, Alain Hurtevent, Rémi Gandy), the Director of the “Fédération Départementale  
489 des Chasseurs de la Drôme” (Denis Rix) and all board members of the “Fédération Départementale  
490 des Chasseurs de la Drôme” for providing all means (technical, funding, staff) to carry out this  
491 research. We also thank the ONF technicians of the Vercors and Lente-Léoncel for their invaluable  
492 help with data collection and our fruitful discussions, particularly Jean-Pierre Lacour, Eric Rousset,  
493 Yves Pesenti, Gaël Gauthier, Franck Millat Carus, Philippe Joanin and Thierry Rozand. We are  
494 indebted to all the hunters, and particularly to all the Presidents of the ACCA, without whom this

495 study would not have been possible. We thank Simon Chamaillé-Jammes for fruitful discussions  
496 about the interpretation of the results of this study, and Eric Marboutin and Maryline Pellerin for  
497 comments on the manuscript. Finally, we thank Jean-Pierre Fermond (“Bubu”), Jérôme Guilloud and  
498 Christophe Randon who have supported this study since the beginning, provided guidance  
499 throughout and commented earlier versions of this draft. We thank two anonymous reviewers for  
500 their helpful suggestions that improved the quality of this manuscript.

501

502

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727

728 **Table 1**

729 Composition of the study areas in terms of land use type (data from the Corine Land Cover 2006  
 730 database). Numbers in brackets show the proportion each land use type represent.

731

Code from Corine Land Cover	Land use type	Central area	Peripheral area
		(ha)	(ha)
112 + 142	Discontinuous urban fabric + Sport and leisure facilities	114 [0.01]	0 [0.00]
211 + 242 + 243	Land principally occupied by agriculture	822 [0.05]	249 [0.02]
231	Pastures	2,238 [0.14]	1,955 [0.14]
311	Broad-leaved forest	5,295 [0.32]	2,380 [0.17]
312	Coniferous forest	323 [0.02]	3471 [0.24]
313	Mixed forest	5,300 [0.32]	4,983 [0.35]
321	Natural grasslands	2012 [0.12]	709 [0.05]
322 + 324	Moors and heathland + Transitional woodland-shrub	236 [0.01]	371 [0.02]
332 + 333	Bare rocks + Sparsely vegetated areas	117 [0.01]	201 [0.01]
<b>TOTAL</b>		<b>16,457</b>	<b>14,319</b>

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743



744 **Table 2**

745 Model selection with Widely Application Information Criterion (WAIC) for the state-space Bayesian  
746 models used to describe the spatio-temporal variation in roe deer abundance in the west Vercors  
747 mountain range, France, between 2001 and 2017. We compared here the temporal variation in roe  
748 deer abundance between the central and peripheral wolf areas.

749

<b>Model description</b>	<b>WAIC</b>	<b><math>\Delta</math>WAIC</b>
Different temporal variation in roe deer abundance between wolf areas	-27.79	0.00
Same temporal variation in roe deer abundance in the wolf areas	-26.18	1.61
No temporal variation in roe deer abundance	2.32	30.11

750

751 **Table 3**

752 Effects of ecological variables on the annual population growth rate of roe deer in the west Vercors  
 753 mountain range between 2001 and 2017, France. We computed annual population growth rates  
 754 from roe deer abundance accounting for sampling variance with a Bayesian state-space model. We  
 755 considered the additive and interactive effects of 4 ecological variables on annual population growth  
 756 rates and present the estimated slope (estimates) along with its 95% credible intervals (95 CI\_low; 95  
 757 CI\_up). We standardized all ecological variables to ease comparison of relative effects.

758

Tested ecological variable	Estimate	95 CI_low	95 CI_up
wolf area	-0.001	-0.141	0.141
spring Gausсен	0.122	0.012	0.242
summer Gausсен	0.066	-0.050	0.178
winter harshness	0.027	-0.081	0.136
red deer abundance	0.000	-0.083	0.075
wolf area x spring Gausсен	0.004	-0.239	0.253
wolf area x summer Gausсен	0.096	-0.155	0.352
wolf area x winter harshness	-0.023	-0.262	0.210
wolf area x red deer abundance	-0.072	-0.255	0.107

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765 **Table 4**

766 Effects of the five ecological variables tested on dressed body mass of roe deer fawns ( $n = 422$ )  
 767 harvested during the autumn-winter of years 2002 to 2016 in the west Vercors mountain range (both  
 768 the central and peripheral areas of the wolf pack territory). We present the standardized coefficients  
 769 (and their 95% confidence limits) and the analysis of deviance (ANODEV) of the effect of  
 770 environmental covariates on roe deer fawn body mass, accounting for the harvest date and the sex.  
 771 The ANODEV quantifies the proportion of temporal variability in the yearly average body mass of roe  
 772 deer fawns accounted for by the cohort-specific ecological variable. No interaction term between  
 773 'wolf area' and an ecological variable was found significant so that only the additive effect is  
 774 presented.

