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

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20   *manuscript. All authors revised the manuscript.*

21

22   **Abstract**

23   In a context of rapidly changing carnivore populations worldwide, it is crucial to understand the

24   consequences of these changes for prey populations. The recolonization by wolves of the French

25   Vercors mountain range and the long-term monitoring (2001-2017) of roe deer populations provided

26   us a unique opportunity to assess both lethal and non-lethal effects of wolves on these populations.

27   We compared roe deer population abundance and growth, fawn body mass, and browsing intensity

28   in two contrasted areas: a central area (core of a wolf pack territory characterized by an intense use

29   by wolves) and a peripheral area (used more occasionally). Both populations of roe deer strongly

30   dropped after an extremely severe winter but the population of the central area facing with wolves

31   was slower to recover (due to a much lower growth rate the following year) and remained at lower

32   abundance levels for 5 years. Fawn body mass was lower in the central area during that period and

33   was not influenced by weather conditions or population abundance. The browsing index in the

34   forests in presence of wolves decreased for a longer period, suggesting that possible habitat shifts

35   have occurred. Altogether, the effects of wolves on the roe deer population in the central area

36   occurred mainly during a 5-year period following the establishment of wolves, with effects at the

37   population level in the first years only through the interplay between wolf predation (before wolves

38   started preying on red deer), harsh winter conditions and naïveté of prey to this recolonizing

39   predator.

40

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

42 **Introduction**

43 The main drivers of population dynamics of large herbivores have been studied into much details

44 over the last decades (e.g. Coulson et al. 2001; Gaillard et al. 2013 for case studies). The

45 consequences of density, weather, habitat quality or hunting on age-specific survival and

46 reproduction are well documented in many species of large herbivores, with increasing empirical

47 evidence of interactions among those limiting factors (Hone and Clutton-Brock 2007; Bonenfant et al.

48 2009). Predation is clearly a major driver of evolution and population dynamics of prey (Volterra

49 1931; Reznick et al. 2004). Understanding and measuring the consequences of predation on the

50 population dynamics of large herbivores is, however, much more complex than for most other

51 environmental variables. Consequently, important ecological questions such as whether large

52 herbivores are undergoing a bottom-up or to-down limitation are still debated (Hopcraft et al. 2010;

53 Laundré et al. 2014).

54 By killing prey and increasing mortality, predators are strongly expected to limit the

55 population growth rate of their prey but there are several arguments suggesting that prey

56 populations can support strong predation pressure. If mortality from predation is compensatory

57 because of density-dependence, population dynamics of prey may remain little affected by predation

58 until attack rates become really high and mortality from predation becomes additive to other sources

59 of mortality (Errington 1946). Similarly, the difference in spatial scale between the ranging behaviour

60 of large carnivores and herbivores leads to differences in densities of several orders of magnitude

61 between predators and prey (Skogland 1991). Consequently, large predators may have limited

62 consequences for population growth rate of prey and particularly so if predators are generalists and

63 can switch between different prey species (Murdoch 1969) or if they select juvenile or senescent

64 individuals because in large herbivores, the population growth rate is most sensitive to variation in

65 the survival of prime-aged adults (Gaillard et al. 2000). However, highly specialized predator species

66 or individuals can clearly reduce population growth rate and the abundance of large herbivores

67 (Festa-Bianchet et al. 2006; Bourbeau-Lémieux et al. 2011). For instance, roe deer *Capreolus*

68   *capreolus* dynamics is markedly affected by lynx *Lynx lynx* predation (Heurich et al. 2012; Andrén and

69   Liberg 2015) particularly so in winter when snow layer is thick, which greatly limits roe deer mobility

70   (Heurich et al. 2012).

71   In a context of rapidly changing abundance and distribution of mammalian apex carnivore

72   populations worldwide (Chapron et al. 2014; Ripple et al. 2014), it is important to understand the

73   consequences of these changes for prey populations and ultimately for ecosystem functioning. Even

74   though studies on these consequences have accumulated over the past decades, most of our current

75   knowledge comes from studies from North American National Parks (and particularly from the grey

76   wolf *Canis lupus* and elk *Cervus canadensis* of the Greater Yellowstone Ecosystem) as pointed out by

77   Kuijper et al. (2016). There is thus a need for studies from different contexts, particularly in Europe

78   where large carnivores live in or are recolonizing anthropogenic landscapes (Chapron et al. 2014).

79   Further, whether prey have continuously co-evolved with their predator or have evolved in a

80   predator-free environment for several generations due to predator extirpation from some

81   ecosystems may ultimately influence the extent to which prey are vulnerable to predators (Byers

82   1997; Berger et al. 2001). Indeed, naïve prey may fail to recognise the cues of a novel predator (but

83   see Chamaillé-Jammes et al. 2014) or may fail to respond appropriately and effectively to the risk of

84   predation by this predator due to the lack of experience (Banks and Dickman 2007; Carthey and

85   Banks 2014). For instance, along brown bear *Ursus arctos* recolonization fronts, brown bears killed

86   adult moose *Alces alces* at disproportionately high rates compared to sites where brown bears have

87   always been present (Berger et al. 2001). However, very little is known on how naïve prey respond to

88   recolonizing predators and how quickly they become effective at efficiently escaping these

89   predators.

