Population responses of roe deer to the recolonization of the French Vercors by wolves

Malory Randon, Christophe Bonenfant, Jacques Michallet, Thierry Chevrier,
Carole Toïgo, Jean-Michel Gaillard, Marion Valeix

1 **Population responses of roe deer to the recolonization of the French Vercors by wolves**

2

3

4 Malory Randon[1,*], Christophe Bonenfant[2], Jacques Michallet[3], Thierry Chevrier[3], Carole Toïgo[3], Jean-

5 Michel Gaillard[2], Marion Valeix[2]

6

7

8 [1] Fédération Départementale des Chasseurs de la Drôme, les Hautes Sétérées, 26400 Crest, France.

9 [2] CNRS, Université de Lyon, Université de Lyon 1, Laboratoire de Biométrie et Biologie Évolutive UMR

10 5558, F-69622 Villeurbanne, France.

11 [3] Office National de la Chasse et de la Faune Sauvage (ONCFS), 5 allée Bethléem, 38610 Gières,

12 France.

13

14 [*] Corresponding author: randon@chasseurs-drome.fr

15

16

Abstract

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

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

Introduction

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

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

3

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 *Albies 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

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 (χ^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

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

6

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 Gaussen 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 Gaussen index is a proxy of the balance

147   between rainfall and evapo-transpiration of plants (Gaussen and Bagnouls 1953). High values of the

148   Gaussen 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

7

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 x full body

214   mass) - 1.054; R^2 = 0.92) and used this relationship to estimate dressed body mass of roe deer

215   harvested during 2002-2007. We used dressed body mass in all subsequent analyses. Because roe

216   deer are income breeders with limited fat reserves (Andersen et al. 2000), and variation in adult body

217   mass is mainly caused by early-life conditions (Pettorelli et al. 2002), we analyzed body mass of roe

9

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 χ^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:

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

242   where $AI_{z,t}$ is the number of observed roe deer in each transect per year, μ 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:

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

248   where $D_{z,t}$ is a normally distributed random variable of mean $\hat{AI}_{z,t}$ and variance σ^2_{proc}. 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 Knape et al. 2011 for a similar approach). This was achieved by adding the following constrains

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   σ_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:

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

278   where γ_0 and γ_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 Gaussen 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 γ_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 1st 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 Gaussen index at year t,

305   summer Gaussen 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 Gaussen index, we modelled fawn body

311   mass depending on 'spring Gaussen index', 'wolf area', and the interaction term between the effects

312   of 'spring Gaussen 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

13

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 ± 95% confidence interval unless otherwise stated.

319

320

321   **Results**

322

323   Weather variables (i.e. winter harshness index, spring and summer Gaussen 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 (χ^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: χ^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 Gaussen 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 ± 0.24 kg (males heavier, as expected;

366   Douhard et al. 2017), and fawns gained on average 0.29 ± 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 ± 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   (≤ 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

16

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-pear 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

19

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

501

502

503   **References**

504   Andersen R, Gaillard J-M, Linnell JDC, Duncan P (2000) Factors affecting maternal care in an income

505   breeder, the European roe deer. Journal of Animal Ecology 69: 672-682.

506   https://doi.org/10.1046/j.1365-2656.2000.00425.x.

507   Andrén H, Liberg O (2015) Large impacts of Eurasian lynx predation on roe deer population dynamics.

508   PLoS ONE e0120570. https://doi.org/10.1371/journal.pone.0120570.

509   Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté.

510   Trends in Ecology and Evolution 22: 229-230. https://doi.org/10.1016/j.tree.2007.02.006.

511   Barnier F, Valeix M, Duncan P, Chamaillé-Jammes S, Barre P, Loveridge AJ, Macdonald DW, Fritz H

512   (2014) Diet quality in a wild grazer declines under the threat of an ambush predator.

513   Proceedings of the Royal Society of London B 281: e20140446.

514   https://doi.org/10.1098/rspb.2014.0446.

515   Berger J, Swenson JE, Persson I-L (2001) Recolonizing carnivores and naïve prey: conservation lessons

516   from Pleistocene extinctions. Science 291: 1036-1039.

517   https://doi.org/10.1126/science.1056466.

518   Bonenfant C, Gaillard J-M, Coulson T, Festa-Bianchet M, Loison A, Garel M, Loe LE et al. (2009)

519   Empirical evidence of density-dependence in populations of large herbivores. Advances in

520   Ecological Research 41: 313-357. https://doi.org/10.1016/S0065-2504(09)00405-X.

521   Bourbeau-Lemieux A, Festa-Bianchet M, Gaillard J-M, Pelletier F (2011) Predator-driven component

522   Allee effects in a wild ungulate. Ecology letters 14: 358-363.

523   https://doi.org/10.1111/j.1461.0248.2011.01595.x.

524   Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations.

525   Journal of Computational and Graphical Statistics 7: 434-455.

526   https://www.jstor.org/stable/1390675.

527   Byers JA (1997) American pronghorns: social adaptations and ghosts of predators past. University of

528   Chicago Press, Chicago.

529   Carthey AJR, Banks PB (2014) Naïveté in novel ecological interactions: lessons from theory and

530   experimental evidence. Biological Reviews 89: 932-949. https://doi.org/10.1111/brv.12087.

531   Cederlund G, Bergqvist J, Kjellander P, Gaillard J-M, Boisaubert B, Ballon P, Duncan P (1998)

532   Managing roe deer and their impact on the environment: maximising the net benefits to society.

533   In R Andersen, P Duncan & JDC Linnell (Eds.), The European Roe Deer: The Biology of Success

534   (pp. 337-372). Scandinavian University Press.

535   Chamaillé-Jammes S, Malcuit H, Le Saout S, Martin J-L (2014) Innate threat-sensitive foraging: black-

536   tailed deer remain more fearful of wolves than of the less dangerous black bear even after 100

537   years of wolf absence. Oecologia 174: 1151-1158. https://doi.org/10.1007/s00442-013-2843-0.

538   Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H, Lopez-Bao JV et al. (2014)

539   Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:

540   1517-1519. https://doi.org/10.1126/science.1257553.

541   Coulson T, Catchpole EA, Albon SD, Morgan BJT, Pemberton JM, Clutton-Borck TH, Carwley MJ et al.

542   (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:

543   1528-1531. https://doi.org/10.1126/science.292.5521.1528.

