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2   **Role of prey and intraspecific density dependence on the population growth of an**

3   **avian top predator**

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23   **ABSTRACT**

24   Exploring predator–prey systems in diverse ecosystems increases our knowledge about

25   ecological processes. Predator population growth may be positive when conspecific

26   density is low but predators also need areas with prey availability, associated with

27   competition, which increases the risk of suffering losses but stabilizes populations. We

28   studied relationships between European rabbits *Oryctolagus cuniculus* (prey) and adult

29   eagle owls *Bubo bubo* (predators) in south–western Europe. We assessed models

30   explaining the predator population growth and stability. We estimated the abundance of

31   rabbits and adult eagle owls during three years in eight localities of central–southern

32   Spain. We explored models including rabbit and adult eagle owl abundance, accounting

33   for yearly variations and including the locality as a random variable. We found that

34   population growth of adult eagle owls was positive in situations with low conspecific

35   abundance and tended to be negative but approaching equilibrium in situations of higher

36   conspecific abundance. Population growth was also positively related to previous

37   summer rabbit density when taking into account eagle owl conspecific abundance,

38   possibly indicating that rabbits may support recruitment. Furthermore, abundance

39   stability of adult eagle owls was positively related to previous winter–spring rabbit

40   density, which could suggest predator population stabilization through quick territory

41   occupation in high–quality areas. These results exemplify the trade–off between prey

42   availability and abundance of adult predators related to population growth and

43   abundance stability in the eagle owl–rabbit system in south–western Europe. Despite

44   rabbits have greatly declined during the last decades and eagle owls locally specialize

45   on them, eagle owls currently have a favourable conservation status. As eagle owls are

46   the only nocturnal raptor with such dependence on rabbits, this could point out that

47   predators may overcome prey decreases in areas with favourable climate and prey in the

48   absence of superior competitors with similar foraging mode.

Abbreviations: RHD is rabbit hemorrhagic disease. N represents rabbit density, being $N_{W–Sp}$ the estimates in winter-spring and N_{Su} the estimates in summer. P is the abundance of adult eagle owls. PPG is the annual predator population growth. PRR is the predator rate of return to equilibrium

51 **1. Introduction**

52 Food availability is an essential requirement in predator populations, especially for

53 species linked to a given single prey species (Begon et al., 1996). In territorial species,

54 individuals wait for an opportunity to occupy territories with high food resources. These

55 territories may allow them to meet their objectives e.g. survival and reproduction

56 (Stamps, 1994). However, it may also imply high competition, which increases the risk

57 of suffering losses in the population, especially in species that are highly territorial and

58 aggressive (López–Sepulcre and Kokko, 2005). If a territory becomes vacant it would

59 be quickly occupied, benefiting predator population stability (López–Sepulcre and

60 Kokko, 2005). This is especially clear in avian top predators, which have higher ability

61 to quickly move between areas in order to find locations with the best conditions

62 (Penteriani et al., 2005b). Nevertheless, poor territories may not permit continued use

63 and predators may have to continue searching in other areas (Penteriani et al., 2005b).

64 Altogether, food availability and intraspecific density could be important factors

65 determining population dynamics of predators.

66 Eagle owls *Bubo bubo* are sit–and–wait top predators that are widely distributed

67 in Eurasia and northern Africa (Mikkola, 1983). In the Iberian Peninsula this species is

68 relatively common and shows high reproductive performance, mainly because of

69 favourable climate and dietary local specialization on European rabbits *Oryctolagus*

70 *cuniculus* (Donázar, 1990; Pérez–García et al., 2010). This lagomorph species is highly

71 rewarding because of its suitable size for large predators, and relative ease of capture

72 (Delibes–Mateos et al., 2008a; Ferrer and Negro, 2004; Penteriani et al., 2008). In

73 recent decades rabbit populations have undergone dramatic declines as a result of the

74 incidence of myxomatosis and the rabbit hemorrhagic disease (RHD). For instance,

75 Moreno et al. (2007) recorded a rabbit population crash in Doñana (south–western

76   Spain), where rabbit abundance is currently less than 10% prior to the arrival of the

77   disease. Similar rabbit abundance reductions have allowed reporting the eagle owl

78   numerical response in terms of population size and breeding performance (Martínez and

79   Calvo, 2001; Martínez and Zuberogoitia, 2001). Despite these reports, the relationships

80   between eagle owls and rabbits have not yet been adequately assessed in south–western

81   Europe. All this information is especially relevant after the recent arrival of a new RHD

82   strain to Iberia (Abrantes et al., 2013) that may cause further declines of rabbit

83   populations and unexpected consequences for the rabbit dependent predators, such as

84   the eagle owl (Penteriani et al., 2008).

