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Role of prey and intraspecific density dependence on the population growth of an avian top predator

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ABSTRACT

Exploring predator–prey systems in diverse ecosystems increases our knowledge about ecological processes. Predator population growth may be positive when conspecific density is low but predators also need areas with prey availability, associated with competition, which increases the risk of suffering losses but stabilizes populations. We studied relationships between European rabbits *Oryctolagus cuniculus* (prey) and adult eagle owls *Bubo bubo* (predators) in south–western Europe. We assessed models explaining the predator population growth and stability. We estimated the abundance of rabbits and adult eagle owls during three years in eight localities of central–southern Spain. We explored models including rabbit and adult eagle owl abundance, accounting for yearly variations and including the locality as a random variable. We found that population growth of adult eagle owls was positive in situations with low conspecific abundance and tended to be negative but approaching equilibrium in situations of higher conspecific abundance. Population growth was also positively related to previous summer rabbit density when taking into account eagle owl conspecific abundance, possibly indicating that rabbits may support recruitment. Furthermore, abundance stability of adult eagle owls was positively related to previous winter–spring rabbit density, which could suggest predator population stabilization through quick territory occupation in high–quality areas. These results exemplify the trade–off between prey availability and abundance of adult predators related to population growth and abundance stability in the eagle owl–rabbit system in south–western Europe. Despite rabbits have greatly declined during the last decades and eagle owls locally specialize on them, eagle owls currently have a favourable conservation status. As eagle owls are 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.

- 49 *Keywords:* abundance stability; *Bubo bubo*; conspecifics; Mediterranean Iberia;
50 *Oryctolagus cuniculus*; predator–prey relationships

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

1. Introduction

Food availability is an essential requirement in predator populations, especially for species linked to a given single prey species (Begon et al., 1996). In territorial species, individuals wait for an opportunity to occupy territories with high food resources. These territories may allow them to meet their objectives e.g. survival and reproduction (Stamps, 1994). However, it may also imply high competition, which increases the risk of suffering losses in the population, especially in species that are highly territorial and aggressive (López-Sepulcre and Kokko, 2005). If a territory becomes vacant it would be quickly occupied, benefiting predator population stability (López-Sepulcre and Kokko, 2005). This is especially clear in avian top predators, which have higher ability to quickly move between areas in order to find locations with the best conditions (Penteriani et al., 2005b). Nevertheless, poor territories may not permit continued use and predators may have to continue searching in other areas (Penteriani et al., 2005b). Altogether, food availability and intraspecific density could be important factors determining population dynamics of predators.

Eagle owls *Bubo bubo* are sit-and-wait top predators that are widely distributed in Eurasia and northern Africa (Mikkola, 1983). In the Iberian Peninsula this species is relatively common and shows high reproductive performance, mainly because of favourable climate and dietary local specialization on European rabbits *Oryctolagus cuniculus* (Donázar, 1990; Pérez-García et al., 2010). This lagomorph species is highly rewarding because of its suitable size for large predators, and relative ease of capture (Delibes-Mateos et al., 2008a; Ferrer and Negro, 2004; Penteriani et al., 2008). In recent decades rabbit populations have undergone dramatic declines as a result of the incidence of myxomatosis and the rabbit hemorrhagic disease (RHD). For instance, Moreno et al. (2007) recorded a rabbit population crash in Doñana (south-western

Spain), where rabbit abundance is currently less than 10% prior to the arrival of the disease. Similar rabbit abundance reductions have allowed reporting the eagle owl numerical response in terms of population size and breeding performance (Martínez and Calvo, 2001; Martínez and Zuberogoitia, 2001). Despite these reports, the relationships between eagle owls and rabbits have not yet been adequately assessed in south–western Europe. All this information is especially relevant after the recent arrival of a new RHD strain to Iberia (Abrantes et al., 2013) that may cause further declines of rabbit populations and unexpected consequences for the rabbit dependent predators, such as the eagle owl (Penteriani et al., 2008).