90   In 1992, wolves crossed the Italian border to recolonize eastern France from where the

91   predator had been missing for ca. 100 years (Valière et al. 2003). In this work, we took advantage of

92   the long-term monitoring (17 years) of roe deer populations in the west Vercors mountain range

93   covering contrasting areas in terms on wolf occupancy and abundance to assess the occurrence and

94   relative impact of lethal and non-lethal effects of wolves on these roe deer populations, and the

95   duration of the naïve period in these roe deer populations. If predation by wolves and the associated

96   predation risk affect roe deer, we expect (1) a decrease in the roe deer population abundance and

97   growth rate, (2) a decrease in roe deer fawn body mass, and (3) a decrease in the herbivore pressure

98   on the vegetation, following the return of wolves.

99

100

101   **Materials and Methods**

102

103   *Study area*

104   The study was carried out between 2001 and 2017 over a study area of 30 776 ha encompassing six

105   neighbouring counties (Bouvante (8 431 ha), La Chapelle-en-Vercors (4 562 ha), Vassieux-en-Vercors

106   (4 798 ha), Saint-Julien-en-Vercors (1 867 ha), Saint-Martin-en-Vercors (2 700 ha), Saint-Agnan-en-

107   Vercors (8418 ha)) in the French department of Drôme, in the west Vercors mountain range (Fig. 1).

108   The west Vercors mountain range is characterized by an Alpine climate (identical to the Northern

109   Alps) with a forest dominated by beech *Fagus sylvatica* and silver fir *Albies alba*. The large herbivore

110   community is composed of roe deer, red deer *Cervus elaphus*, chamois *Rupicapra rupicapra*, mouflon

111   *Ovis gmelini*, and wild boar *Sus scrofa*. The six counties are used by people for agriculture, livestock

112   breeding, forestry, hunting, and outdoor recreational activities.

113

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

115   Wolves were extirpated from the Drôme department in 1901 (Faton and Ladreyt 1982). In 1998, the

116   first field evidence from prey carcasses, tracks and faeces suggesting the return of wolves from the

117   Italian Alps to the west Vercors mountain range were found (Valière et al. 2003). The ONCFS (French

118   National Hunting and Wildlife Agency) network "Grands Prédateurs" later confirmed the permanent

119   occupancy (3 individuals identified based on DNA analyses) and reproduction of wolves in the west

120   Vercors mountain range in 2003/2004 (ONCFS 2006). At this early stage of the recolonization, only

121   lone wolves or single pairs were observed. Since 2007/2008, wolves form packs of a minimum of five

122   individuals. In this study, we contrasted two main study areas based on the intensity of use by

123   wolves. The central area is the core of the west Vercors wolf pack territory (central area hereafter),

124   and encompasses the counties of Bouvante, Vassieux-en-Vercors and the western sector of La

125   Chapelle-en-Vercors (Fig. 1). The central area is characterized by an intensive use of the area by

126   wolves where sightings of wolves, wolf tracks, and wild prey carcasses are frequently reported. In

127   contrast, the peripheral area is used by wolves more occasionally, and encompasses the eastern

128   sector of La Chapelle-en-Vercors, Saint-Julien-en-Vercors, Saint-Martin-en-Vercors, and Saint-Agnan-

129   en-Vercors (Fig. 1).

130

131   ***Weather data***

132   We obtained weather data (daily rainfall and mean daily temperature) from Météo France for the

133   weather station La Chapelle-en-Vercors, which is representative of the west Vercors mountain range.

134   We calculated the Gaussen index (i.e. the amount of precipitation minus twice the mean

135   temperature) to measure the water deficit of plants in spring (April-June) and summer (July-August)

136   (e.g. Gaillard et al. 1997; Garel et al. 2004) to which roe deer are particularly susceptible (Pettorelli et

137   al. 2005). The Gaussen index is a proxy of the balance between rainfall and evapo-transpiration of

138   plants (Gaussen and Bagnouls 1953). High values of the Gaussen index mean positive water balance,

139   higher plant growth, and hence better foraging conditions for large herbivores, and conversely (Toïgo

140   et al. 2006). Winter can be very long in the west Vercors mountain range so this season was defined

141   from October to March. To characterize winter conditions, we collected information on snow-fall,

142   snow depth, and number of days with snow cover from the local skiing resorts in Bouvante. Because

143   of the strong correlation existing among winter variables, we performed a principal component

144   analysis (PCA) on these standardized variables. The first principal component (PC1) accounted for

145   62% of the overall variance, so we used the point projections on PC1 as a winter harshness index.

146   Low values of this index were associated with severe winters and hence more difficult conditions for

147   roe deer as harsh winters are generally associated with a lower survival of fawns (Gaillard et al. 1993)

148   and costly movements for large herbivores (Parker et al. 1984), which, in turn, could increase

149   predation rates (Mech et al. 2001).