544   Courbin N, Loveridge AJ, Macdonald DW, Fritz H, Valeix M, Makuwe ET, Chamaillé-Jammes S (2016)

545   Reactive response of zebras to lion encounters shape their predator-prey space game at large

546   scale. Oikos 125: 829-838. https://doi.org/10.1111/oik.02555.

547 Creel S, Winnie J, Maxwell B, Hamlin K, Creel M (2005) Elk alter habitat selection as an anti-predator

548   response to wolves. Ecology 86: 3387-3397. https://doi.org/10.1890/05-0032.

549 Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and

550   demography of elk. Science 315: 960. https://doi.org/10.1126/science.1135918.

551 Creel S, Winnie JA, Christianson D (2009) Glucocorticoid stress hormones and the effect of predation

552   risk on elf reproduction. Proceedings of the National Academy of Sciences 106: 12388-12393.

553   https://doi.org/10.1073/pnas.0902235106.

554 Creel S, Schuette P, Christianson D (2014) Effects of predation risk on group size, vigilance and

555   foraging behaviour in an African ungulate community. Behavioral Ecology 25: 773-784.

556   https://doi.org/10.1093/beheco/aru050.

557 Creel S (2018) The control of risk hypothesis: reactive vs. proactive antipredator responses and

558   stress-mediated vs. food-mediated costs of response. Ecology letters 21: 947-956.

559   https://doi.org/10.1111/ele.12975.

560 DelGiudice GD, Riggs MR, Joly P, Pan W (2002) Winter severity, survival, and cause-specific mortality

561   of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:

562   698-717. https://www.jstor.org/stable/3803136.

563 de Valpine P, Hastings A (2002) Fitting population models incorporating process noise and

564   observation error. Ecological Monographs 72: 57-76. https://doi.org/10.1890/0012-

565   9615(2002)072[0057:FPMIPN]2.0.C0;2.

566 Douhard M, Gaillard J-M, Delorme D, Capron G, Duncan P, Klein F, Bonenfant C (2013) Variation in

567   adult body mass of roe deer: early environmental conditions influence early and late body

568   growth of females. Ecology 94: 1805-1814. https://doi.org/10.1890/13-0034.1.

569 Douhard M, Gaillard J-M, Pellerin M, Jacob L, Lemaître J-F (2017) The cost of growing large: costs of

570   post-weaning growth on body mass senescence in a wild mammal. Oikos 126: 1329-1338.

571   https://doi.org/10.1111/oik.04421.

572   Errington PL (1946) Predation and vertebrate populations. The Quaterly Review of Biology 21: 144-

573   177. https://doi.org/10.1086/395220.

574   Farhig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis.

575   Ecology and Society 14: 21. http://www.ecologyandsociety.org/vol14/iss1/art21.

576   Faton J-M, Ladreyt R (1982) Mammifères (*Mammalia*) drômois : ongulés et carnivores. DDA, FDC,

577   FRAPNA, ONF, Valence, 92p.

578   Festa-Bianchet M, Coulson T, Gaillard J-M, Hogg JT, Pelletier F (2006) Stochastic predation events and

579   population persistence in bighorn sheep. Proceedings of the Royal Society B 273. doi:

580   10.1098/rspb.2006.3467.

581   Fluhr J (2011) Analyse spatio-temporelle du régime alimentaire du loup (*Canis lupus*) dans les Alpes

582   françaises. Master Report, University of Montpellier, France.

583   Fortin D, Fortin M-E, Beyer HL, Duchesne T, Courant S, Dancose K (2009) Group-size-mediated habitat

584   selection and group fusion-fission dynamics of bison under predation risk. Ecology 90: 2480-

585   2490. https://doi.org/10.1890/08-0345.1.

586   Gaillard J-M, Delorme D, Boutin J-M, Van Laere G, Boisaubert B, Pradel R (1993) Roe deer survival

587   patterns: a comparative analysis of contrasting populations. Journal of Animal Ecology 62: 778-

588   791. https://www.jstor.org/stable/5396.

589   Gaillard J-M, Boutin J-M, Delorme D, Van Laere G, Duncan P, Lebreton J-D (1997) Early survival in roe

590   deer: causes and consequences of cohort variation in two contrasted populations. Oecologia

591   112: 502-513. https://doi.org/10.1007/s004420050338.

592   Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness

593   components and population dynamics of large herbivores. Annual Review of Ecology and

594   Systematics 31: 367-393. https://doi.org/10.1146/annurev.ecolsys.31.1.367.

595   Gaillard J-M, Hewison AJM, Klein F, Plard F, Douhard M, Davison R, Bonenfant C (2013) How does

596   climate change influence demographic processes of widespread species? Lessons from the

597   comparative analysis of contrasted populations of roe deer. Ecology Letters 16: 48-57.

598   https://doi.org/10.1111/ele.12059.

599   Garel M, Loison A, Gaillard J-M, Cugnasse J-M, Maillard D (2004) The effects of a severe drought on

600   mouflon lamb survival. Proceedings of the Royal Society B 271: 471-473.

601   https://doi.org/10.1098/rsbl.2004.0219.

602   Garel M, Bonenfant C, Hamann J-L, Klein F, Gaillard J-M (2010) Are abundance indices derived from

603   spotlight counts reliable to monitor red deer *Cervus elaphus* populations? Wildlife Biology 16:

604   77-84. https://doi.org/10.2981/09-022.

605   Gaussen H, Bagnouls F (1953) Les climats biologiques et leur classification. Annales de Géographie 6.

606   https://doi.org/10.3406/geo.1957.18273.

607   Grosbois V, Gimenez O, Gaillard J-M, Pradel R, Barbraud C, Clobert J, Möller AP, Weimerskirch H

608   (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biological

609   Reviews 83: 357-399. https://doi.org/10.1111/j.1469-185X.2008.00047.x.

610   Hebblewhite M, Pletscher DH, Paquet PC (2002) Elk population dynamics in areas with and without

611   predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology

612   80: 789-799. https://doi.org/10.1139/Z02-058.