85   To improve understanding of the effects of food availability and abundance of

86   adult conspecifics on predator population growth and stability we estimated rabbit and

87   adult eagle owl abundance in several localities of central–southern Spain during several

88   years. Rabbits were the main prey of eagle owls, at least at the localities with higher

89   densities of rabbits (range of biomass consumed by eagle owls = 73–89%, Tobajas,

90   2012). We performed several analyses accounting for locality and seasonal variations.

91   We assessed models for explaining eagle owl population growth that included rabbit

92   and adult eagle owl abundance. We also assessed similar models for explaining

93   abundance stability of adult eagle owls. Finally, in the light of our results, we discussed

94   the potential of predators to overcome main prey declines.

95

96   **2. Materials and methods**

97   **2.1. Study areas**

98   We carried out field work in 8 sites of central–southern Spain (localities 1–8 in

99   Fernandez–de–Simon et al., 2011) that differed in rabbit density. All localities have

100   Mediterranean climate characterized by mild wet winters, and warm dry summers.

101 Habitat composition was also similar in all localities and mainly consisted of

102 Mediterranean scrublands, pastures, croplands, dehesas (savanna–like formations that

103 combine pasture with intermittent cereal cultivation in park–like oak woodlands;

104 Blondel and Aronson, 1999) and tree plantations. Localities had gentle slopes and

105 ecotones between Mediterranean scrublands and pastures or croplands favourable for

106 rabbits (Lombardi et al., 2003). Low cliffs that are the preferred nesting habitat for eagle

107 owls were also available.

108 **2.2. Rabbit surveys**

109 We counted rabbits at each locality along a transect (mean ± SE = 14.91 ± 0.59 km,

110 range = 7.1–17.2 km) driven at night (starting 2 h after sunset) and using a spotlight.

111 The surveys were conducted in good weather conditions (no strong winds or rainfall;

112 Fernandez–de–Simon et al., 2011) and traversing ecotone areas which are favourable to

113 rabbits but also to eagle owls in order to hunt rabbits (Lombardi et al., 2003; Ortego and

114 Díaz, 2004). Counts were performed in different yearly seasonal periods to account for

115 varying rabbit densities according to the annual cycle of rabbit reproduction and

116 abundance (Moreno et al., 2007). The surveys were carried out in winter–spring (mainly

117 February–March) of years 2007, 2008 and 2009, and in summer (mainly June–July) of

118 years 2007 and 2008. Because of logistical limitations we could not conduct the counts

119 in a locality during the winter–spring of year 2009 (see locality 5 in Appendix). We

120 counted rabbits at each locality on three–four consecutive nights unless climatic or

121 logistical factors prevented from doing so. We estimated rabbit density (individuals per

122 hectare, hereafter N) at each locality and season using the distance sampling method

123 (Buckland et al., 1993), with the Fourier series estimator as the detection function in

124 TRANSECT software (Burnham et al., 1980). For a detailed description of the method,

125 see Fernandez–de–Simon et al. (2011).

126   **2.3. Adult eagle owl surveys**

127   Adult eagle owls typically call during twilight hours for either mating or territorial

128   purposes (Delgado and Penteriani, 2007). The annual eagle owl pre–laying period

129   occurs from September to January in our study areas (Delgado and Penteriani, 2007).