150

151   ***Roe deer population abundance***

152   We monitored the abundance of roe deer populations in 5 of the 6 study counties because Bouvante

153   could not be monitored due to the deep snow cover that made most roads in this county inaccessible

154   at the time of surveys in all years. We drove along 3 transects located in the central area (1 transect

155   in the western sector of La Chapelle-en-Vercors and 2 transects in Vassieux-en-Vercors) and 3

156   transects in the peripheral area (1 transect in Saint-Agnan-en-Vercors, 1 transect across St-Julien-en-

157   Vercors and St-Martin-en-Vercors, and 1 transect in the eastern sector of La Chapelle-en-Vercors –

158   see Fig. 1). We carried out counts at night with a powerful spotlight reflecting animals' eyes. We

159   counted roe deer after winter, in March-April, when vegetation flush has not started yet, along roads

160   known to be practicable at that time of the year. We drove transects at low speed (10-15 km/h) with

161   one driver, two observers who spotted and identified all animals seen, and one person who recorded

162   the observations. We repeated counts twice a year between 2001 and 2004, three times a year

163   between 2005 and 2012, and four times a year since 2013. For the central and peripheral areas, we

164   obtained an abundance index of roe deer population (AI) by calculating the mean number of roe deer

165   seen per kilometre (see Pellerin et al. 2017 for a similar approach applied to diurnal car counts).

166   Finally, we derived the annual growth rate (r_t) of the yearly abundance indices as follows:

167    $r_t = \ln(AI_{t+1}/AI_t)$. We assumed that this growth rate provided a reliable proxy of roe deer population

168   growth from year t to year $t+1$.

169

170   ***Roe deer fawn body mass***

171   Twenty local hunting associations (which encompass 500 hunters) contributed to this study and were

172   equipped with a digital scale with an accuracy of 100 grams to weigh hunted roe deer. Between 2002

173   and 2007, hunters measured the full body mass of harvested roe deer, but have switched to dressed

174   body mass (i.e. guts, liver, heart and lungs removed) since 2007. Between 2007 and 2009, 43 local

175   hunting associations in the whole Drôme department were asked to measure both full and dressed

176   body masses. From a sample of 170 roe deer with the two measurements, we checked that a close

177   relationship existed between dressed and full body masses (dressed body mass = (0.837 x full body

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

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

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

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

182   deer fawns (individuals < 1 year when shot). We excluded body mass data from la Chapelle-en-

183   Vercors because the exact locations of where animals were shot were not recorded, which prevented

184   us from assigning the hunted roe deer of this county to the central vs. peripheral area.

185

186   ***Herbivore pressure on the woody vegetation***

187   Because changes in browsing pressure correlate with changes in the abundance of populations of

188   large herbivores (Morellet et al. 2001; Chevrier et al. 2012), we monitored the browsing pressure in

189   the forest habitats of the central area of the wolf pack territory (Bouvante, Vassieux-en-Vercors, and

190   the western sector of La Chapelle-en-Vercors) from 2001 to 2014. Unfortunately, such monitoring did

191   not take place in the peripheral area. One limit of such index is that it encompasses the browsing

192   pressure from all herbivore species. In the study system, this index encompasses the browsing

193   pressure from both roe deer and red deer. For this monitoring, we focused on the four main woody

194   plant species of the west Vercors mountain range (beech, silver fir, Norway spruce *Picea abies*, and

195   sycamore *Acer pseudoplatanus*). Every year in April-May, between snow melt and spring vegetation

196   flush, we monitored 86 quadrats (1 m²) distributed in the central area. In each quadrat, we recorded

197   whether one of these four species was present and whether these plants had been browsed in the

198   past growing season. Following Morellet et al. (2001), the browsing index was defined as

199      $B = (n_c + 1)/(n_p + 2)$ where n_p is the number of plots where at least one of the monitored species was

200   present, and n_c is the number of plots with at least one species consumed.

201

202   ***Analyses***

203   ***Roe deer abundance***

204   We analysed variation in roe deer abundance (assessed using the AI) with Generalised Linear Models

205   (GLMs) setting a logarithmic link function and a negative binomial distribution. We opted for a

206   negative binomial distribution because the model with a Poisson distribution did not fit the data well

207   (goodness-of-fit test: $\chi^2 = 1\,451.71$, df = 287, P < 0.001) resulting from over-dispersed count data (ver

208   Hoef and Boveng 2007). Even if we did our best not to change the road count protocol, transect

209   length did vary among years and across transects. Including an offset variable (log-transformed

210   number of kilometres) accounted for this heterogeneity in the data collection. We included a

211   categorical variable 'year' with 16 levels to test for temporal variation in roe deer abundance. We

212   investigated whether the temporal dynamics of roe deer abundance differed between the central

213   and peripheral areas by testing the first-order interaction between the effects of 'year' and 'wolf

214   area' (a 2-level categorical variable: "central area" and "peripheral area"). Finally, we fitted a model

215   where environmental covariates accounted for temporal variation in roe deer abundance and tested

216   the prediction that predation and winter conditions lead to decreasing population abundance with

217   the interaction term between the effects of the 'winter harshness index' and 'wolf area'. For the

218   population growth rate (r assessed from AI), we investigated the time variation using Gaussian linear

219   models; 'year' being entered as a categorical variable. We also fitted a model with first-order

220   interaction term between the effects of 'year' and 'wolf area'. For both AI and population growth

221   rate r assessed from AI, we assessed the statistical significance of all variables with likelihood-ratio-

222   tests (LRT).