613   Heurich M, Möst L, Schauberger G, Reulen H, Sustr P, Hothorn T (2012) Survival and causes of death

614   of European roe deer before and after Eurasian lynx reintroduction in the Bavarian Forest

615   National Park. European Journal of Wildlife Research 58: 567-578.

616   https://doi.org/10.1007/s10344-011-0606-y.

617   Hone J, Clutton-Brock TH (2007) Climate, food, density and wildlife population growth rate. Journal

618   of Animal Ecology 76: 361-367. https://doi.org/10.1111/j.1365-2656.2006.01200.x.

619   Hopcraft JGC, Olff H, Sinclair ARE (2010) Herbivores, resources and risks: alternating regulation along

620   primary environmental gradients in savannas. Trends in Ecology and Evolution 25: 119-128.

621   https://doi.org/10.1016/j.tree.2009.08.001.

622 Kéry M, Schaub M (2011) Bayesian population analysis using WinBUGS: a hierarchical perspective.

623   Academic Press.

624 Knape J, Jonzén N, Sköld M (2011) On observation distributions for state space models of population

625   survey data. Journal of Animal Ecology 80: 1269-1277. https://doi.org/10.1111/j.1365-

626   2656.2011.01868.x.

627 Kuijper DPJ, Sahlén E, Elmhagen B, Chamaillé-Jammes S, Sand H, Lone K, Cromsigt J (2016) Paws

628   without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proceedings

629   of the Royal Society B 283: 20161625. https://doi.org/10.1098/rspb.2016.1625.

630 Laundré JW, Hernandez L, Medina PL, Campanella A, Lopez-Portillo J, Gonzalez-Romero A, Grajales-

631   Tam KM et al. (2014) The landscape of fear: the missing link to understand top-down and

632   bottom-up controls of prey abundance? Ecology 95: 1141-1152. https://doi.org/10.1890/13-

633   1083.1.

634 MacLeod KJ, Krebs CJ, Boonstra R, Sheriff MJ (2018) Fear and lethality in snowshoe hares: the deadly

635   effects of non-consumptive predation risk. Oikos 127: 375-380.

636   https://doi.org/10.1111/oik.04890.

637 MacNulty DR, Smith DW, Mech DL, Vucetich JA, Packer C (2012) Nonlinear effects of group size on

638   the success of wolves hunting elk. Behavioral Ecology 23: 75-82.

639   https://doi.org/10.1093/beheco/arr159.

640 Mech DL, Smith DW, Murphy KM, MacNulty DR (2001) Winter severity and wolf predation on a

641   formerly wolf-free elk herd. Journal of Wildlife Management 65: 998-1003.

642   https://www.jstor.org/stable/3803048.

643 Middleton et al. 2013. Linking anti-predator behaviour to prey demography reveals limited effects of

644   an actively hunting large carnivore. Ecology Letters 16: 1023-1030.

645   https://doi.org/10.1111/ele.12133.

646   Murdoch WW (1969) Switching in general predators: experiments on predator specificity and

647   stability of prey populations. Ecological Monographs 39: 335-354.

648   https://doi.org/10.2307/1942352.

649   ONCFS (2006) Quoi de neuf n°15 – Juin 2006 – Bulletin d'information du réseau loup.

650   Parker KL, Robbins CT, Hanley TA (1984) Energy expenditures for locomotion by mule deer and elk.

651   Journal of Wildlife Management 48: 474-488. https://www.jstor.org/stable/3801180.

652   Pellerin M, Bessière A, Maillard D, Capron G, Gaillard J-M, Michallet J, Bonenfant C (2017) Saving

653   time and money by using diurnal vehicle counts to monitor roe deer abundance. Wildlife

654   Biology. https://doi.org/10.2981/wlb.00274.

655   Pettorelli N, Gaillard J-M, Van Laere G, Duncan P, Kjellander P, Liberg O, Delorme D et al. (2002)

656   Variations in adult body mass in roe deer: the effects of population density at birth and of

657   habitat quality. Proceedings of the Royal Society London B 269. https://doi.org/10.1098/

658   rspb.2001.1791.

659   Pettorelli N, Dray S, Gaillard J-M, Chessel D, Duncan P, Illius A, Guillon N et al. (2003) Spatial

660   variations in springtime food resources influences the winter body mass of roe deer fawns.

661   Oecologia 137: 363-369. https://doi.org/10.1007/s00442-003-1364-7.

662   Pettorelli N, Gaillard J-M, Yoccoz NG, Duncan P, Maillard D, Delorme D, Van Laere G et al. (2005) The

663   response of fawn survival to changes in habitat quality varies according to cohort quality and

664   spatial scale. Journal of Animal Ecology 74: 972-981. https://doi.org/10.1111/j.1365-

665   2656.2005.00988.x.

666   Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

667   In Proceedings of the 3rd international workshop on distributed statistical computing (vol. 124,

668   No 125, p.10)

669   Post E, Peterson RO, Stenseth NC, McLaren BE (1999) Ecosystem consequences of wolf behavioural

670   response to climate. Nature 401: 905-907. https://doi.org/10.1038/44814.

671   Ramler JP, Hebblewhite M, Kellenberg D, Sime C (2014) Crying wolves? A spatial analysis of wolf

672   location and depredations on calf weight. American Journal of Agricultural Economics 96: 631-

673   656. https://doi.org/10.1093/ajae/aat100.

674   R Core Team (2018) R: a language and environment for statistical computing. R Foundation for

675   Statistical Computing, Vienna, Austria. (https://www.R-project.org/).

676   Reznick DN, Bryant MJ, Roff D, Ghalambor CK, Ghalambor DE (2004) Effect of extrinsic mortality on

677   the evolution of senescence in guppies. Nature 431: 1095-1099.

678   https://doi.org/10.1038/nature02936.

679   Richard E, Gaillard J-M, Saïd S, Hamann J-L, Klein F (2010) High red deer density depresses body mass

680   of roe deer fawns. Oecologia 163: 91-97. https://doi.org/10.1007/s00442-009-1538-z.

681   Ripple WJ, Estes JA, Beschta RL, Wilmers C, Ritchie EG, Hebblewhite M, Berger J et al. (2014) Status

682   and ecological effects of the world's largest carnivores. Science 343: 1241484.

683   https://doi.org/10.1126/science.1241484.

684   Saether B-E (1997) Environmental stochasticity and population dynamics of large herbivores: a

685   search for mechanisms. Trends in Ecology and Evolution 12: 143-149.