To improve understanding of the effects of food availability and abundance of adult conspecifics on predator population growth and stability we estimated rabbit and adult eagle owl abundance in several localities of central–southern Spain during several years. Rabbits were the main prey of eagle owls, at least at the localities with higher densities of rabbits (range of biomass consumed by eagle owls = 73–89%, Tobajas, 2012). We performed several analyses accounting for locality and seasonal variations. We assessed models for explaining eagle owl population growth that included rabbit and adult eagle owl abundance. We also assessed similar models for explaining abundance stability of adult eagle owls. Finally, in the light of our results, we discussed the potential of predators to overcome main prey declines.

2. Materials and methods

2.1. Study areas

We carried out field work in 8 sites of central–southern Spain (localities 1–8 in Fernandez–de–Simon et al., 2011) that differed in rabbit density. All localities have Mediterranean climate characterized by mild wet winters, and warm dry summers.

Habitat composition was also similar in all localities and mainly consisted of Mediterranean scrublands, pastures, croplands, dehesas (savanna-like formations that combine pasture with intermittent cereal cultivation in park-like oak woodlands; Blondel and Aronson, 1999) and tree plantations. Localities had gentle slopes and ecotones between Mediterranean scrublands and pastures or croplands favourable for rabbits (Lombardi et al., 2003). Low cliffs that are the preferred nesting habitat for eagle owls were also available.

2.2. Rabbit surveys

We counted rabbits at each locality along a transect (mean $\pm$ SE = 14.91 $\pm$ 0.59 km, range = 7.1–17.2 km) driven at night (starting 2 h after sunset) and using a spotlight. The surveys were conducted in good weather conditions (no strong winds or rainfall; Fernandez-de-Simon et al., 2011) and traversing ecotone areas which are favourable to rabbits but also to eagle owls in order to hunt rabbits (Lombardi et al., 2003; Ortego and Díaz, 2004). Counts were performed in different yearly seasonal periods to account for varying rabbit densities according to the annual cycle of rabbit reproduction and abundance (Moreno et al., 2007). The surveys were carried out in winter–spring (mainly February–March) of years 2007, 2008 and 2009, and in summer (mainly June–July) of years 2007 and 2008. Because of logistical limitations we could not conduct the counts in a locality during the winter–spring of year 2009 (see locality 5 in Appendix). We counted rabbits at each locality on three–four consecutive nights unless climatic or logistical factors prevented from doing so. We estimated rabbit density (individuals per hectare, hereafter N) at each locality and season using the distance sampling method (Buckland et al., 1993), with the Fourier series estimator as the detection function in TRANSECT software (Burnham et al., 1980). For a detailed description of the method, see Fernandez-de-Simon et al. (2011).

2.3. Adult eagle owl surveys

Adult eagle owls typically call during twilight hours for either mating or territorial purposes (Delgado and Penteriani, 2007). The annual eagle owl pre-laying period occurs from September to January in our study areas (Delgado and Penteriani, 2007). Playback surveys were conducted during winters (November–January) of years 2006–2007, 2007–2008 and 2008–2009. As for spotlight rabbit counts, surveys were carried out on nights with good weather (no strong winds or rainfall; Penteriani, 2003). Each survey commenced 15 min after sunset and lasted 2 h at most. Surveys involved five stations per night and locality although, because of weather or logistic limitations, exceptionally less than five stations per night were surveyed. Stations were located along the spotlighting transect with a separation of 1.5–2 km between them. At each station a three-minute recording of the “oohu” hoot of adults was broadcasted from a CD/MP3 device connected to a pair of loudspeakers (PRO BASIC 10W PMPO) (Fuller and Mosher, 1987). We listened for eagle owl calls for 10 min following the broadcast, which were considered adequate because 85% of eagle owl calls occurred within the first five minutes. Calls from different directions were considered to correspond to different individuals. During winter 2006–2007 we undertook only one survey per locality but, in order to reduce variability (authors, unpublished data; Penteriani et al., 2002a), we repeated the surveys on three–four consecutive sunsets per locality at the same stations in subsequent winters. As for spotlight rabbit counts, the survey could not be conducted in a locality during 2008–2009 winter. The mean number of individuals per playback for each winter and locality was used as a predator (adult eagle owls) abundance index (hereafter P). We also estimated the annual population growth of adult eagle owls for each locality and consecutive years by applying the formula:

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

Where PPG is the annual predator (adult eagle owls) population growth and P_t and P_{t-1} are the abundance indices of adult eagle owls in a given winter and in the previous winter respectively.