775

<b>Environmental variable</b>	<b>Estimate</b>	<b>R<sup>2</sup></b>	<b>ANODEV</b>
Winter harshness index	0.210 (0.112)	0.08	F = 2.09, df = (1, 14), P = 0.15
Spring Gausсен index	-0.093 (0.116)	0.02	F = 1.41, df = (1, 15), P = 0.52
Summer Gausсен index	0.052 (0.115)	0.00	F = 0.13, df = (1, 15), P = 0.72
Roe deer population abundance index	0.254 (0.120)	0.11	F = 3.12, df = (1, 15), P = 0.09
Red deer population abundance index	0.168 (0.117)	0.05	F = 1.36, df = (1, 15), P = 0.25

776

777

778 **Figure legends**

779

780 **Figure 1:** Map of the study area in the French department of Drôme with the location of the six study  
781 counties (the small map of France shows the location of the Drôme department in France). The dark  
782 grey area represents the central area of the west Vercors wolf pack territory, while the pale grey area  
783 represents the peripheral area. Lines show transects for the monitoring of roe deer population  
784 abundance.

785

786 **Figure 2:** Changes in the contribution of large herbivore species to the diet of wolves in the west  
787 Vercors mountain range, based on carcasses retrieved in winter months, between the early stage of  
788 the recolonization, when only lone wolves or a single pair were observed, and the later stage of the  
789 recolonization, when wolves formed a pack of a minimum of five individuals. It is worth noting that  
790 the number of carcasses detected reflects the prey's perspective of predation, and not necessarily  
791 the predator's perspective, as the results presented are not controlled for prey biomass.

792

793 **Figure 3: (A)** Changes in the roe deer population abundance index (AI; small circles) and in the  
794 predicted roe deer abundance per km, accounting for the sampling variance of the counts ( $D_{z,t}$ ; large  
795 circles) in the central and peripheral areas of a wolf pack territory in the French west Vercors  
796 mountain range for the period 2001-2017. The shaded areas represent the 95% credible intervals.  
797 The horizontal grey bar represent the years for which the roe deer abundance differed between the  
798 central and peripheral areas.

799 **(B)** Changes in the annual population growth rate of the roe deer population in the central and  
800 peripheral areas of a wolf pack territory in the French west Vercors mountain range for the period  
801 2001-2017. The annual population growth rates represented are calculated from our baseline state-  
802 space model (see details in the text). The horizontal grey bar represent the period for which the roe

803 deer population growth rate differed between the central and peripheral areas. The dotted  
804 horizontal line shows a null population growth rate.

805

806 **Figure 4:** Changes in the roe deer fawn body mass (small circles: corrected dressed body mass – see  
807 text for details; large circles: predicted values of dressed body mass from the model) in the central  
808 and peripheral areas of a wolf pack territory in the French west Vercors mountain range. Bars  
809 represent the 95% confidence interval.

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812 **Figure 1**

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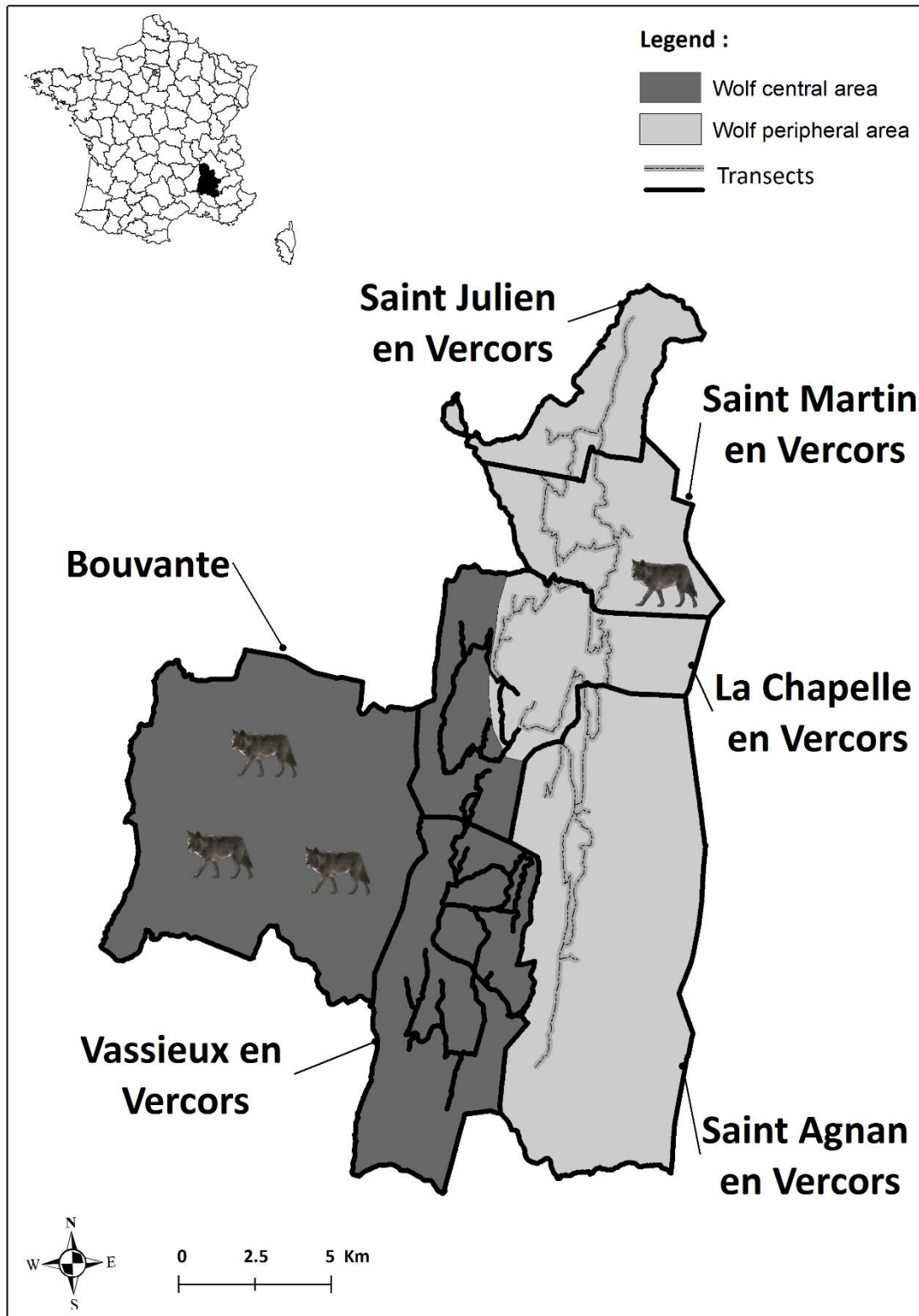
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837 **Figure 2**