223

Fawn body mass

225 We analysed fawn body mass of roe deer using Gaussian linear models. All models, consistently

226 included both sex (a 2-level categorical variable) and date of harvest (the number of days elapsed

227 since June 1st of the year of birth) as explanatory variables to account for fawn body growth over the

228 hunting season. We tested for temporal variation in average body mass of fawns by including 'year'

229 as a categorical variable. The interaction term between the effects of 'year' and 'wolf area' was also

230 included to test for possible difference in time variation in fawn body mass between the central and

231 peripheral wolf areas. We then quantified and tested for the effects of spring and summer Gaussen

232 index at year t, and of winter harshness for the winter season covering years t and $t+1$ on fawn body

233 mass from the hunting season covering years t and $t+1$ by replacing year with the corresponding

234 weather index in the model, one at a time. Again, we included the interaction term between the

235 effects of 'wolf area' and weather indices. For our model selection, we sequentially removed non-

236 statistically significant variables starting from the most complex model. We tested for the effect of

237 sex, date of harvest and year using LRT. For the effect of environmental covariates, we tested their

238 significance using an analysis of deviance (ANODEV) (Skalski 1996; Grosbois et al. 2008).

239

Browsing index

241 The browsing index can reasonably be approximated by a proportion of consumed plants by

242 herbivores. We hence modelled the browsing index using GLMs, with a logistic link function and a

243 binomial distribution to constrain the response variable within the 0–1 interval. Our model included

244 a random effect of the plot identity because of repeated measurements at the same place over

245 years. We found no evidence for spatial correlation among the plots, so we did not specifically model

246 plot location. We then added a year effect (a 14-level categorical variable) to test for an effect of

247 time on the average browsing rate. Again, we assessed the statistical significance of time variation in

248 the browsing index using LRT tests.

249

250   We performed all analyses with the statistical software R 3.4 (R Core Team 2018) extended with the

251   *MASS* package (Venables and Ripley 2002). We set the significance level to α = 0.05 and reported

252   estimates as mean ± 95% confidence interval unless otherwise stated.

253

254

255   **Results**

256

257   Weather variables (i.e. winter harshness index, spring and summer Gaussen indices) during the study

258   period are provided in Appendix 1. Winter 2004/2005 was the harshest of the time series, with a

259   record of snow-fall (total snow-fall = 498 mm, max snow depth = 140 mm) and snow duration

260   (number of days with snow cover = 110).

261

262   *Roe deer population abundance and growth rate*

263   The negative binomial model fitted the data satisfactorily (goodness-of-fit test: χ^2 = 292.55, df = 287,

264   P = 0.40). The AI of the roe deer population varied a lot between 2001 and 2017 (χ^2 = 97.60, df = 16, P

265   < 0.0001), with different patterns between the central and peripheral areas (interaction between

266   'year' and 'wolf area': χ^2 = 41.39, df = 16, P < 0.0001; Fig. 2A). Roe deer AIs were positively associated

267   between the central and peripheral areas except during the 2005-2010 period. In 2005, roe deer AI

268   decreased dramatically in both areas, coinciding with the most severe winter of the study period

269   (2004-2005). Between 2005 and 2010, roe deer AI remained low in the central area while it increased

270   in the peripheral area (Fig. 2A). Since 2011, the annual variation in roe deer AI was synchronous in

271   the two areas, as for the period 2001-2005 (Fig. 2A). Winter harshness did not account for temporal

272   variation observed in roe deer AI (χ^2 = 0.10, df = 16, P = 0.99).

273

274   All annual growth rates of AI were biologically realistic (i.e. < 0.4) except for two years (Fig. 2B),

275   which could be explained either by methodological biases (e.g. exceptional local conditions during

276   the counts) or by immigration. Figure 2B shows that the difference in roe deer AI between the two

277   areas for the period 2005-2010 resulted from the much lower growth rate in the central wolf area

278   between 2005 and 2006 compared to the peripheral area. After 2006, the annual growth rates were

279   rather similar in the two study areas (Fig. 2B). Despite the lowest growth rate occurred between

280   2004 and 2005 henceforth including the harshest winter, we could not detect any effect of any

281   weather variable on annual growth rates over the study period (spring Gaussen index: β = -0.00019 ±

282   0.00057, t = -0.34, P = 0.74; summer Gaussen index: β = 0.00036 ± 0.00061, t = 0.59, P = 0.56; winter

283   harshness index: β = 0.00018 ± 0.00038, t = 0.474, P = 0.64).

284

285   ***Roe deer fawn body mass***

286   Overall, we collected dressed body mass measurements for *n* = 428 roe deer fawns in the study area

287   from 2002 to 2016, both in the central (Vassieux-en-Vercors, Bouvante; n = 243) and the peripheral

288   (Saint-Julien-en-Vercors, Saint-Martin-en-Vercors, Saint-Agnan-en-Vercors; n = 185) areas. The mean

289   difference in fawn body mass between sexes was 372 ± 230 g (males heavier, as expected; Douhard

290   et al. 2017), and fawns gained on average 250 ± 90.3 g per month over the hunting season from

291   September to the following March. Mean body mass of fawns varied among years (*F* = 1.10, df = (14,

292   410), P < 0.01) but not differently between the central and peripheral wolf areas (interaction term

293   between 'year' and 'wolf area': *F* = 1.10, df = (12, 398), P = 0.35). Fawn body mass was on average

294   lower in the central than in the peripheral wolf area (0.700 ± 0.253 kg, *t* = 2.75, P < 0.01), consistently

295   between 2006 and 2011 but no clear patterns were detected before and after that period (Fig. 3).