686   https://doi.org/10.1016/S0169-5347(97)10068-9.

687   Say-Sallaz E, Chamaillé-Jammes S, Fritz H, Valeix M (2019) Non-consumptive effects of predation in

688   large terrestrial mammals: mapping our knowledge and revealing the tip of the iceberg.

689   Biological Conservation 235: 36-52. https://doi.org/10.1016/j.biocon.2019.03.044.

690   Skalski JR (1996) Regression of abundance estimates from mark-recapture surveys against

691   environmental covariates. Canadian Journal of Fisheries and aquatic Sciences 53: 196-204.

692   https://doi.org/10.1139/f95-169.

693   Skogland T (1991) What are the effects of predators on large ungulate populations? Oikos 61: 401-

694   411. https://doi.org/10.2307/3545248.

695   Theuerkauf J, Jedrzejewski W, Schmidt K, Gula R (2003) Spatiotemporal segregation of wolves from

696   humans in the Bialoweza Forest (Poland). Journal of Wildlife Management 67: 706-716.

697   https://www.jstor.org/stable/3802677.

698   Toïgo C, Gaillard J-M, Van Laere G, Hewison M, Morellet N (2006) How does environmental variation

699   influence body mass, body size, and body condition? Roe deer as a case study. Ecography 29:

700   301-308. https://doi.org/10.1111/j.2006.0906-7590.04394.x.

701   Valeix M, Fritz H, Loveridge AJ, Davidson Z, Hunt JE, Murindagomo F, Macdonald DW (2009a) Does

702   the risk of encountering lions influence African herbivore behaviour at waterholes? Behavioral

703   Ecology and Sociobiology 63: 1483-1494. https://doi.org/10.1007/s00265-009-0760-3.

704   Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW

705   (2009b) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal

706   variations influence habitat use. Ecology 90: 23-30. https://doi.org/10.1890/08-0607.1.

707   Valière N, Fumagalli L, Gielly L, Miquel C, Lequette B, Poulle M-L, Weber J-M et al. (2003) Long-

708   distance wolf recolonization of France and Switzerland inferred from non-invasive genetic

709   sampling over a period of 10 years. Animal Conservation 6: 83-92.

710   https://doi.org/10.1017/s1367943003003111.

711   Ver Hoef JM, Boveng PL (2007) Quasi-Poisson vs. negative binomial regression: how should we model

712   overdispersed count data? Ecology 88: 2766-2772. https://doi.org/10.1890/07-0043.1.

713   Volterra V (1931) Leçons sur la théorie mathématique de la lutte pour la vie. Goutliers-Vallars, Paris.

714   Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-

715   validation and WAIC. Statistics and Computing 27: 1413-1432.

716   http://dx.doi.org/10.1007/s11222-016-9709-3.

717   Venables WN, Ripley BD (2002) Modern Applied Statistics with S. Springer, New York, ISBN 0-387-

718   95457-0.

719   Watanabe S (2010) Asymptotic equivalence of Bayes cross validation and widely applicable

720   information criterion in singular learning theory. Journal of Machine Learning Research 11:

721   3571-3594.

722   White PJ, Garrott RA, Hamlin KL, Cook RC, Cook JG, Cunningham JA (2011) Body condition and

723   pregnancy in northern Yellowstone elk: evidence for predation risk effects? Ecological

724   Applications 21: 3-8. https://doi.org/10.1890/09-2123.1.

725   Whittington J, St Clair CC, Mercer G (2005) Spatial responses of wolves to roads and trails in

726   mountain valleys. Ecological Applications 15: 543-553. https://doi.org/10.1890/03-5317.

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 (ha)	Peripheral area (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]
TOTAL		16,457	14,319

732

733

734

735

736

737

738

739

740

741

742

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

Model description	WAIC	ΔWAIC
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

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 Gaussen	0.122	0.012	0.242
summer Gaussen	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 Gaussen	0.004	-0.239	0.253
wolf area x summer Gaussen	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

759

760

761

762

763

764

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

Environmental variable	Estimate	R^2	ANODEV
Winter harshness index	0.210 (0.112)	0.08	F = 2.09, df = (1, 14), P = 0.15
Spring Gaussen index	-0.093 (0.116)	0.02	F = 1.41, df = (1, 15), P = 0.52
Summer Gaussen 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

Figure legends

Figure 1: Map of the study area in the French department of Drôme with the location of the six study

counties (the small map of France shows the location of the Drôme department in France). The dark

grey area represents the central area of the west Vercors wolf pack territory, while the pale grey area

represents the peripheral area. Lines show transects for the monitoring of roe deer population

abundance.

Figure 2: Changes in the contribution of large herbivore species to the diet of wolves in the west

Vercors mountain range, based on carcasses retrieved in winter months, between the early stage of

the recolonization, when only lone wolves or a single pair were observed, and the later stage of the

recolonization, when wolves formed a pack of a minimum of five individuals. It is worth noting that

the number of carcasses detected reflects the prey's perspective of predation, and not necessarily

the predator's perspective, as the results presented are not controlled for prey biomass.

Figure 3: (A) Changes in the roe deer population abundance index (AI; small circles) and in the

predicted roe deer abundance per km, accounting for the sampling variance of the counts ($D_{z,t}$; large

circles) in the central and peripheral areas of a wolf pack territory in the French west Vercors

mountain range for the period 2001-2017. The shaded areas represent the 95% credible intervals.

The horizontal grey bar represent the years for which the roe deer abundance differed between the

central and peripheral areas.

(B) Changes in the annual population growth rate of the roe deer population in the central and

peripheral areas of a wolf pack territory in the French west Vercors mountain range for the period

2001-2017. The annual population growth rates represented are calculated from our baseline state-

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.