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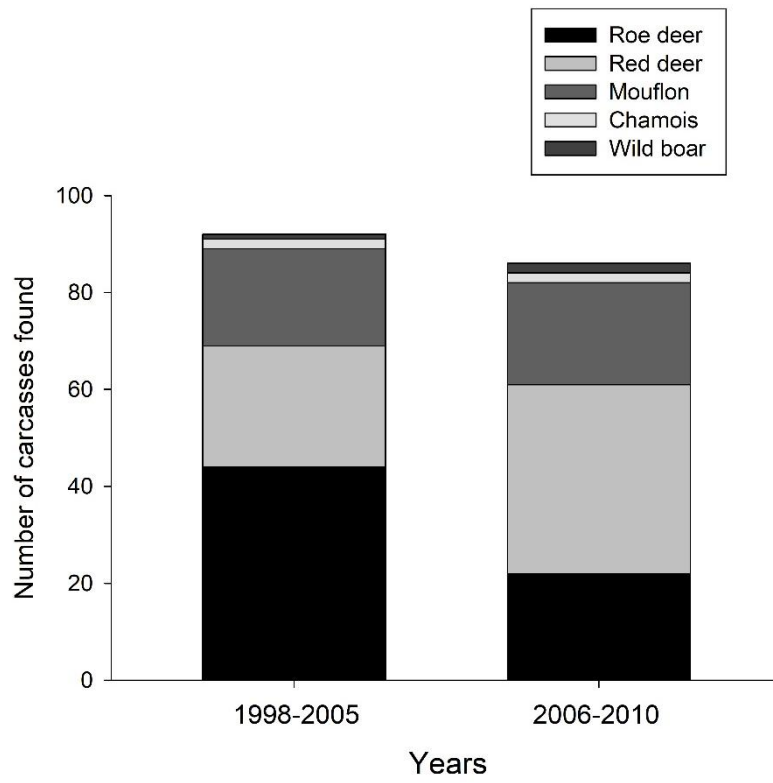
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855 **Figure 3**

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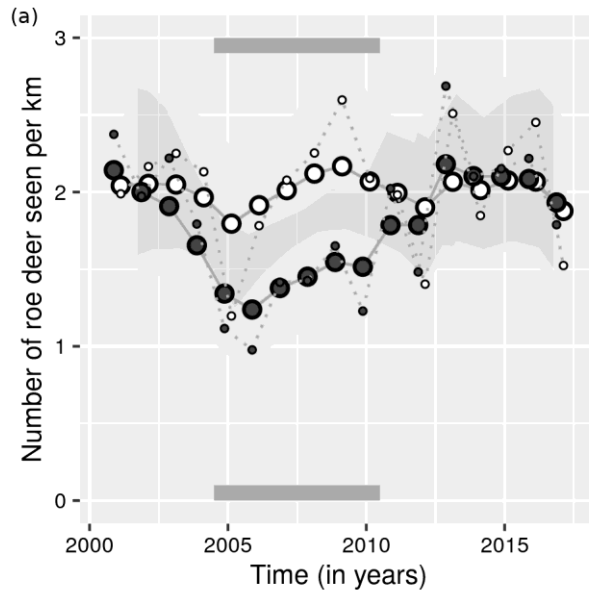
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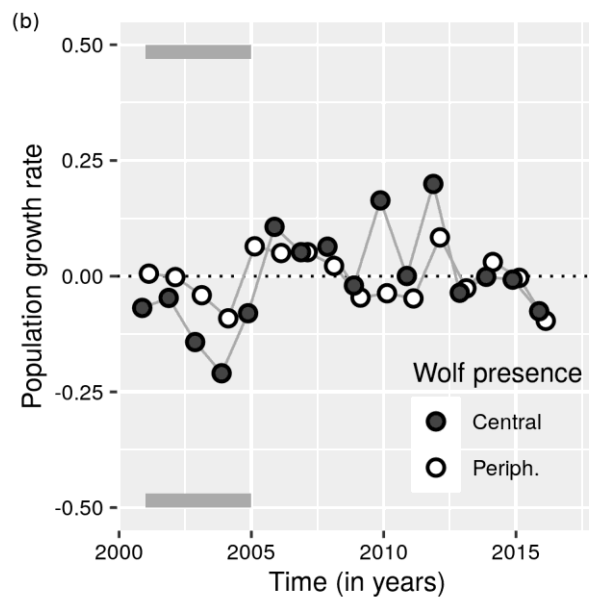
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876 **Figure 4**