130   Playback surveys were conducted during winters (November–January) of years 2006–

131   2007, 2007–2008 and 2008–2009. As for spotlight rabbit counts, surveys were carried

132   out on nights with good weather (no strong winds or rainfall; Penteriani, 2003). Each

133   survey commenced 15 min after sunset and lasted 2 h at most. Surveys involved five

134   stations per night and locality although, because of weather or logistic limitations,

135   exceptionally less than five stations per night were surveyed. Stations were located

136   along the spotlighting transect with a separation of 1.5–2 km between them. At each

137   station a three–minute recording of the "oohu" hoot of adults was broadcasted from a

138   CD/MP3 device connected to a pair of loudspeakers (PRO BASIC 10W PMPO) (Fuller

139   and Mosher, 1987). We listened for eagle owl calls for 10 min following the broadcast,

140   which were considered adequate because 85% of eagle owl calls occurred within the

141   first five minutes. Calls from different directions were considered to correspond to

142   different individuals. During winter 2006–2007 we undertook only one survey per

143   locality but, in order to reduce variability (authors, unpublished data; Penteriani et al.,

144   2002a), we repeated the surveys on three–four consecutive sunsets per locality at the

145   same stations in subsequent winters. As for spotlight rabbit counts, the survey could not

146   be conducted in a locality during 2008–2009 winter. The mean number of individuals

147   per playback for each winter and locality was used as a predator (adult eagle owls)

148   abundance index (hereafter P). We also estimated the annual population growth of adult

149   eagle owls for each locality and consecutive years by applying the formula:

150        $PPG = \ln(P_t/P_{t-1})$

151   Where *PPG* is the annual predator (adult eagle owls) population growth and P_t

152   and P_{t-1} are the abundance indices of adult eagle owls in a given winter and in the

153   previous winter respectively.

154   Furthermore, we computed the predator rate of return to equilibrium (hereafter

155   *PRR*) as the absolute value of the *PPG* (Sibly et al., 2005). This allows to test if

156   abundance of adult eagle owls changed between years or was rather stable (i.e. rate of

157   return close to zero).

158   **2.4. Statistical analyses**

159   *2.4.1. Which model best explains the annual population growth of adult eagle owls?*

160   We compared various generalised mixed models, using *PPG* as dependent variable

161   (Table 1). They were based on the linear response to previous winter–spring rabbit

162   density ($N_{\text{W–Sp}}$), and the linear response to previous summer rabbit density (N_{Su}) as

163   independent variables. We also used the natural logarithm of *P* in previous winter (Sibly

164   et al., 2005). The locality was included in the models as a random variable (Zuur et al.,

165   2009). The year variable was also included to control the possible effect of year in our

166   models (Hurlbert, 1984). We also included a model with the year variable only. The

167   comparison with a null model (intercept only) served as an overall performance

168   indicator of the models. This summed 9 single–effect models and we considered as the

169   most parsimonious model that with the lowest AICc value (Burnham and Anderson,

170   2002). Differences in AICc (Δi) > 2 between a given model and the model with the

171   lowest AICc indicated little or no empirical support for that model. In addition to model

172   weights, we calculated the weights of individual variables to look for informative

173   parameters and models (Arnold, 2010). Sample size (n = 15) was equal for all models.

174   We tested the normality, linearity and homocedasticity of model residuals and variables

175   used. If necessary we transformed variables by means of e.g. using the decimal

176 logarithm. We also show parameters and probability values of individual variables in

177 the best models but do not set a critical probability threshold since we are more

178 interested in inference than in hypothesis testing. Thus we have considered models with

179 non-significant variables ($p > 0.05$), even so included for inference purposes (Burnham

180 and Anderson, 2002).

181 *2.4.2. Which model best explains the annual rate of return to equilibrium of adult eagle*

182 *owls?*

183 We developed generalised mixed models similarly as in the previous section but using

184 *PRR* as dependent variable. We again assessed models with rabbit and adult eagle owl

185 abundance (see also Table 1). In this case we used *P* instead of its natural logarithm as

186 independent variable as we did not have a previous hypothesis that the relationship

187 could have a curvilinear natural logarithmic shape. We accounted for seasonal and

188 locality variations. Model selection was performed according to the AICc criteria. We

189 also tested the normality, linearity and homocedasticity of model residuals and variables

190 used (see section 2.4.1). We used R version 3.0.1 (R Development Core Team, 2013) to

191 perform all the analyses.

192

193 **3. Results**

194 **3.1. Rabbit and adult eagle owl abundance**

195 Mean *N* estimated for each locality ranged from 0.01 to 1.22 rabbits per hectare in

196 winter–spring, and 0–1.5 rabbits per hectare in summer (Appendix). We recorded adult

197 eagle owl presence at all localities and years (mean $\pm$ SE = 0.98 $\pm$ 0.16 individuals per

198 playback, range of means of all localities = 0.31–2.2 individuals per playback,

199 Appendix), and population was close to stability (i.e. mean *PPG* was close to zero,

200 mean $\pm$ SE = –0.06 $\pm$ 0.24).