Furthermore, we computed the predator rate of return to equilibrium (hereafter PRR) as the absolute value of the PPG (Sibly et al., 2005). This allows to test if abundance of adult eagle owls changed between years or was rather stable (i.e. rate of return close to zero).

2.4. Statistical analyses

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

We compared various generalised mixed models, using PPG as dependent variable (Table 1). They were based on the linear response to previous winter–spring rabbit density (N_{W-Sp}), and the linear response to previous summer rabbit density (N_{Su}) as independent variables. We also used the natural logarithm of P in previous winter (Sibly et al., 2005). The locality was included in the models as a random variable (Zuur et al., 2009). The year variable was also included to control the possible effect of year in our models (Hurlbert, 1984). We also included a model with the year variable only. The comparison with a null model (intercept only) served as an overall performance indicator of the models. This summed 9 single–effect models and we considered as the most parsimonious model that with the lowest AICc value (Burnham and Anderson, 2002). Differences in AICc (Δi) > 2 between a given model and the model with the lowest AICc indicated little or no empirical support for that model. In addition to model weights, we calculated the weights of individual variables to look for informative parameters and models (Arnold, 2010). Sample size ($n = 15$) was equal for all models. We tested the normality, linearity and homocedasticity of model residuals and variables used. If necessary we transformed variables by means of e.g. using the decimal

logarithm. We also show parameters and probability values of individual variables in the best models but do not set a critical probability threshold since we are more interested in inference than in hypothesis testing. Thus we have considered models with non-significant variables ($p > 0.05$), even so included for inference purposes (Burnham and Anderson, 2002).

2.4.2. Which model best explains the annual rate of return to equilibrium of adult eagle owls?

We developed generalised mixed models similarly as in the previous section but using *PRR* as dependent variable. We again assessed models with rabbit and adult eagle owl abundance (see also Table 1). In this case we used *P* instead of its natural logarithm as independent variable as we did not have a previous hypothesis that the relationship could have a curvilinear natural logarithmic shape. We accounted for seasonal and locality variations. Model selection was performed according to the AICc criteria. We also tested the normality, linearity and homocedasticity of model residuals and variables used (see section 2.4.1). We used R version 3.0.1 (R Development Core Team, 2013) to perform all the analyses.

3. Results

3.1. Rabbit and adult eagle owl abundance

Mean *N* estimated for each locality ranged from 0.01 to 1.22 rabbits per hectare in winter–spring, and 0–1.5 rabbits per hectare in summer (Appendix). We recorded adult eagle owl presence at all localities and years (mean $\pm$ SE = 0.98 ± 0.16 individuals per playback, range of means of all localities = 0.31–2.2 individuals per playback, Appendix), and population was close to stability (i.e. mean *PPG* was close to zero, mean $\pm$ SE = -0.06 ± 0.24).

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

Two models of *PPG* obtained $\Delta i < 2$. The first model included *P* in the previous winter, *N_{Su}* (log-transformed) and the effect of year (Table 1 and 2). The second model included *P* in the previous winter and the year variable (Fig. 1; Table 1 and 2). Summing their model weights totalled 0.61. The largest individual weight was obtained by *P* in the previous winter (weight = 0.77), followed by *N_{Su}* (0.46) and then *N_{W-Sp}* (0.19).

3.3. Which model best explains the rate of return to equilibrium of adult eagle owls?

The model of *PRR* including *N_{W-Sp}* (log-transformed) and year was the only one with $\Delta i < 2$ (Table 1 and 2). It also accounted the largest model weight (0.68). Hence, *PRR* was negatively related to *N_{W-Sp}* (Fig. 2). This model indicates that *P* was more stable at high *N* in the previous winter–spring (Fig. 2; Table 1 and 2). We found the largest individual weight in *N_{W-Sp}* (weight= 0.77), followed by *N_{Su}* (0.11) and *P* (0.1).