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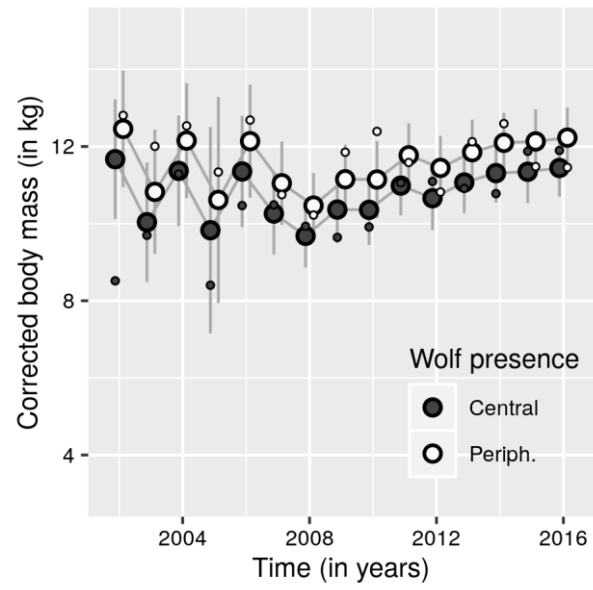
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### Supporting Information

**Supporting Information 1:** Picture of a wolf in the French Vercors mountain range (picture from a camera trap).

**Supporting Information 2: (a)** Composition of the study counties in terms of land use type (data extracted from Corine Land Cover). **(b)** Information on the altitude in the study counties.

**Supporting Information 3:** JAGS code used for our baseline model for the analysis of roe deer abundance and population growth rate.

**Supporting Information 4:** Weather conditions in the French west Vercors mountain range between 2001 and 2017. Weather indices (**(a)** winter harshness index, **(b)** Spring Gausсен index, and **(c)** Summer Gausсен index) were calculated from weather data from Météo France for the weather station La Chapelle-en-Vercors. See text for details.

**Supporting Information 5:** Coefficients of the effect of the interaction “year”\*“wolf area” on roe deer fawn body mass in the French west Vercors mountain range between 2002 and 2016.

**Supporting Information 6:** Changes in the number of roe deer quotas and off-takes for the period 2001-2017 in **(a)** the central area of the west Vercors wolf pack territory, and **(b)** the peripheral area of the west Vercors wolf pack territory. The county of La Chapelle-en-Vercors was excluded as it belongs to both the central and peripheral areas.

**Supporting Information 7:** Changes in the browsing index in the central area of a wolf pack territory in the French west Vercors mountain range.



917 **Supporting Information 1**

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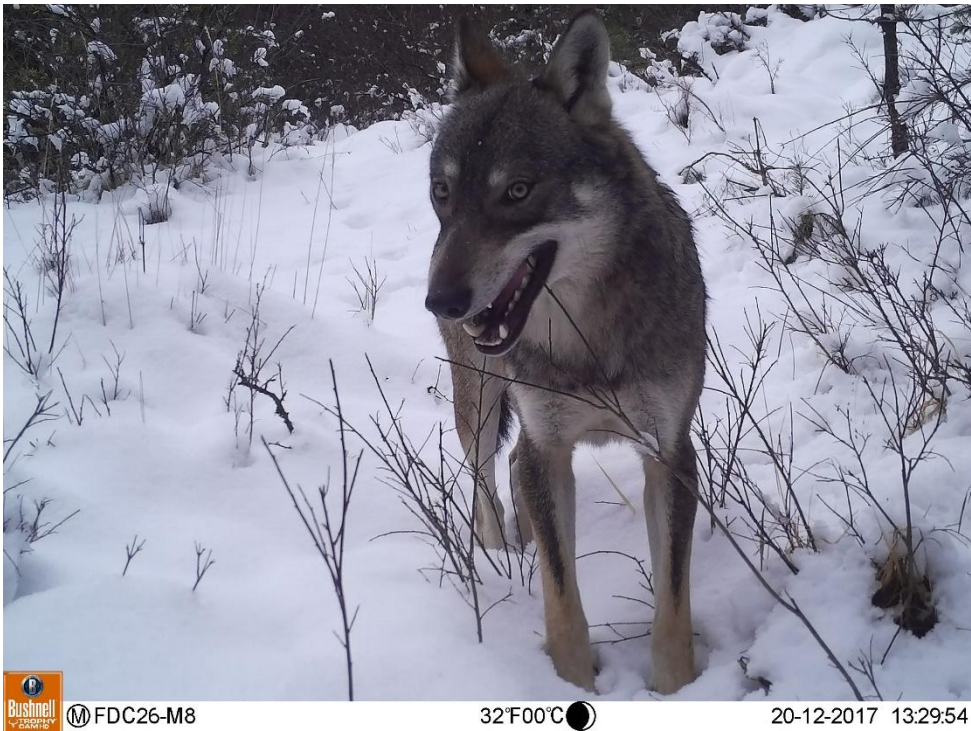
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930 **Supporting Information 2**931 **(a)**

