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Original article

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



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#### A R T I C L E I N F O

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#### ABSTRACT

Exploring predator-prev 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 stabilises 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 stabilisation 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 specialise 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 predators may overcome prey decreases in areas with favourable climate and prey in the absence of superior competitors with similar foraging mode.

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#### 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

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

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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 specialisation 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 fieldwork 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 characterised 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 3-min 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 5 min. 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 (J. Fernandez-de-Simon et al., 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).

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