201 **3.2. Which model best explains the annual population growth of adult eagle owls?**

202 Two models of *PPG* obtained $\Delta i < 2$. The first model included P in the previous winter,

203 N_{Su} (log–transformed) and the effect of year (Table 1 and 2). The second model

204 included P in the previous winter and the year variable (Fig. 1; Table 1 and 2).

205 Summing their model weights totalled 0.61. The largest individual weight was obtained

206 by P in the previous winter (weight = 0.77), followed by N_{Su} (0.46) and then N_{W-Sp}

207 (0.19).

208 **3.3. Which model best explains the rate of return to equilibrium of adult eagle**

209 **owls?**

210 The model of *PRR* including N_{W-Sp} (log-transformed) and year was the only one with Δi

211 < 2 (Table 1 and 2). It also accounted the largest model weight (0.68). Hence, *PRR* was

212 negatively related to N_{W-Sp} (Fig. 2). This model indicates that P was more stable at high

213 N in the previous winter–spring (Fig. 2; Table 1 and 2). We found the largest individual

214 weight in N_{W-Sp} (weight= 0.77), followed by N_{Su} (0.11) and P (0.1).

215

216 **4. Discussion**

217 Eagle owl population growth was related to rabbit density and abundance of adult

218 conspecifics in the previous winter, according to models taking into account year and

219 locality variations. These results could reflect the trade–off between food and

220 intraspecific competition in predator–prey systems such as the eagle owl–rabbit system

221 of south–western Europe.

222 Rabbits could partly determine adult eagle owl abundance changes in southern

223 Europe (Martínez and Calvo, 2001; Martínez and Zuberogoitia, 2001; Penteriani et al.,

224 2002b). We found a positive relationship between N_{Su} and population growth of adult

225 eagle owls when controlling for eagle owl conspecific abundance in the models. This

226 could indicate the important role of rabbits for eagle owl juveniles, as the postfledging

227 period prior to dispersal is risky for their survival (Penteriani et al., 2005a) and enough

228 food availability could be helpful for them (but see Sergio et al., 2004). In addition, the

229 estimates of *PRR* showed that changes in adult eagle owl abundance between years

230 were less pronounced with higher $N_{\text{W–Sp}}$. The latter could be the result of a stabilizing

231 effect of rabbit density in high–quality conditions (Pérez–García et al., 2012). Though

232 we lack information of breeding territories in these areas, this abundance stabilization

233 might be explained by floaters that would quickly occupy vacant territories with high

234 $N_{\text{W–Sp}}$ when available (Delgado et al., 2010). In the opposite situation could be localities

235 with low $N_{\text{W–Sp}}$ and with abundance of adult eagle owls either strongly decreasing or

236 increasing. This could be a consequence of individuals searching a territory with

237 sufficient food resources such as alternative prey of medium size (Donázar, 1989;

238 Martínez and Zuberogoitia, 2001; Serrano, 2000; Tobajas, 2012). If eagle owls do not

239 find these food resources, they might not persist (Penteriani et al., 2002b).

240   We found a logarithmic and negative curvilinear relationship between the *PPG*

241 and *P*. Eagle owls are territorial birds, and form nesting pairs that mate annually for

242 several years (Mikkola, 1983). As it occurs in other territorial raptor species (Valkama

243 et al., 2005), the greatest densities appear in high–quality territories with high food

244 availability (see above). In these conditions intraspecific density dependence with adult

245 conspecifics could play a prominent role. Our results show that population growth of

246 adult eagle owls between consecutive years is positive at low eagle owl abundance and

247 negative at higher abundance, promoting eagle owl stability near abundance

248 equilibriums (López–Sepulcre and Kokko, 2005). This result would suggest the

249 existence of some degree of interference between individuals in the populations

250 surveyed.

251   These results show the dynamics of the eagle owl–rabbit system in the range of

252   low to moderate densities for both species. To our knowledge, the only density

253   estimation of eagle owl for our localities corresponds to moderate values (1.96

254   territories/100 km^2 in locality 3 in winter 2004–2005; De la Dueña and López, 2007).