Code from Corine Land Cover	Land use type	Central area			Peripheral area			
		Bouvante (ha)	Vassieux-en- Vercors (ha)	La Chapelle- en-Vercors (ha)	La Chapelle- en-Vercors (ha)	St-Agnan-en- Vercors (ha)	St-Julien- en-Vercors (ha)	St-Martin- en-Vercors (ha)
112 + 142	Discontinuous urban fabric + Sport and leisure facilities	26	27	61	0	0	0	0
211 + 242 + 243	Land principally occupied by agriculture	124	408	290	1	105	0	143
231	Pastures	557	897	784	97	861	405	592
311	Broad-leaved forest	2,520	1,116	1,659	198	961	660	561
312	Coniferous forest	165	95	63	289	2,792	10	380
313	Mixed forest	3,706	1,357	237	623	2,738	677	945
321	Natural grasslands	1,177	782	53	63	621	0	25
322 + 324	Moors and heathland + Transitional woodland-shrub	82	107	47	63	275	14	19
332 + 333	Bare rocks + Sparsely vegetated areas	74	9	34	0	65	101	35
<b>TOTAL</b>		<b>8,431</b>	<b>4,798</b>	<b>3,228</b>	<b>1,334</b>	<b>8,418</b>	<b>1,867</b>	<b>2,700</b>

932

933

934 **(b)**

935

County	Mean altitude (m)	SD altitude (m)	Minimal altitude (m)	Maximal altitude (m)
Bouvante	1,120	305	305	1,690
Vassieux-en-Vercors	1,204	141	1,036	1,647
La Chapelle-en-Vercors	1,026	192	598	1,508
St-Agnan-en-Vercors	1,275	238	728	1,729
St-Julien-en-Vercors	992	162	413	1,591
St-Martin-en-Vercors	1,044	228	565	1,559

936

937

938 **Supporting Information 3**

939

```

940 sink(file = "pois.bug")
941 cat("
942 model{
943   ## ----- ##
944   ##           ##
945   ## Definition of priors ##
946   ##           ##
947   ## ----- ##
948
949   theta ~ dunif(0, 50)
950   beta ~ dnorm(mu.beta, tau.beta)
951   for(i in 1:2){
952     sigma.r[i] ~ dunif(0, 100)      # Prior for sd of observation process
953     sigma2.r[i] <- pow(sigma.r[i], 2)
954     tau.r[i] <- pow(sigma.r[i], -2)
955     mean.r[i] ~ dnorm(0, 0.001)
956   }
957   sigma.proc ~ dunif(0, 100)
958   sigma2.proc <- pow(sigma.proc, 2)
959   tau.proc <- pow(sigma.proc, -2)
960
961   ## ----- ##
962   ##           ##
963   ## Likelihood for the negative binomial regression model ##
964   ##           ##
965   ## ----- ##
966
967   for(i in 1:n){
968     y[i] ~ dnegbin(p[i], theta)
969     p[i] <- theta/(theta + lambda[i])
970     log(lambda[i]) <- f[i]
971     f[i] <- inprod(beta[, ], X[i, ]) + offset[i]
972   }
973
974   ## ----- ##
975   ##           ##
976   ## Likelihood for the state-space model ##
977   ##           ##
978   ## ----- ##
979
980   C <- 10000

```

```

981   for(i in 1:34){
982     fit[i] <- inprod(beta[], X.fit[i, ])
983     zeros[i] ~ dpois(zero.mean[i])
984     zero.mean[i] <- -L[i] + C
985     l1[i] <- -0.5 * log(2 * pi) - 0.5 * log(sigma2.proc)
986     l2[i] <- -0.5 * pow(fit[i] - fit.tild[i], 2) / sigma2.proc
987     L[i] <- l1[i] + l2[i]
988     Lik[i] <- dnorm(fit[i], fit.tild[i], tau.proc)
989   }
990
991   ## ----- ##
992   ##           ##
993   ## Annual population growth estimation ##
994   ##           ##
995   ## ----- ##
996
997   ## ## Recursive equation linking Nt and Nt+1 for central zone
998   fit.tild[1] ~ dnorm(0, 0.001)
999   for(i in 1:16){
1000     r[i, 1] ~ dnorm(mean.r[1], tau.r[1])
1001     fit.tild[i+1] <- r[i, 1] + fit.tild[i]
1002   }
1003
1004   ## Recursive equation linking Nt and Nt+1 for periphery zone
1005   fit.tild[18] ~ dnorm(0, 0.001)
1006   for(i in (1:16 + 17)){
1007     r[i, 2] ~ dnorm(mean.r[2], tau.r[2])
1008     fit.tild[i+1] <- r[i, 2] + fit.tild[i]
1009   }
1010
1011 }")
1012 sink()
1013
1014 forJags <- list(
1015   X = model.matrix(~ as.factor(yr) * zone, data = ikchev),
1016   X.fit = model.matrix(~ as.factor(yr) * zone, data = ikout),
1017   offset = log(ikchev$km),
1018   y = as.numeric(ikchev$N),
1019   n = dim(ikchev)[1],
1020   mu.beta = rep(0, 34),
1021   tau.beta = diag(.0001, 34),
1022   zeros = rep(0, 34),
1023   pi = pi
1024 )
1025