4. Discussion

Eagle owl population growth was related to rabbit density and abundance of adult conspecifics in the previous winter, according to models taking into account year and locality variations. These results could reflect the trade-off between food and intraspecific competition in predator–prey systems such as the eagle owl–rabbit system of south–western Europe.

Rabbits could partly determine adult eagle owl abundance changes in southern Europe (Martínez and Calvo, 2001; Martínez and Zuberogoitia, 2001; Penteriani et al., 2002b). We found a positive relationship between *N_{Su}* and population growth of adult eagle owls when controlling for eagle owl conspecific abundance in the models. This

could indicate the important role of rabbits for eagle owl juveniles, as the postfledging period prior to dispersal is risky for their survival (Penteriani et al., 2005a) and enough food availability could be helpful for them (but see Sergio et al., 2004). In addition, the estimates of *PRR* showed that changes in adult eagle owl abundance between years were less pronounced with higher N_{W-sp} . The latter could be the result of a stabilizing effect of rabbit density in high-quality conditions (Pérez-García et al., 2012). Though we lack information of breeding territories in these areas, this abundance stabilization might be explained by floaters that would quickly occupy vacant territories with high N_{W-sp} when available (Delgado et al., 2010). In the opposite situation could be localities with low N_{W-sp} and with abundance of adult eagle owls either strongly decreasing or increasing. This could be a consequence of individuals searching a territory with sufficient food resources such as alternative prey of medium size (Donazar, 1989; Martínez and Zuberogoitia, 2001; Serrano, 2000; Tobajas, 2012). If eagle owls do not find these food resources, they might not persist (Penteriani et al., 2002b).

We found a logarithmic and negative curvilinear relationship between the *PPG* and *P*. Eagle owls are territorial birds, and form nesting pairs that mate annually for several years (Mikkola, 1983). As it occurs in other territorial raptor species (Valkama et al., 2005), the greatest densities appear in high-quality territories with high food availability (see above). In these conditions intraspecific density dependence with adult conspecifics could play a prominent role. Our results show that population growth of adult eagle owls between consecutive years is positive at low eagle owl abundance and negative at higher abundance, promoting eagle owl stability near abundance equilibriums (López-Sepulcre and Kokko, 2005). This result would suggest the existence of some degree of interference between individuals in the populations surveyed.

These results show the dynamics of the eagle owl–rabbit system in the range of low to moderate densities for both species. To our knowledge, the only density estimation of eagle owl for our localities corresponds to moderate values (1.96 territories/100 km² in locality 3 in winter 2004–2005; De la Dueña and López, 2007). This density could have remained close to this value during our study as (i) our surveys began two years later (winter 2006–2007), (ii) rabbit densities did not greatly change during these years (0–1 rabbits per hectare, De la Dueña and López, 2007), and (iii) large modifications in habitat composition or structure did not occur since it is a protected area (Lagunas de Ruidera Natural Park). As this locality ranked 2nd in *P* (Appendix), eagle owl density may be low to moderate in most localities. This could also be applicable to rabbits as the densities estimated are in the range 0–1.5 rabbits per hectare. Therefore future studies should try to elucidate these relationships in higher densities of both eagle owls and rabbits for a better understanding of the system (but see Pérez–García et al., 2012).