255   This density could have remained close to this value during our study as (i) our surveys

256   began two years later (winter 2006–2007), (ii) rabbit densities did not greatly change

257   during these years (0–1 rabbits per hectare, De la Dueña and López, 2007), and (iii)

258   large modifications in habitat composition or structure did not occur since it is a

259   protected area (Lagunas de Ruidera Natural Park). As this locality ranked 2nd in P

260   (Appendix), eagle owl density may be low to moderate in most localities. This could

261   also be applicable to rabbits as the densities estimated are in the range 0–1.5 rabbits per

262   hectare. Therefore future studies should try to elucidate these relationships in higher

263   densities of both eagle owls and rabbits for a better understanding of the system (but see

264   Pérez–García et al., 2012).

265   Several facts about our eagle owl and rabbit abundance estimates should be

266   considered. First, eagle owls might move between posts (Delgado and Penteriani, 2007),

267   and we rarely saw them during playbacks (authors, unpublished data). This could inflate

268   abundance estimates as detection of individuals is based on calls from different

269   directions. Nevertheless, the mean P and its standard error were relatively low,

270   indicating that large numbers per playback were rare and estimates should not be

271   excessively affected. Second, calling behaviour might change depending on eagle owl

272   activity (Delgado and Penteriani, 2007). In this sense, we always used the same method

273   in the same time period and then the error should always be similar. Third, we preferred

274   the use of playbacks instead of listening of spontaneous calls (Martínez and

275   Zuberogoitia, 2002), as adult eagle owls usually are more silent at low densities (see

276   above; Penteriani, 2003), and otherwise it would be difficult to detect their presence (De

277   la Dueña and López, 2007). Fourth, although the distance between call posts of the

278   nearest neighbour adult eagle owl males could be up to 2.5 km, the mean value was 1.16

279   km (Delgado and Penteriani, 2007) which suggests that our 1.5–2 km distance between

280   playback stations provides a great probability of detection of different individuals. Fifth,

281   both P and N estimates are relatively low and the results could be more sensitive to the

282   imprecision of these estimates. However, the information from these variables was

283   obtained from several replicates of the methods used, which provide more reliable

284   results (Hurlbert, 1984). Altogether, future studies should improve abundance estimates

285   by including additional methods that allow individual standardisation as, for instance,

286   studying eagle owl sonograms (see Penteriani, 2003). This could also be applicable to

287   our N estimates from spotlight rabbit counts. Although the latter have been considered a

288   reference method (Fernandez–de–Simon et al., 2011), it may also need further testing

289   by comparisons against e.g. live–trapping and capture–mark–recapture density estimates

290   (King and Wheeler, 1985; Marchandeau et al., 2006). Nevertheless in this study with a

291   regional scale and the resources available we could consider our indices as cost–

292   efficient (Sutherland, 2006).

293   Another potential downside arises from the fact that, while generally studies of

294   this kind have surveyed predators and prey during decades (e.g. moose–wolf

295   interactions at Isle Royale, Jost et al., 2005), our monitoring period covered only three

296   years. Although PPG could be meaningful to detect annual changes of adult abundance,

297   it might not capture potential variation that could appear on the long run, especially for

298   a long–lived species such as the eagle owl (Mikkola, 1983). However as young eagle

299   owls reach sexual maturity in their first year (König and Weick, 2008) we still feel that

300   PPG and PRR are measures of abundance change as they compare abundance of adult

301   individuals between two consecutive years which may differ annually due not only to

302   productivity and survival, but also to immigration and emigration (Begon et al., 1996).

303   We encourage future studies with intensive monitoring of predator and prey populations

304   to provide more understanding of the numerical response (see e.g. Hone et al., 2007;

305   Rohner 1995, 1996). Anyway, in this study the use of a regional approach provided a

306   wide range of abundance estimates and valuable large–scale observations of dynamics

307   of natural species in their home–range conditions.