```



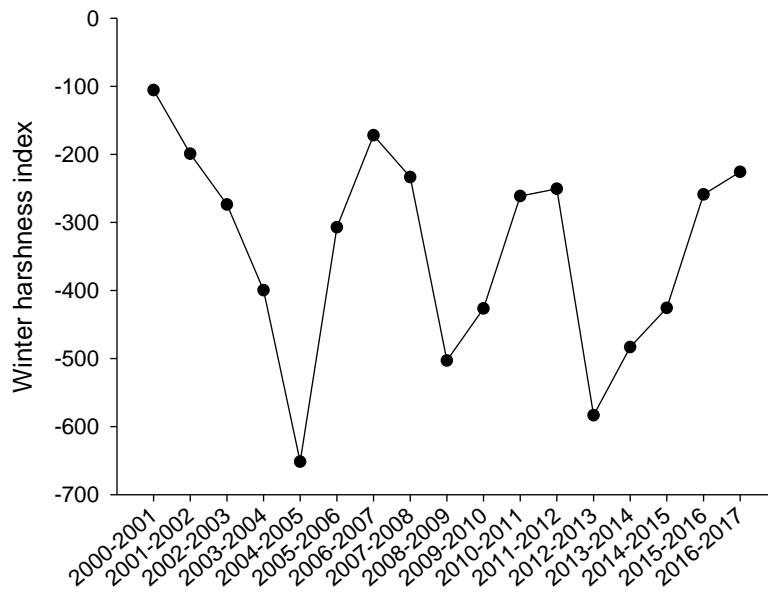
```

1026 # Initial values
1027 inits <- function(){list(
1028   sigma.r = runif(2, 0, 2),
1029   fit.tild = c(0.5, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA,
1030   NA, NA, NA, NA, 0.5, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA,
1031   NA, NA, NA, NA, NA)
1032 )}
1033
1034 # Parameters monitored
1035 parameters <- c("fit", "fit.tild", "r", "mean.r", "sigma.r", "sigma.proc")#, "Lik")
1036
1037 # MCMC settings
1038 ni <- 20000
1039 nt <- 5
1040 nb <- 15000
1041 nc <- 3
1042
1043 # Call JAGS
1044 jagsmodel <- jags(forJags,
1045   inits,
1046   parameters,
1047   "pois.bug",
1048   n.chains = nc,
1049   n.thin = nt,
1050   n.iter = ni,
1051   n.burnin = nb,
1052   working.directory = getwd()
1053 )
1054 jagsmodel
1055 #save(jagsmodel, file = "jagsmodel.RData")
1056 #load("jagsmodel.RData")

```

1057 **Supporting Information 4**

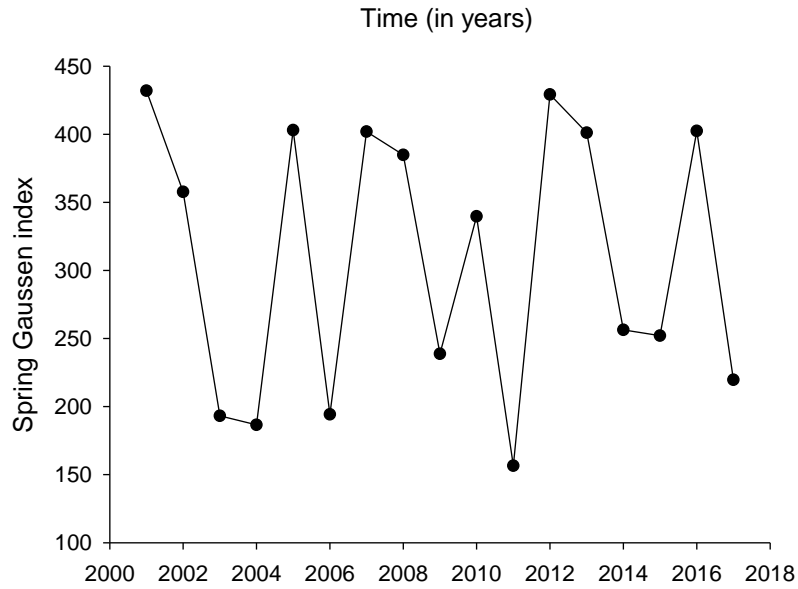
1058 **(a)**



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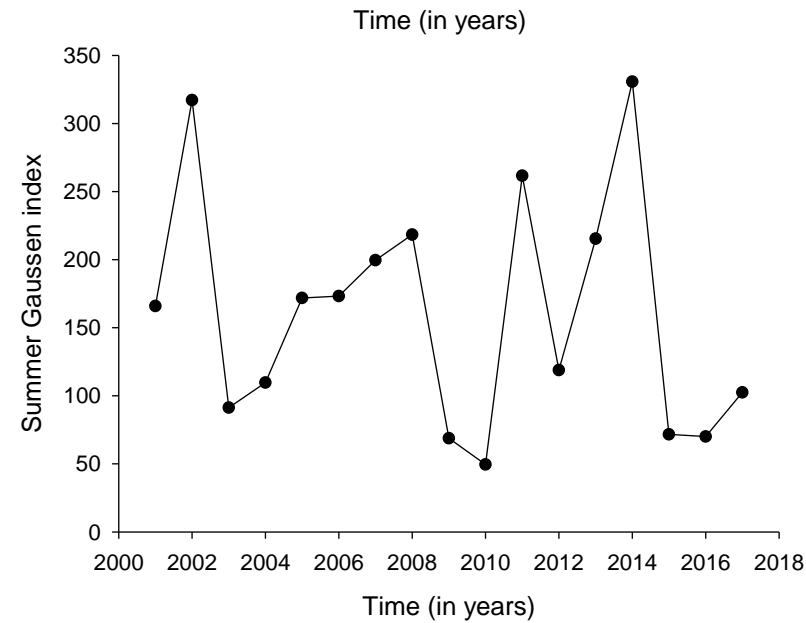
1067 **(b)**