296   The differences in mean fawn body mass among years and between areas were, however, rather low

297   (≤ 1 kg). Of the four environmental covariates (i.e. the 3 weather indices and the population

298   abundance index), none accounted for annual variation in fawn body mass (Table 1).

299

300   *Herbivore pressure on the vegetation*

301   The mean browsing index varied among years, between 0.10 in 2008 and 0.54 in 2001 (F = 22.27, df =

302   (13, 5046), P < 0.01; Fig. 4). In the central wolf area, the browsing indices markedly decreased in the

303   Vercors forests between 2001 and 2008, and continuously (but moderately) increased afterwards

304   (Fig. 4).

305

306

307   **Discussion**

308   Over the 17 years of our study, the roe deer population abundance patterns, as measured by the AI,

309   were similar in the central and peripheral areas but during the 5-year period between 2006 and

310   2010. During that period, roe deer abundance was lower in the central area, which corresponds to

311   the core of a wolf pack territory and is characterized by an intense use of the area by wolves.

312   Populations of roe deer strongly dropped between 2004 and 2005 in both the central and the

313   peripheral areas most likely because of the extreme severity of the winter 2004-2005, which was the

314   harshest winter throughout the 17-year study period. This is consistent with several previous studies

315   that showed that severe winters decrease survival of young and old individuals in populations of

316   large herbivores (e.g. Saether 1997; Gaillard et al. 2000 for reviews). Wolf predation is expected to

317   increase with snow depth. For instance, on the Isle Royale, wolves hunted in larger packs and tripled

318   the number of moose they killed per day in the snowiest years (Post et al. 1999). Likewise, the

319   relative importance of wolf predation on white-tailed deer *Odocoileus virginianus* mortality increased

320   with winter severity in Minnesota (DelGiudice et al. 2002). Such higher susceptibility of ungulates to

321   wolf predation during severe winters is associated with costlier and less efficient movements if

322   ungulates in deep snow (Parker et al. 1984).

323   The steep decrease of roe deer AI occurred in both the central and peripheral areas, but the

324   roe deer population was slower to recover in the central area. Something different occurred

325   between the two study areas during the period 2006-2010. As no change in forest management

326   occurred (Randon, pers. obs.), we can discard big change in resource availability to account for such a

327   difference. Likewise, possible competition with red deer (Richard et al. 2010) cannot be involved

328   because no detectable change in the red deer population abundance was detected during that

329   period (unpublished data; supported by the lack of increase of the browsing index). The two wolf

330   areas being very close geographically, differences in local weather conditions can also be excluded.

331   No disease outbreak was reported over the study period (Randon, pers. obs.). The yearly variation in

332   roe deer harvest bags was also similar in the two areas (Appendix 2). Predation by wolves is thus a

333   likely factor to explain the difference we observe in population dynamics between the central and

334   peripheral areas. This difference in population dynamics between 2006 and 2010 is due to a marked

335   difference in the growth rate reported in the AI between 2005 and 2006 only. Because growth rates

336   were not generally lower in the central area in the following years, this means that the mortality

337   caused by wolf predation on roe deer in the central area influenced roe deer populations for 2 years

338   only (2005 in interaction with the extreme winter severity and 2006 possibly still benefiting from the

339   naïveté of roe deer) and after may not be large enough to be captured in the abundance index.

340   The sample sizes of roe deer fawn body mass were rather low but allowed us to depict a

341   period (2006-2011) when body mass was lower in the central area than in the peripheral area. The

342   positive relationship between roe deer fawn body mass and roe deer AI we reported is opposite to

343   what was expected in presence of density-dependence (Bonenfant et al. 2009). Indeed, fawn body

344   masses were lower in 2006-2010 when roe deer AI was low abundance in the central area. Such

345   positive relationship has already been demonstrated in a study whereby bighorn sheep *Ovis*

346   *canadensis* lambs suffered mortality through reduced growth during years of high predation by

347   cougars *Puma concolor*, contributing a third of the total impact of predation on lamb survival

348   (Bourbeau-Lémieux et al. 2011); a study that illustrated a case of non-consumptive effects of

349   predation on a prey population. While our results may suggest such a mechanism, the alternative of

350   a delayed effect of the extremely rigorous winter 2004/2005 that led several consecutive cohorts to

351   be light, and hence prevented any relationship between average fawn body mass and population AI

352   cannot be discarded.

353   The changes of the browsing index in the central area indicates a decrease of the browsing

354   pressure on woody plants in forest habitats of the west Vercors mountain range. This decreased deer

355   pressure on vegetation may result from either a decline in deer abundance (which does not seem to

356   be the case when considering temporal variation in AI) or a change in foraging behaviour with an

357   increased use of suboptimal habitats (as shown in other systems, e.g. Creel et al. 2005; Valeix et al.

358   2009). This may be the case here but future studies involving detailed GPS monitoring of individual

359   roe deer are needed to investigate whether they alter their habitat use and selection as a response

360   to predation risk by wolves. The risk of predation alone can affect prey individual performance

361   through stress-mediated and food-mediated costs (Creel 2018; MacLeod et al. 2018). A study on

362   wolves in the Greater Yellowstone Ecosystem, where wolves are wide-ranging and active predators,

363   revealed that the behavioural responses of elk were not strong or frequent enough to lead to major

364   changes in individual performance and, hence, on population abundance (Middleton et al. 2013).