810

811

812   **Figure 1**

813

Figure 1

814

815

816

817

818

819

820

821

822

823

824

825

826

827

828

829

830

831

832

833

834

835

836
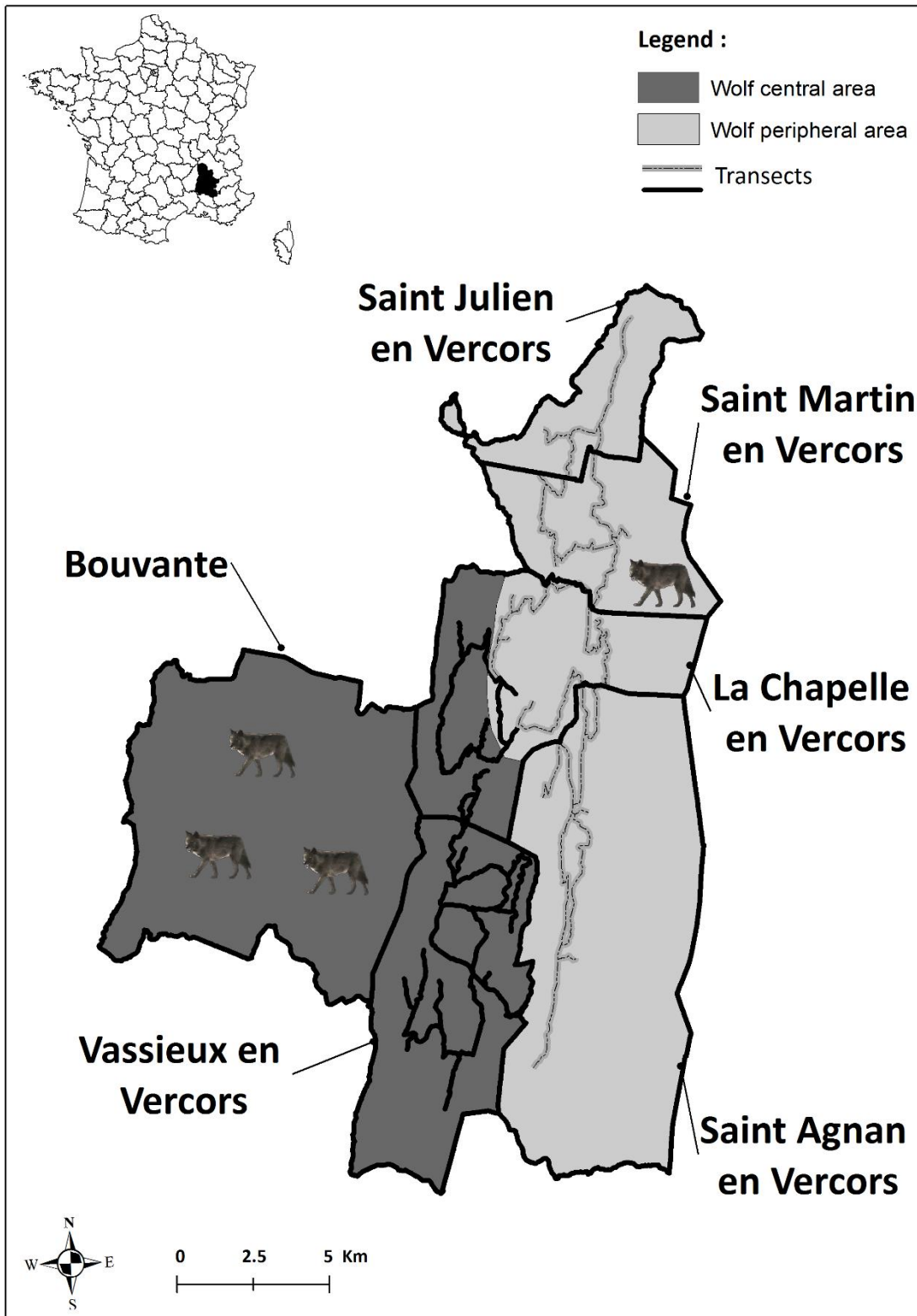
837   **Figure 2**

838

839

840

841

842
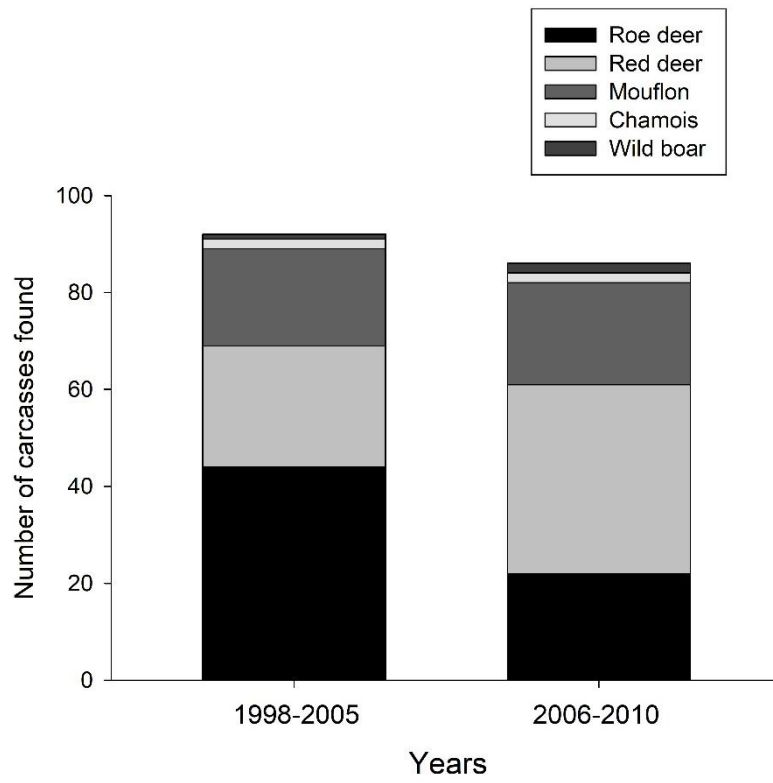

850   Years

851

852

853

854
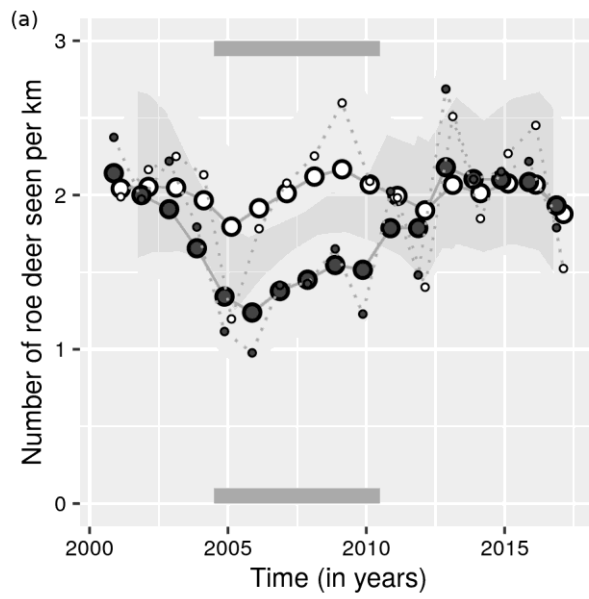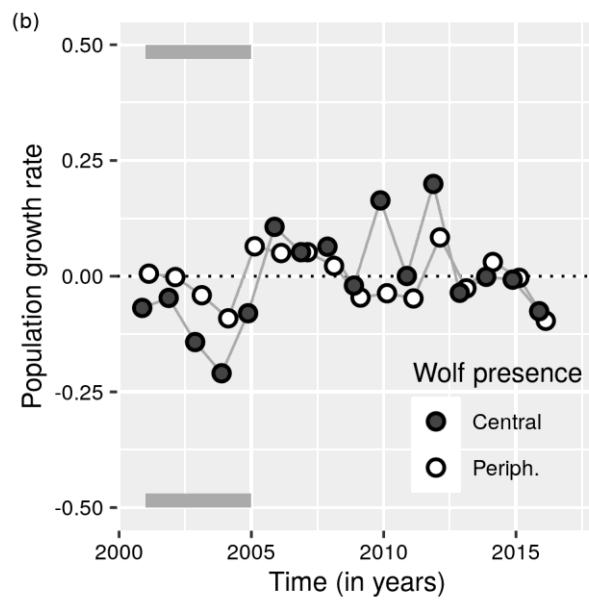
Figure 3

876   **Figure 4**

877

878

879

880

881

882

883

884

885

886

887

888

889
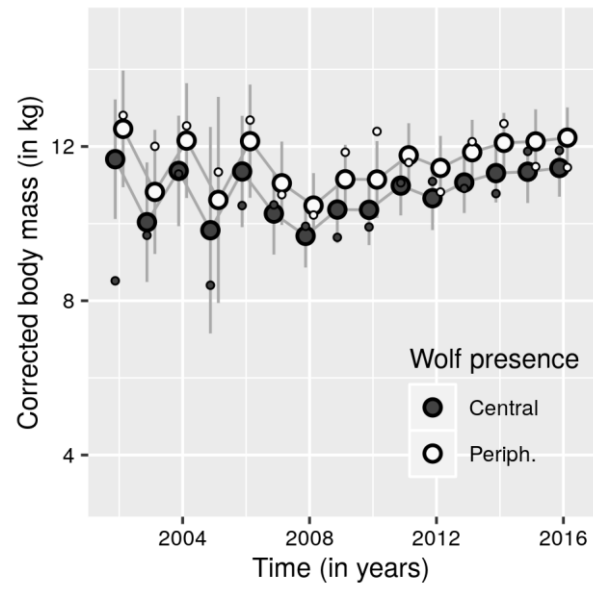
890   **Supporting Information**

891

892   **Supporting Information 1:** Picture of a wolf in the French Vercors mountain range (picture from a

893   camera trap).

894

895   **Supporting Information 2: (a)** Composition of the study counties in terms of land use type (data

896   extracted from Corine Land Cover). **(b)** Information on the altitude in the study counties.

897

898   **Supporting Information 3:** JAGS code used for our baseline model for the analysis of roe deer

899   abundance and population growth rate.

900

901   **Supporting Information 4:** Weather conditions in the French west Vercors mountain range between