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1075 **(c)**



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1083 **Supporting Information 5**

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<b>Term</b>	<b>Estimate</b>	<b>Standard error</b>
(Intercept)	11.75	1.35
Sex_Male	0.34	0.24
Julian_date	0.01	0
as.factor(year)2002	-4.58	2.61
as.factor(year)2003	-3.4	1.48
as.factor(year)2004	-1.81	1.41
as.factor(year)2005	-4.69	2.6
as.factor(year)2006	-2.62	1.65
as.factor(year)2007	-2.61	1.38
as.factor(year)2008	-3.16	1.32
as.factor(year)2009	-3.45	1.33
as.factor(year)2010	-3.18	1.3
as.factor(year)2011	-2.03	1.27
as.factor(year)2012	-2	1.31
as.factor(year)2013	-2.18	1.28
as.factor(year)2014	-2.31	1.29
as.factor(year)2015	-1.22	1.3
as.factor(year)2016	-1.2	1.12
area_periphery	-0.44	0.68
as.factor(year)2002:area_periphery	4.73	2.57
as.factor(year)2003:area_periphery	2.75	1.99
as.factor(year)2004:area_periphery	1.69	2.54
as.factor(year)2005:area_periphery	3.38	2.94
as.factor(year)2006:area_periphery	2.66	1.62
as.factor(year)2007:area_periphery	0.71	1.25
as.factor(year)2008:area_periphery	0.73	1.03
as.factor(year)2009:area_periphery	2.65	1.07
as.factor(year)2010:area_periphery	2.92	1.24
as.factor(year)2011:area_periphery	0.97	1
as.factor(year)2012:area_periphery	0.17	1.03
as.factor(year)2013:area_periphery	1.65	1.05
as.factor(year)2014:area_periphery	2.25	0.96
as.factor(year)2015:area_periphery	0.05	1

1085

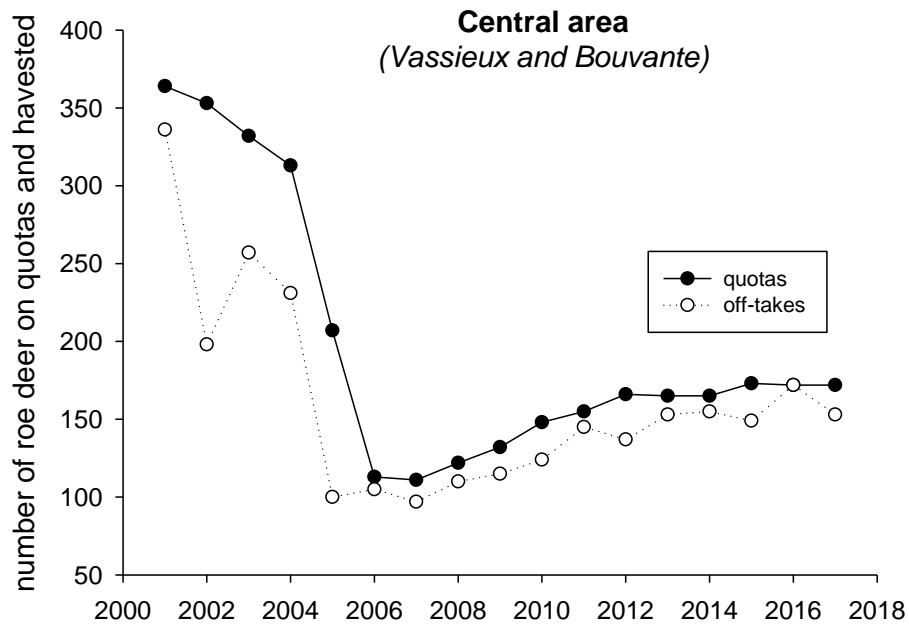
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1088 **Supporting Information 6**

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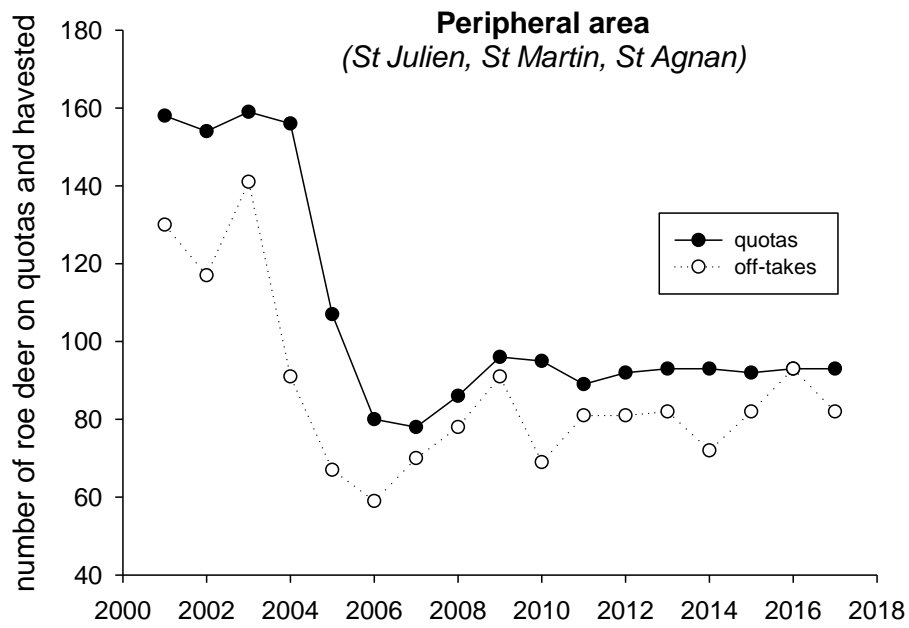
1090 **(a)**