308   The best models obtained intermediate levels of support (sum of model weights

309   for the best models, i.e. $\Delta i < 2$, explaining *PPG* and *PRR* are 0.61 and 0.68

310   respectively). Moreover, some of the variables included were not significant, which

311   provide discordant results considering that they appear in the best models. That is the

312   case of the year variable, which was kept in all models to control for its effect on the

313   response variable (Hurlbert, 1984). With our model selection procedure we maximise

314   inference (Burnham and Anderson, 2002), getting the most parsimonious models that

315   depict a valuable picture of the role of rabbit abundance and intraspecific density

316   dependence on eagle owl population growth, while taking into account year and locality

317   variations. Again future studies should make further progress by conducting refined

318   surveys with intensive and long term monitoring of populations of both prey and

319   predators (see e.g. Penteriani et al., 2005b; Fargallo et al., 2009) but also experimentally

320   test the effect of the variables studied here (Begon et al., 1996).

321   The abundance of rabbit populations in Iberia is undoubtedly very low if

322   compared to few decades ago (Moreno et al., 2007; Delibes–Mateos et al., 2008b;

323   2009). Eagle owls have also experienced human–induced mortality and habitat

324   modifications (Marchesi et al., 2002). Nevertheless the contraction in the eagle owl

325   distribution has been relatively small (mainly in northern Spain, Martínez et al., 2006).

326 In fact, eagle owls were present in all localities in our study, according to their good

327 conservation status in central–southern Spain (Martínez and Zuberogoitia, 2003). Then,

328 how have eagle owls overcome the rabbit decline? From the 24 predator species that

329 frequently consume rabbits in Mediterranean Iberia (i.e. those with >5% of rabbits in

330 diet, Delibes–Mateos et al., 2008a), only two are nocturnal raptor species: Eagle owls

331 and tawny owls *Strix aluco*, but the latter mainly prefer prey of smaller size (Villarán,

332 2000). Therefore, the eagle owl is the only nocturnal raptor that preys heavily on

333 rabbits, where they are available (Penteriani et al., 2008) in an area that is already

334 favourable climatically for eagle owls (Donázar, 1990). Although they may also feed on

335 other prey (see above), their productivity in Iberia is highest when rabbits are abundant

336 (Pérez–García et al., 2010). This altogether suggests that with optimum climatic

337 conditions and prey (Donázar, 1990; Penteriani et al., 2008) predators could overcome

338 their main prey declines in the absence of superior competitors with similar foraging

339 mode (Schoener, 1974).

340

341 **5. Conclusions**

342 This study shows the potential relationship of food density and adult conspecifics on the

343 abundance changes of this bird of prey. On the one hand, the role of rabbits seemed

344 directly related to boost the abundance of adult eagle owls but also stabilize their

345 population. On the other hand, adult conspecifics may reduce population growth of

346 adult eagle owls with a trend towards stabilization in situations of relative high

347 abundance of adult conspecifics. This reflects an ecological trade–off that may influence

348 population dynamics. We show these patterns from a regional approach which could

349 help us to understand the interrelations between predators and their main prey when

350 studies with long–term datasets collected at specific localities are absent. For that

351   reason, more research is needed to complete our understanding of the factors that

352   explain predator and prey abundance. In Iberia, this will be greatly welcome as a new

353   strain of RHD could be producing again high mortalities in European wild rabbit

354   populations and the consequences for their dependent predators remain largely

355   unexplored.

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538 **Tables**

539 **Table 1**

540 Generalised mixed models used to explain the annual population growth (PPG) and the

541 rate of return to equilibrium (PRR) of adult eagle owls. P is the abundance index of

542 adult eagle owls in winter, $N_{W–Sp}$ is winter–spring rabbit density and N_{Su} is summer

543 rabbit density (see text for further details). The locality is included as a random variable.

544 The models with $\Delta i < 2$ are shown in bold and labelled with numbers between

545 parenthesis (1, 2 and 3, see also Table 2). The degrees of freedom may vary between

546 models.

Dependent variable	Model and independent variables	AICc	Δi	Weight
PPG	**(1) ln(P) + Log(N_{Su}) + Year**	**42.95**	**0**	**0.42**
	(2) ln(P) + Year	**44.58**	**1.63**	**0.19**
	Year	44.97	2.02	0.15
	ln(P) + Log($N_{W–Sp}$) + Year	45.01	2.06	0.15
	Null model	47.73	4.78	0.04
	Log(N_{Su}) + Year	49.02	6.07	0.02
	ln(P) + Log($N_{W–Sp}$) + Log(N_{Su}) + Year	49.16	6.22	0.02
	Log($N_{W–Sp}$) + Year	49.54	6.6	0.02
	Log($N_{W–Sp}$) + Log(N_{Su}) + Year	54.74	11.79	<0.01
PRR	**(3) Log($N_{W–Sp}$) + Year**	**29.03**	**0**	**0.68**
	Null model	33.02	3.99	0.09
	Log(N_{Su}) + Year	33.7	4.67	0.07
	Year	33.92	4.89	0.06