902   2001 and 2017. Weather indices (**(a)** winter harshness index, **(b)** Spring Gaussen index, and **(c)**

903   Summer Gaussen index) were calculated from weather data from Météo France for the weather

904   station La Chapelle-en-Vercors. See text for details.

905

906   **Supporting Information 5:** Coefficients of the effect of the interaction "year"*"wolf area" on roe

907   deer fawn body mass in the French west Vercors mountain range between 2002 and 2016.

908

909   **Supporting Information 6:** Changes in the number of roe deer quotas and off-takes for the period

910   2001-2017 in **(a)** the central area of the west Vercors wolf pack territory, and **(b)** the peripheral area

911   of the west Vercors wolf pack territory. The county of La Chapelle-en-Vercors was excluded as it

912   belongs to both the central and peripheral areas.

913

914   **Supporting Information 7:** Changes in the browsing index in the central area of a wolf pack territory

915   in the French west Vercors mountain range.

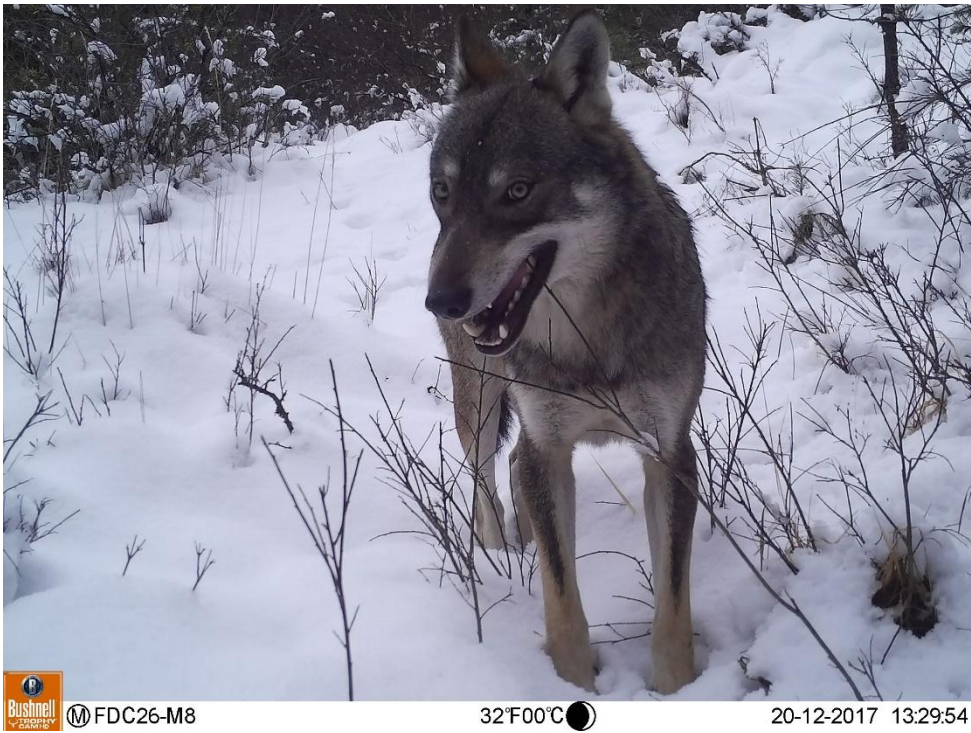917 **Supporting Information 1**

918

919
920
921
922
923
924
925
926
927
928
929

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
TOTAL		8,431	4,798	3,228	1,334	8,418	1,867	2,700