365   This may be the case in the present study because behavioural adjustments of roe deer to the risk of

366   predation by wolves are likely to carry costs at the individual level. However, it is noteworthy that the

367   difference in fawn body mass was low (~1kg) compared to differences previously reported in roe

368   deer in response to changes in density (about 2 kg in response to spatial variation in resources,

369   Pettorelli et al. 2003; > 3kg in response to population density, Douhard et al. 2013)) but these ones

370   do not translate into detectable changes in growth rates of AI, which are similar in the two

371   contrasting study areas.

372   Roe deer populations in the central and peripheral areas had similar patterns of temporal

373   variation of AI, growth rates and fawn body mass after 2011. This suggests that the effects of wolves

374   on the roe deer population in the central area occurred mainly during a five-year period following the

375   establishment of the pack, with effects at the population level in the first years only in interaction

376   with the harshest winter in 2004/2005. The little difference we reported between the central and

377   peripheral areas after 2011 may be explained by (i) a learning process to recognize wolf cues allowing

378   roe deer to escape from wolf predation (end of naïve period), and/or (ii) a predation shift by wolves,

379   which targeted their predation on red deer instead of roe deer (Appendix 3) with increasing pack

380   size.

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557

558 **Table 1**

559 Results from the analysis of deviance of the effect of environmental covariates on roe deer fawn

560 body mass in the west Vercors mountain range (both the central and peripheral areas of the wolf

561 pack territory). Data from dressed body mass measurements for n = 428 roe deer fawns harvested

562 between 2002 and 2016.

563

Environmental variable	Estimate	R²	ANODEV
Winter harshness index	-0.010 (0.118)	0.00	F = 0.004, df = (1, 13), P = 0.95
Spring Gaussen index	0.089 (0.113)	0.07	F = 1.17, df = (1, 14), P = 0.28
Summer Gaussen index	0.136 (0.113)	0.06	F = 0.84, df = (1, 14), P = 0.37
Population abundance index	0.215 (0.118)	0.13	F = 2.06, df = (1, 14), P = 0.17

564

565 **Figure legends**

566

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

568 counties (the small map of France in the left bottom corner shows the location of the Drôme

569 department in France). The red hatched area represents the central area of the west Vercors wolf

570 pack territory, while the dotted blue area represents the peripheral area. Coloured lines show the

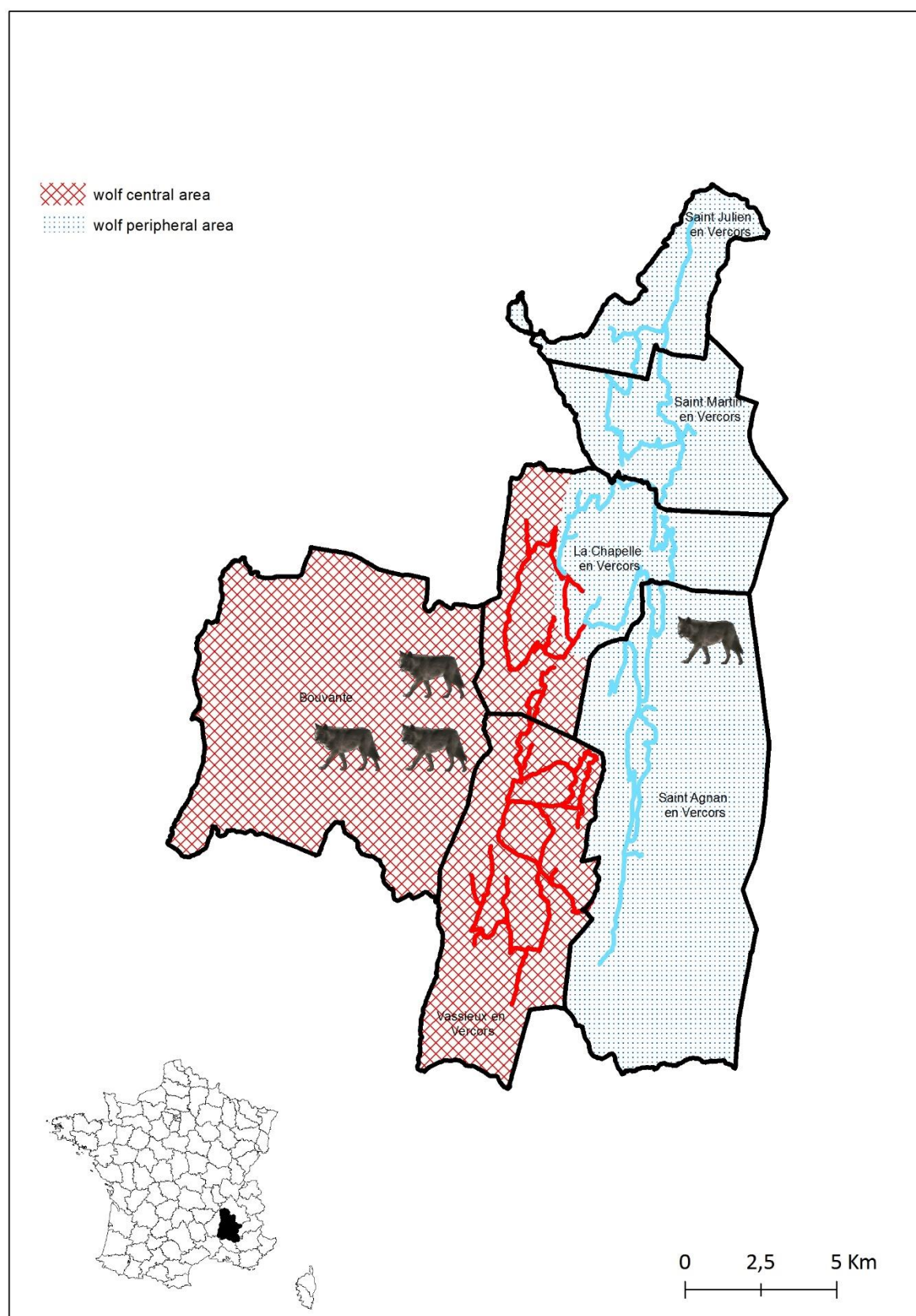571 transects for the monitoring of roe deer population abundance.