Log(P) + Log($N_{\text{W–Sp}}$) + Year	34.33	5.3	0.05
Log($N_{\text{W–Sp}}$) + Log(N_{Su}) + Year	34.61	5.58	0.04
Log(P) + Year	37.64	8.62	0.01
Log(P) + Log(N_{Su}) + Year	39.41	10.39	<0.01
Log(P) + Log($N_{\text{W–Sp}}$) + Log(N_{Su}) + Year	41.56	12.53	<0.01

547

548

549 **Table 2**

550 Parameters of models explaining annual population growth (*PPG*) and the rate of return

551 to equilibrium (*PRR*) of adult eagle owls. ln(*P*) is the natural logarithm of the previous

552 winter abundance of adult eagle owls, Log(N_{W-Sp}) is the decimal logarithm of the

553 previous winter–spring rabbit density and Log(N_{Su}) is the decimal logarithm of the

554 previous summer rabbit density. Only models with $\Delta i < 2$ are shown. These models are

555 labelled with numbers between parentheses in Table 1. See text for further details.

| Model (1)		Coefficient	Std. Error	t value	Probability value
PPG	Intercept	−1	0.25	−3.99	0.005
	Year 2008	0.44	0.34	1.31	0.26
	ln(*P*)	−0.78	0.21	−3.65	0.02
	Log(N_{Su})	3.27	1.23	2.66	0.06
Model (2)					
PPG	Intercept	−0.59	0.24	−2.42	0.05
	Year 2008	0.7	0.39	1.77	0.14
	ln(*P*)	−0.5	0.23	−2.19	0.08
Model (3)					
PRR	Intercept	1.34	0.19	6.97	<0.001
	Year 2008	−0.45	0.21	−2.13	0.09
	Log(N_{W-Sp})	−4.25	1.21	−3.5	0.02

556

557

558 **Figure legends**

559 **Fig. 1.** Annual population growth of adult eagle owls (*PPG*) in years 2007 (white

560 points, solid line), and 2008 (black points, dashed line) as a function of the natural

561 logarithm of the abundance index of adult eagle owls (eagle owls per playback, *P*) in the

562 previous winter, according to one of the most parsimonious generalised mixed models,

563 which takes into account the locality as random variable (Model (2), see Table 1 and 2).

564 The equation of the model is the following: $PPG = -0.59 + 0.7 \times (Year2008) - 0.5 \times \ln(P)$
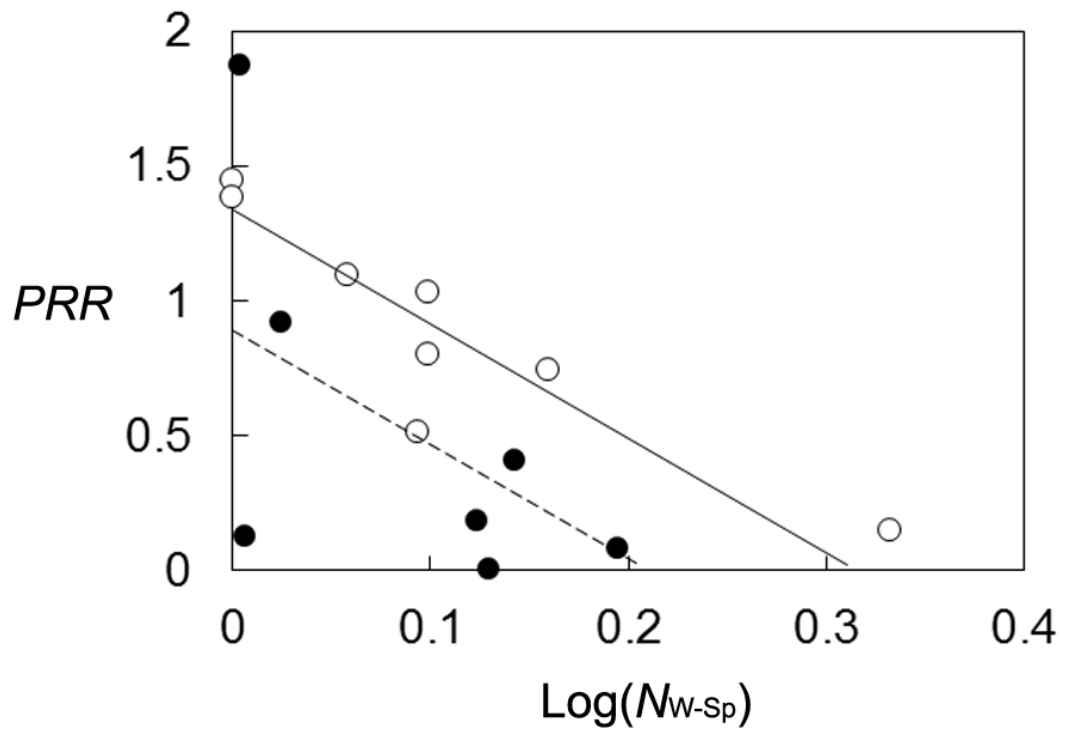
565 **Fig. 2.** Annual rate of return to equilibrium of adult eagle owls (absolute values of