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

Supporting Information 3

```
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 ~ dmnorm(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,
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")
```
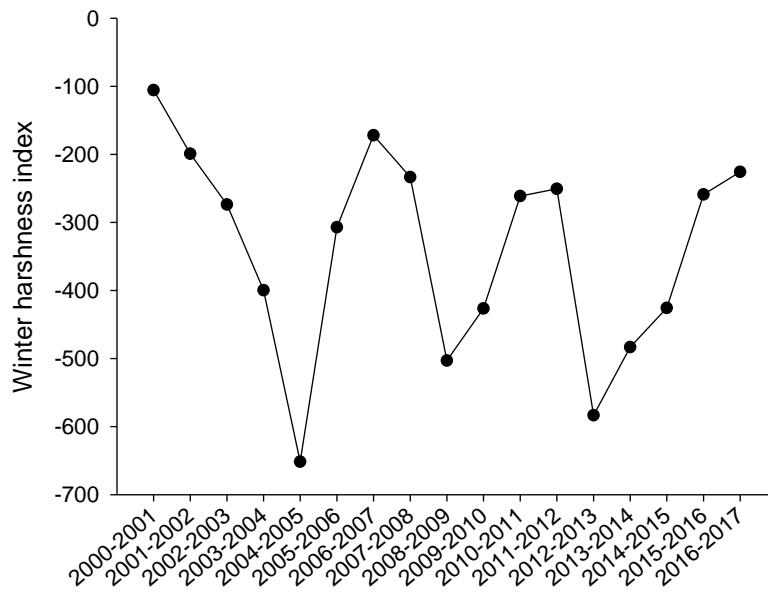
Supporting Information 4
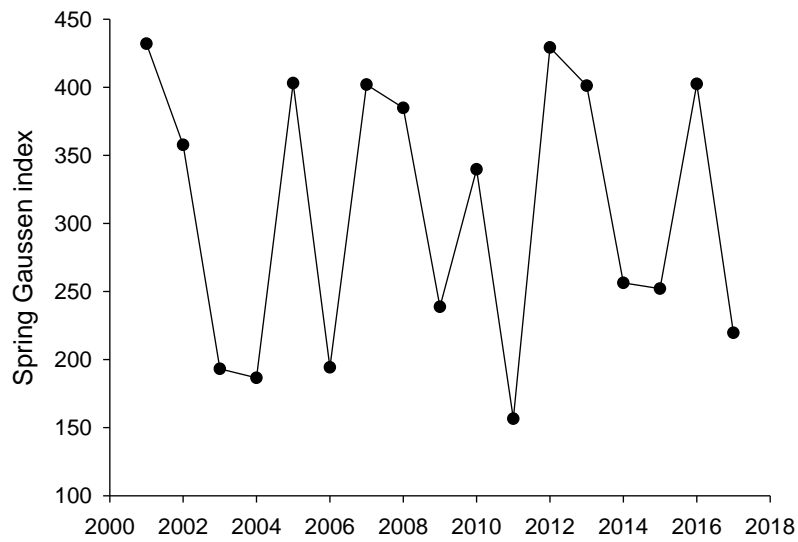
(a)

(b)
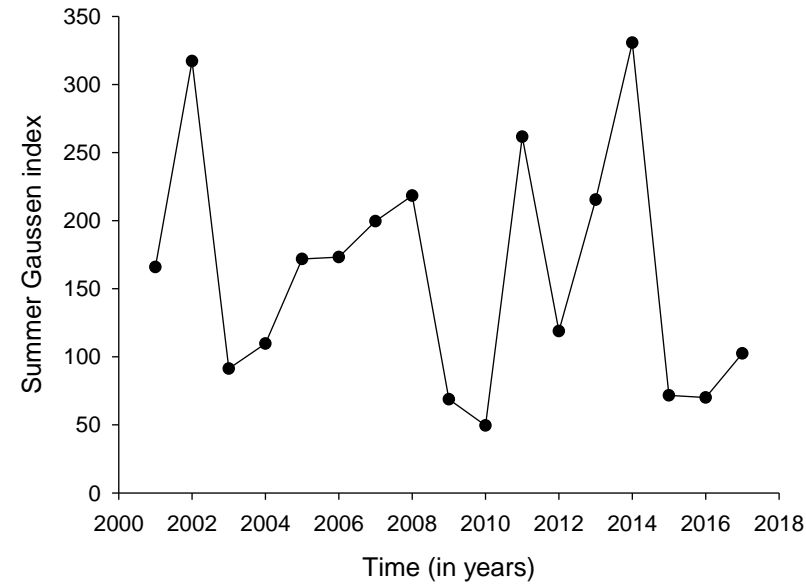

(c)