Several facts about our eagle owl and rabbit abundance estimates should be considered. First, eagle owls might move between posts (Delgado and Penteriani, 2007), and we rarely saw them during playbacks (authors, unpublished data). This could inflate abundance estimates as detection of individuals is based on calls from different directions. Nevertheless, the mean *P* and its standard error were relatively low, indicating that large numbers per playback were rare and estimates should not be excessively affected. Second, calling behaviour might change depending on eagle owl activity (Delgado and Penteriani, 2007). In this sense, we always used the same method in the same time period and then the error should always be similar. Third, we preferred the use of playbacks instead of listening of spontaneous calls (Martínez and Zuberogoitia, 2002), as adult eagle owls usually are more silent at low densities (see

above; Penteriani, 2003), and otherwise it would be difficult to detect their presence (De la Dueña and López, 2007). Fourth, although the distance between call posts of the nearest neighbour adult eagle owl males could be up to 2.5 km, the mean value was 1.16 km (Delgado and Penteriani, 2007) which suggests that our 1.5–2 km distance between playback stations provides a great probability of detection of different individuals. Fifth, both P and N estimates are relatively low and the results could be more sensitive to the imprecision of these estimates. However, the information from these variables was obtained from several replicates of the methods used, which provide more reliable results (Hurlbert, 1984). Altogether, future studies should improve abundance estimates by including additional methods that allow individual standardisation as, for instance, studying eagle owl sonograms (see Penteriani, 2003). This could also be applicable to our N estimates from spotlight rabbit counts. Although the latter have been considered a reference method (Fernandez-de-Simon et al., 2011), it may also need further testing by comparisons against e.g. live-trapping and capture-mark-recapture density estimates (King and Wheeler, 1985; Marchandeu et al., 2006). Nevertheless in this study with a regional scale and the resources available we could consider our indices as cost-efficient (Sutherland, 2006).

Another potential downside arises from the fact that, while generally studies of this kind have surveyed predators and prey during decades (e.g. moose–wolf interactions at Isle Royale, Jost et al., 2005), our monitoring period covered only three years. Although PPG could be meaningful to detect annual changes of adult abundance, it might not capture potential variation that could appear on the long run, especially for a long-lived species such as the eagle owl (Mikkola, 1983). However as young eagle owls reach sexual maturity in their first year (König and Weick, 2008) we still feel that PPG and PRR are measures of abundance change as they compare abundance of adult

individuals between two consecutive years which may differ annually due not only to productivity and survival, but also to immigration and emigration (Begon et al., 1996). We encourage future studies with intensive monitoring of predator and prey populations to provide more understanding of the numerical response (see e.g. Hone et al., 2007; Rohner 1995, 1996). Anyway, in this study the use of a regional approach provided a wide range of abundance estimates and valuable large-scale observations of dynamics of natural species in their home-range conditions.

The best models obtained intermediate levels of support (sum of model weights for the best models, i.e. $\Delta i < 2$, explaining *PPG* and *PRR* are 0.61 and 0.68 respectively). Moreover, some of the variables included were not significant, which provide discordant results considering that they appear in the best models. That is the case of the year variable, which was kept in all models to control for its effect on the response variable (Hurlbert, 1984). With our model selection procedure we maximise inference (Burnham and Anderson, 2002), getting the most parsimonious models that depict a valuable picture of the role of rabbit abundance and intraspecific density dependence on eagle owl population growth, while taking into account year and locality variations. Again future studies should make further progress by conducting refined surveys with intensive and long term monitoring of populations of both prey and predators (see e.g. Penteriani et al., 2005b; Fargallo et al., 2009) but also experimentally test the effect of the variables studied here (Begon et al., 1996).

The abundance of rabbit populations in Iberia is undoubtedly very low if compared to few decades ago (Moreno et al., 2007; Delibes-Mateos et al., 2008b; 2009). Eagle owls have also experienced human-induced mortality and habitat modifications (Marchesi et al., 2002). Nevertheless the contraction in the eagle owl distribution has been relatively small (mainly in northern Spain, Martínez et al., 2006).