572

573 **Figure 2: A)** Changes in the abundance kilometric index of the roe deer populations in the central and

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

575 2001-2017. Bars represent the 95% confidence interval.

576 **B)** Changes in the population growth rates of the roe deer populations in the central and peripheral

577 areas of a wolf pack territory in the French west Vercors mountain range for the period 2001-2017.

578 In A and B, the grey area shows the period for which the abundance kilometric indices are different

579 between the central and peripheral areas.

580

581 **Figure 3:** Changes in the roe deer fawn body mass (corrected dressed body mass – see text for

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

583 mountain range. Bars represent the 95% confidence interval. The grey area shows the period for

584 which the body masses are different between the central and peripheral areas.
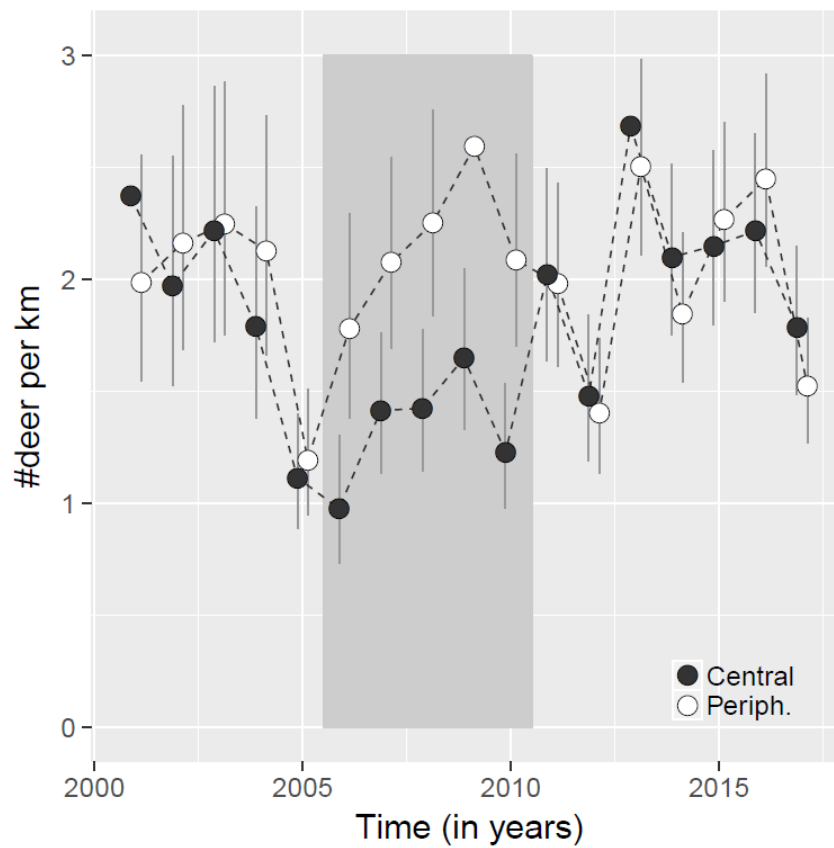
585

586 **Figure 4:** Changes in the browsing index (calculated for the four main woody plant species, i.e. beech,