Supporting Information 5

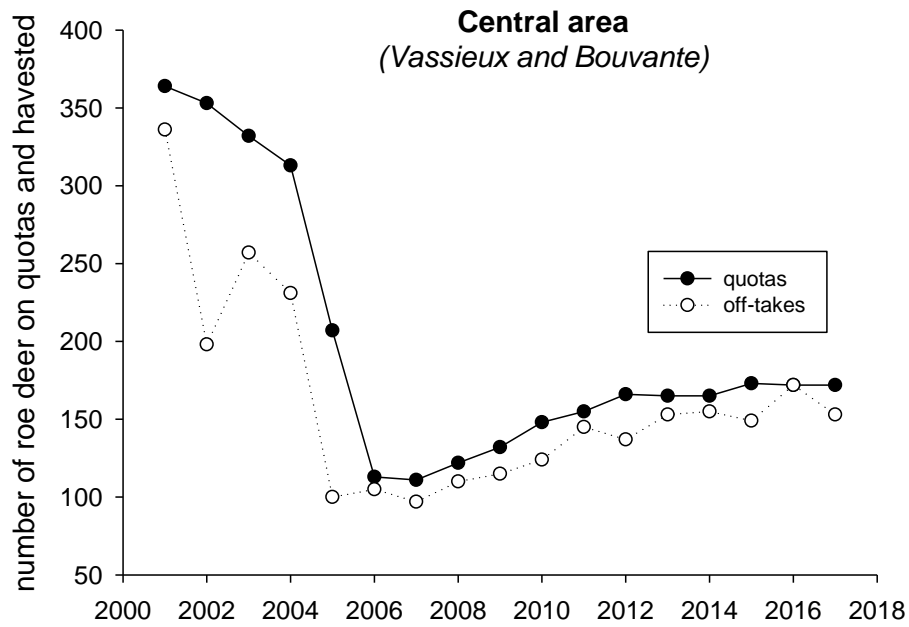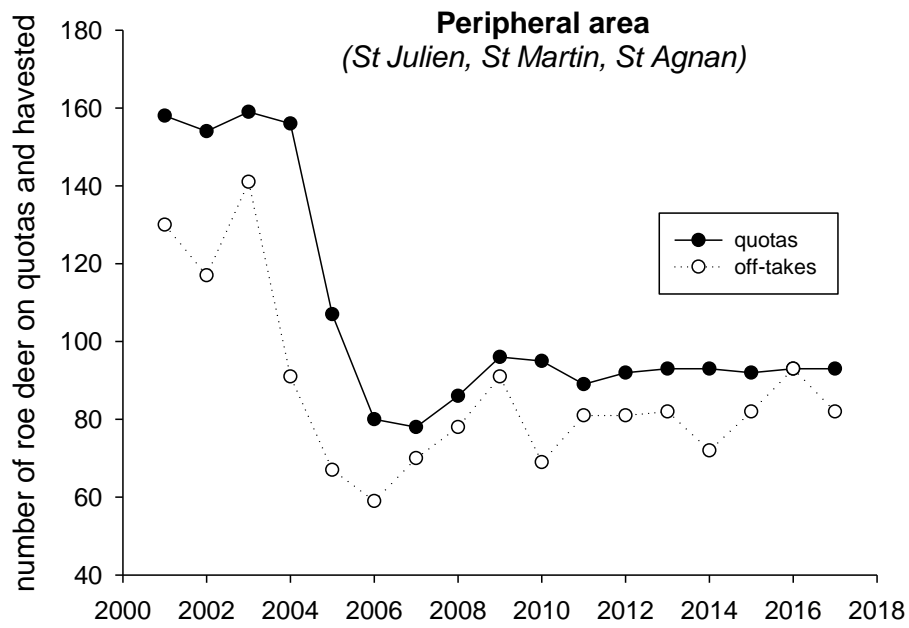| Term	Estimate	Standard error
(Intercept)	11.75	1.35
Sex_Male	0.34	0.24
Julian_date	0.01	0
as.factor(year)2002	-4.58	2.61
as.factor(year)2003	-3.4	1.48
as.factor(year)2004	-1.81	1.41
as.factor(year)2005	-4.69	2.6
as.factor(year)2006	-2.62	1.65
as.factor(year)2007	-2.61	1.38
as.factor(year)2008	-3.16	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

Supporting Information 6

(a)

Central area
(Vassieux and Bouvante)

(b)

Peripheral area
(St Julien, St Martin, St Agnan)

1111 **Supporting Information 7**

1112

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 m²) 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.
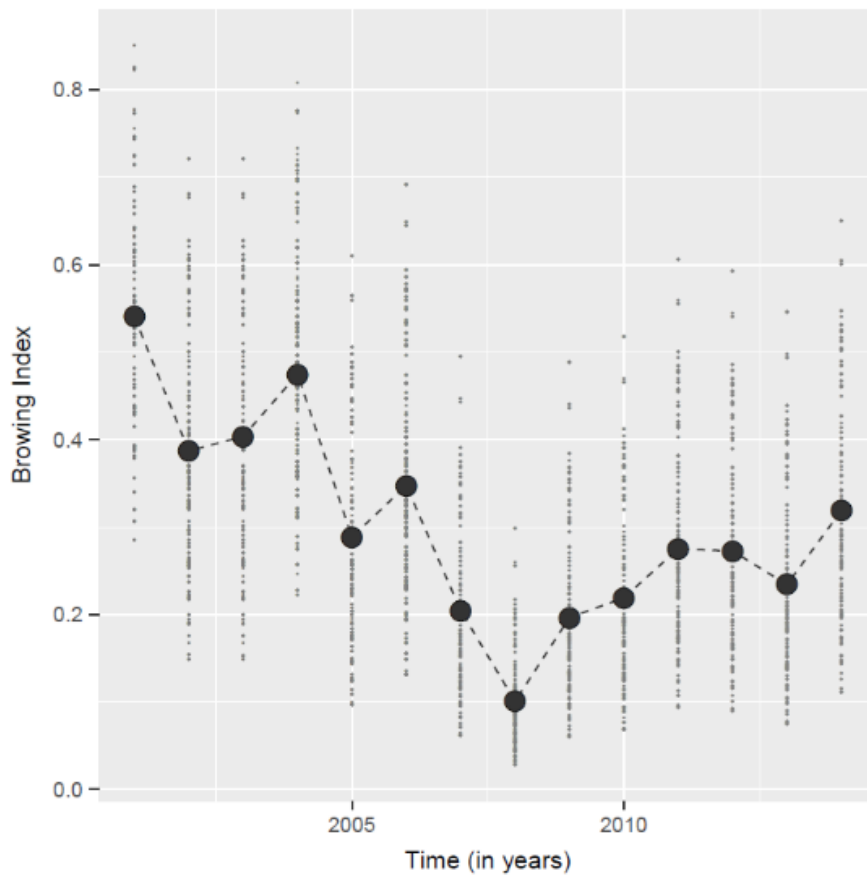
1128

1129

1130

1131

1132

1133

1134

1135

1136

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.