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1100 **(b)**



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1111 **Supporting Information 7**

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1113 ***Herbivore pressure on the woody vegetation***

1114 Because changes in browsing pressure correlate with changes in the abundance of populations of  
1115 large herbivores (Chevrier et al. 2012; Morellet et al. 2001), we monitored the browsing pressure in  
1116 the forest habitats of the central area of the wolf pack territory (Bouvante, Vassieux-en-Vercors, and  
1117 the western sector of La Chapelle-en-Vercors) from 2001 to 2014. Unfortunately, such monitoring did  
1118 not take place in the peripheral area. One limit of such index is that it encompasses the browsing  
1119 pressure from all herbivore species. In the study system, this index encompasses the browsing  
1120 pressure from both roe deer and red deer. For this monitoring, we focused on the four main woody  
1121 plant species of the west Vercors mountain range (beech, silver fir, Norway spruce *Picea abies*, and  
1122 sycamore *Acer pseudoplatanus*). Every year in April-May, between snow melt and spring vegetation  
1123 flush, we monitored 86 quadrats (1 m<sup>2</sup>) distributed in the central area. In each quadrat, we recorded  
1124 whether one of these four species was present and whether these plants had been browsed in the  
1125 past growing season. Following Morellet et al. (2001), the browsing index was defined as  
1126  $B = (n_c + 1)/(n_p + 2)$  where  $n_p$  is the number of plots where at least one of the monitored species was  
1127 present, and  $n_c$  is the number of plots with at least one species consumed.

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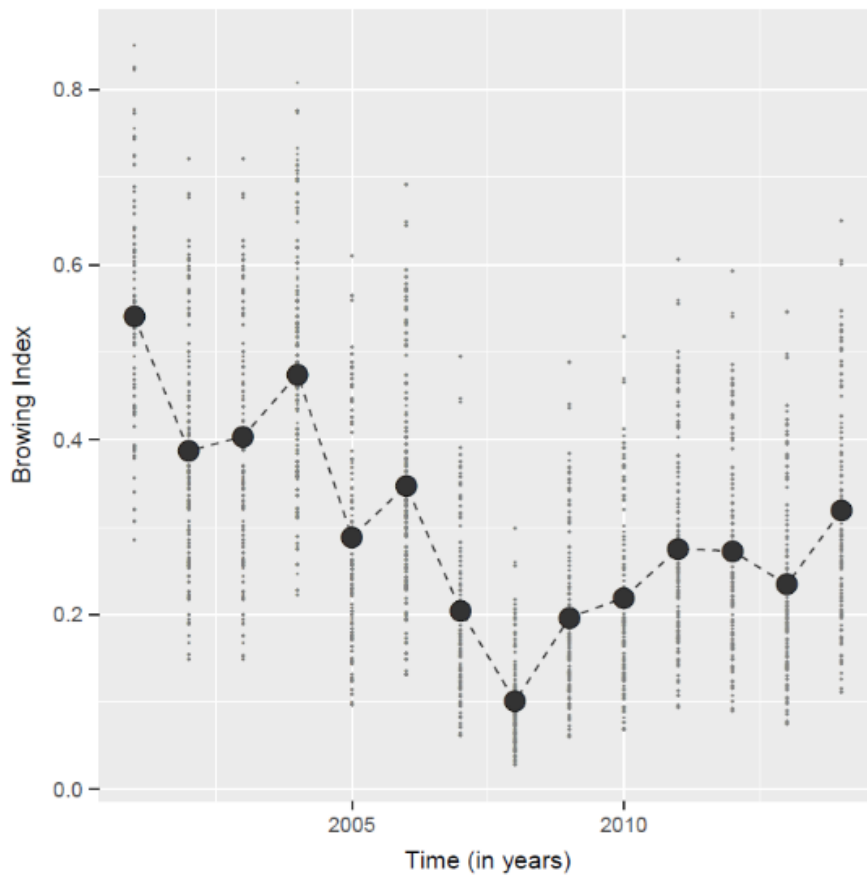
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References

Chevrier T, Saïd S, Widmer O, Hamard J-P, Saint-Andrieux C, Gaillard J-M (2012) The oak browsing index correlates linearly with roe deer density: a new indicator for deer management? *European Journal of Wildlife Research* 58: 17-22. <https://doi.org/10.1007/s10344-011-0535-9>.

Morellet N, Champely S, Gaillard J-M, Ballon P, Boscardin Y (2001) The browsing index: new tool uses browsing pressure to monitor deer populations. *Wildlife Society Bulletin* 29: 1243-1252. <https://www.jstor.org/stable/3784150>.