587 fir, Norway spruce, and sycamore) in the central area of a wolf pack territory in the French west
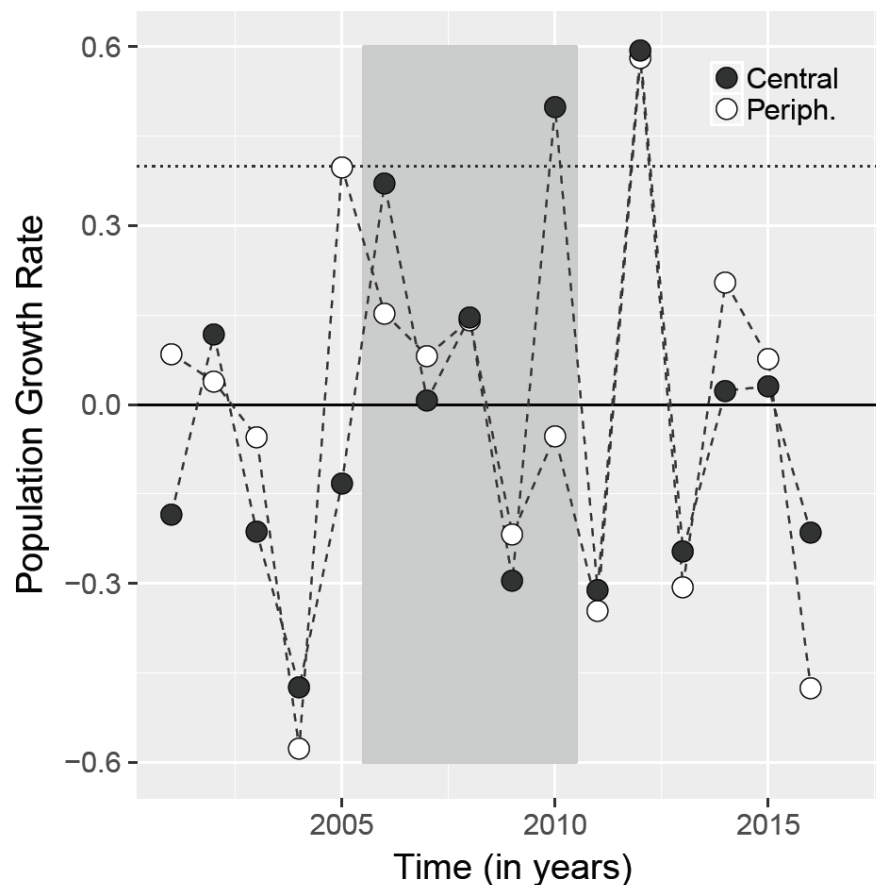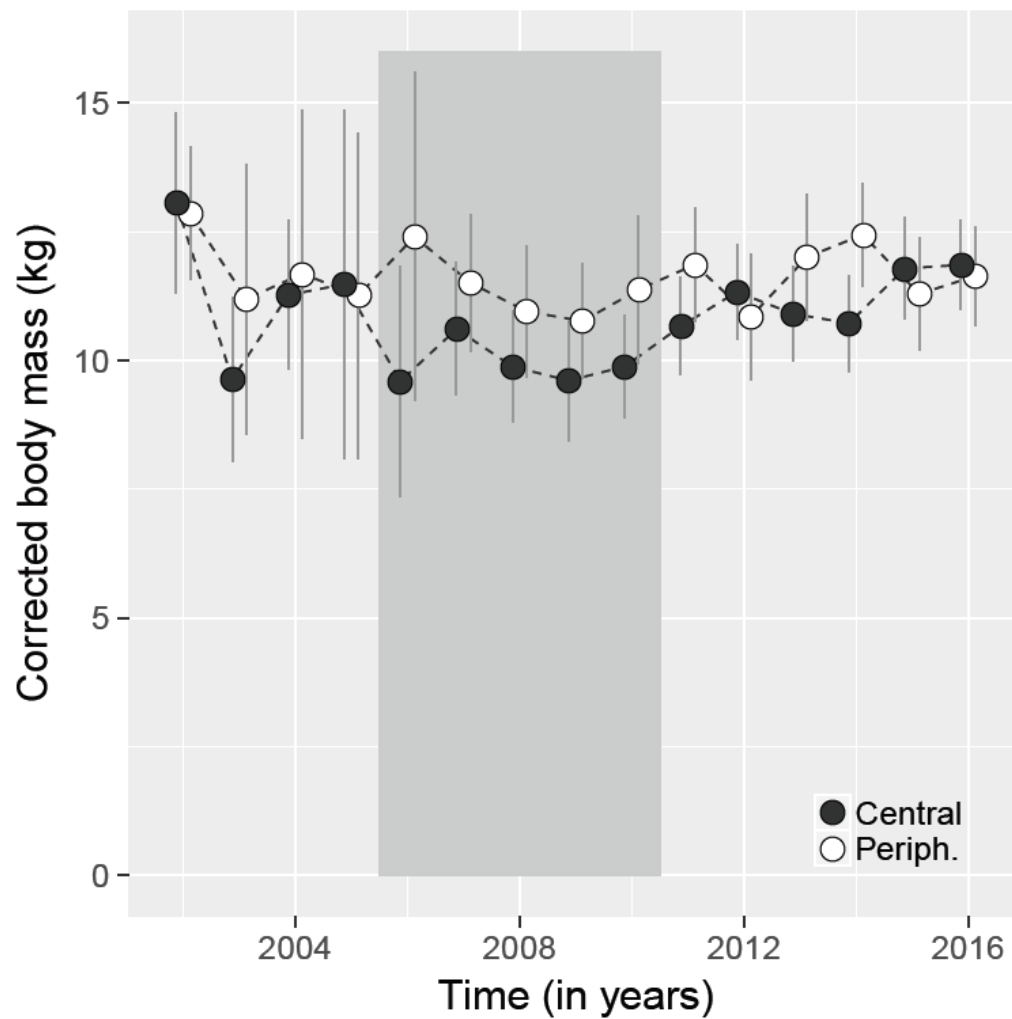
588 Vercors mountain range.

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590   **Figure 1**

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593 **Figure 2**

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595 **A)**

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607 **B)**

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619   **Figure 3**

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637   **Figure 4**

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