566 population growth, *PRR*) in years 2007 (white points, solid line) and 2008 (black points,

567 dashed line) as a function of rabbit density (rabbits per hectare, N_{W-Sp}, log–transformed)

568 in the previous winter–spring, according to the most parsimonious generalised mixed

569 model, which takes into account the locality as random variable (Model (3), see Table 1

570 and 2). The equation of the model is the following: $PRR = 1.34 - 0.45 \times (Year2008) -$

571 $4.25 \times Log(N_{W-Sp})$

572

573   **Fig. 1.** (1.5-column fitting image)
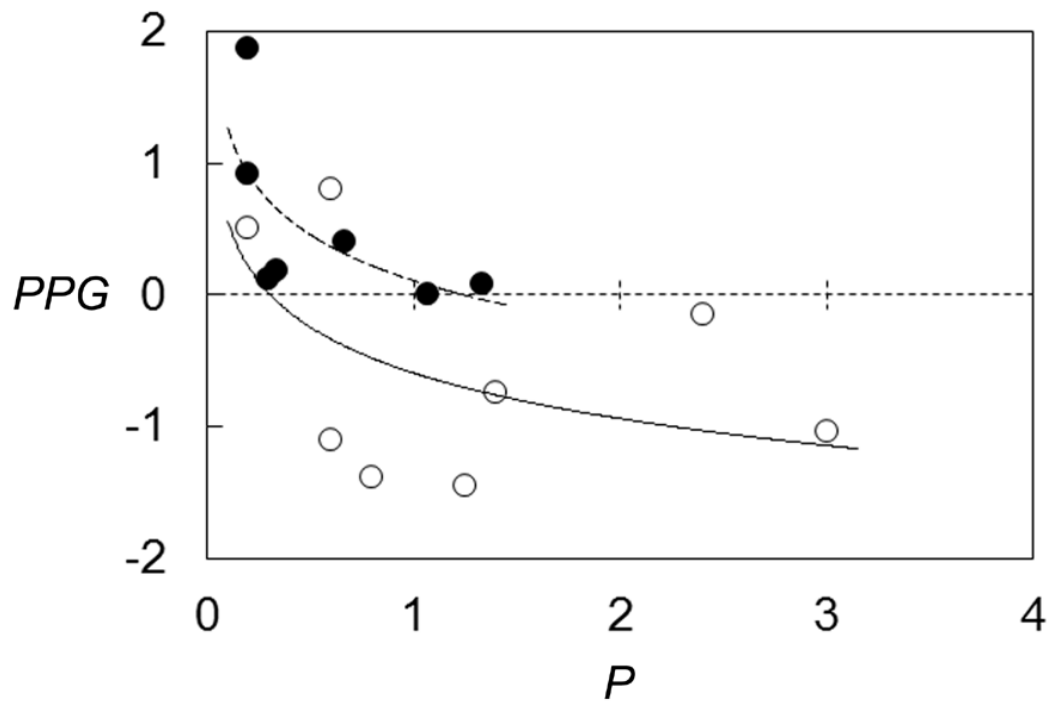
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576   **Fig. 2.** (1.5-column fitting image)

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