In fact, eagle owls were present in all localities in our study, according to their good conservation status in central–southern Spain (Martínez and Zuberogoitia, 2003). Then, how have eagle owls overcome the rabbit decline? From the 24 predator species that frequently consume rabbits in Mediterranean Iberia (i.e. those with >5% of rabbits in diet, Delibes–Mateos et al., 2008a), only two are nocturnal raptor species: Eagle owls and tawny owls *Strix aluco*, but the latter mainly prefer prey of smaller size (Villarán, 2000). Therefore, the eagle owl is the only nocturnal raptor that preys heavily on rabbits, where they are available (Penteriani et al., 2008) in an area that is already favourable climatically for eagle owls (Donazar, 1990). Although they may also feed on other prey (see above), their productivity in Iberia is highest when rabbits are abundant (Pérez–García et al., 2010). This altogether suggests that with optimum climatic conditions and prey (Donazar, 1990; Penteriani et al., 2008) predators could overcome their main prey declines in the absence of superior competitors with similar foraging mode (Schoener, 1974).

5. Conclusions

This study shows the potential relationship of food density and adult conspecifics on the abundance changes of this bird of prey. On the one hand, the role of rabbits seemed directly related to boost the abundance of adult eagle owls but also stabilize their population. On the other hand, adult conspecifics may reduce population growth of adult eagle owls with a trend towards stabilization in situations of relative high abundance of adult conspecifics. This reflects an ecological trade–off that may influence population dynamics. We show these patterns from a regional approach which could help us to understand the interrelations between predators and their main prey when studies with long–term datasets collected at specific localities are absent. For that

reason, more research is needed to complete our understanding of the factors that explain predator and prey abundance. In Iberia, this will be greatly welcome as a new strain of RHD could be producing again high mortalities in European wild rabbit populations and the consequences for their dependent predators remain largely unexplored.

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Tables

Table 1

Generalised mixed models used to explain the annual population growth (*PPG*) and the rate of return to equilibrium (*PRR*) of adult eagle owls. *P* is the abundance index of adult eagle owls in winter, N_{W-sp} is winter–spring rabbit density and N_{Su} is summer rabbit density (see text for further details). The locality is included as a random variable. The models with $\Delta i < 2$ are shown in bold and labelled with numbers between parenthesis (1, 2 and 3, see also Table 2). The degrees of freedom may vary between models.

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

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

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Table 2

Parameters of models explaining annual population growth (*PPG*) and the rate of return to equilibrium (*PRR*) of adult eagle owls. $\ln(P)$ is the natural logarithm of the previous winter abundance of adult eagle owls, $\text{Log}(N_{W-Sp})$ is the decimal logarithm of the previous winter–spring rabbit density and $\text{Log}(N_{Su})$ is the decimal logarithm of the previous summer rabbit density. Only models with $\Delta i < 2$ are shown. These models are labelled with numbers between parentheses in Table 1. See text for further details.

Model (1)		Coefficient	Std. Error	t value	Probability value
<i>PPG</i>	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
	$\text{Log}(N_{Su})$	3.27	1.23	2.66	0.06
Model (2)					
<i>PPG</i>	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)					
<i>PRR</i>	Intercept	1.34	0.19	6.97	<0.001
	Year 2008	−0.45	0.21	−2.13	0.09
	$\text{Log}(N_{W-Sp})$	−4.25	1.21	−3.5	0.02

Figure legends

Fig. 1. Annual population growth of adult eagle owls (*PPG*) in years 2007 (white points, solid line), and 2008 (black points, dashed line) as a function of the natural logarithm of the abundance index of adult eagle owls (eagle owls per playback, *P*) in the previous winter, according to one of the most parsimonious generalised mixed models, which takes into account the locality as random variable (Model (2), see Table 1 and 2).

The equation of the model is the following: $PPG = -0.59 + 0.7 \times (\text{Year}2008) - 0.5 \times \ln(P)$

Fig. 2. Annual rate of return to equilibrium of adult eagle owls (absolute values of population growth, *PRR*) in years 2007 (white points, solid line) and 2008 (black points, dashed line) as a function of rabbit density (rabbits per hectare, N_{W-sp} , log-transformed) in the previous winter–spring, according to the most parsimonious generalised mixed model, which takes into account the locality as random variable (Model (3), see Table 1 and 2). The equation of the model is the following: $PRR = 1.34 - 0.45 \times (\text{Year}2008) -$

$4.25 \times \text{Log}(N_{W-sp})$

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

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575

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

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