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How does optimal prey abundance shape space use by a territorial raptor?

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Abstract

Understanding predator-prey interactions is important to determine the inter-relationships between species. Optimal foraging theory states that predators balance out energy expended with the energy gained from their prey. In the Iberian Peninsula, the European rabbit (*Oryctolagus cuniculus*) is a key prey species for endangered Bonelli's eagle (*Aquila fasciata*). Thus, it is vital to understand how changes in rabbit abundance can influence habitat selection and territory use by Bonelli's eagle. We studied 11 radio-tagged Bonelli's eagles in their territories in Catalonia (NE Iberian Peninsula) and analysed the relationship between rabbit relative abundance, habitat selection and territory use of eagles. Rabbit relative abundance varied between territories, with shrublands hosting more rabbits, and eagles preferred shrublands and open areas for foraging and avoided dense forests. Spatial use by territorial eagles correlated positively with rabbit abundance in rabbit-rich territories, thereby supporting the idea that prey availability influences habitat selection. This result confirms optimal foraging strategies given that open habitats including shrublands tended to host more rabbits, thus providing better opportunities for prey detection and capture. Therefore, maintaining rabbit populations and their habitats (i.e., preserving open Mediterranean shrublands) would seem to be crucial for Bonelli's eagle conservation. Our findings improve our understanding of predator-prey interactions and highlight the relationship between habitat structure, prey abundance and predator behaviour. In addition, our results emphasize the need for targeted conservation strategies designed to safeguard endangered species such as Bonelli's eagle and maintain ecosystem integrity.

Keywords Bonelli's eagle \cdot Conservation \cdot European rabbit \cdot Mediterranean ecosystems \cdot Optimal foraging theory \cdot Territory uses

Introduction

Understanding predator-prey interactions provides critical information on the inter-relationships between the biotic component of ecosystems. Optimal foraging theory (OFT; Krebs 1977; Pyke 1984) posits that predators must balance

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the energy expended in searching, capturing and consuming prey with the energy gained thereby (Stephens and Krebs 1986). Therefore, predators choose optimal prey items that provide the maximum energy per unit of effort (Krebs et al. 1977) by considering factors such as abundance, availability and capture costs (Schweiger et al. 2015; Vettorazzi et al. 2022). Predators may be specialists, exhibiting a logarithmic functional response by targeting specific prey that is abundant, easily accessible and/or offers a high-energy reward, or generalists, with a sigmoidal functional response by preying upon a variety of scarce or unpredictable prey items (Oro and Furness 2002; Rutz and Bijlsma 2006; Spitz et al. 2012; Krebs 2014). OFT involves two key components: patch use and prey choice, both influenced by intrinsic and extrinsic factors of the predator. Intrinsic factors such as predator size, strength and hunting abilities affect prey selection, meaning that optimal prey choice depends on the size and behaviour of both predator and prey (Cresswell

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and Quinn 2011; Schweiger et al. 2015). For example, predators may select slow or weak species that are easier to catch (Moleón et al. 2009, 2012). The predator's ecology and behaviour, along with the costs and benefits associated with different prey types, play crucial roles in determining optimal prey selection (Thirgood et al. 2000; Mougeot et al. 2003). Additionally, extrinsic factors such as perch availability or supplementary food may also influence predator-prey relationships, affecting both patch use and prey choice (Kenward et al. 2001; Redpath et al. 2001).

The European wild rabbit (Oryctolagus cuniculus L.) is a keystone species in Mediterranean ecosystems that is preved upon by a variety of predators (Delibes and Hiraldo 1981; Delibes-Mateos et al. 2007; Puig-Gironès and Real 2022). Consequently, it plays a critical role in supporting endangered species such as the Iberian lynx (Lynx pardinus), red kite (Milvus milvus), Spanish imperial eagle (Aquila adalberti), and Bonelli's eagle (A. fasciata), among others (Valverde 1967; Palomares et al. 2001; Ferrer and Negro 2004; Gonzalez et al. 2006; Delibes-Mateos et al. 2007). Rabbits are social animals that inhabit a variety of open landscapes including shrublands, agricultural mosaics and recently burned areas (Fa et al. 1999; Beja et al. 2007; Rollan and Real 2011). They possess a high reproductive rate that helps offset high mortality through predation (Gibb and Williams 1990; Delibes-Mateos et al. 2022). Changes in rabbit abundance can influence the distribution and abundance of apex predators (Palomares et al. 2001; Margalida et al. 2007; Ferreira and Delibes-Mateos 2010), so outbreaks of myxomatosis and rabbit haemorrhagic disease virus (RHDV), which have significantly reduced rabbit populations since the mid-20th century, can lead to changes in ecosystem functioning (Fa et al. 1999; Fenner and Fantini 1999; Calvete 2006; Virgós et al. 2007) and alterations in predator abundance and distribution (Fernandez 1993; Monterroso et al. 2016; Jiménez et al. 2019). Therefore, understanding the environmental and biological factors that determine the abundance of this species is of great importance for conserving Mediterranean food webs.

Bonelli's eagle is a long-lived, territorial raptor found from South-east Asia through the Middle East to the western Mediterranean (Orta et al. 2019). In Europe, its population is estimated at 1,100–1,200 pairs; it is classified as Near Threatened (BirdLife International 2017) and receives priority status under the EU Birds Directive (79/409/EEC). Negative factors affecting its populations include mortality on power lines (electrocution and collision), persecution, and landscape changes affecting prey availability (Real et al. 2001, 2016; Hernández-Matías et al. 2015). This eagle inhabits Mediterranean environments, typically breeding on cliffs or large trees (Gil-Sánchez et al. 1996), and forages in open habitats where it mainly feeds on lagomorphs, pigeons and partridges (Real 1991; Moleón et al. 2009; Resano-Mayor et al. 2014). One of its main prey items is the European rabbit and some authors suggest that the consumption of this prey is positively correlated to vital rates such as breeding success and survival, which are key factors ensuring population viability (Real and Mañosa 1997; Hernández-Matías et al. 2013; Resano-Mayor et al. 2016; Rollan et al. 2021). However, less is known about its foraging habitat and interaction with prey, two key issues in its ecology and conservation (but see Real et al. 2016 and Balbontín 2005). At a global scale, Bonelli's eagle is found in rocky areas interspersed with scrublands (Beier and Drennan 1997; Carrascal and Seoane 2009b; Martínez-Miranzo et al. 2019). At the home-range scale, foraging areas mainly coincide with scrub where prev such as rabbits and partridges are available (Real et al. 2016). Therefore, identifying foraging areas, suitable prey availability, and their relationship is crucial for the conservation of this raptor. Available evidence suggests that rabbit consumption by Bonelli's eagle is driven by both rabbit abundance in selected foraging habitats (Real 1991; Palma et al. 2006; Moleón et al. 2011, 2012) and the accessibility of rabbits in open habitats, which is claimed to be a more important factor than their absolute abundance (Ontiveros 1999). Wild rabbits play a key role in the Mediterranean biocenosis from an ecological perspective. Their abundance and survival hinge not only on the impact and evolution of the diseases they are afflicted by (Fa et al. 1999; Monterroso et al. 2016) but also on the maintenance of open Mediterranean landscapes (Calvete 2006). Disentangling the optimal habitats selected by rabbits and their abundance in scenarios in which grazing and land abandonment, both current and forecasted in the future, is a key issue in habitat management aimed at conserving adequate environments for rabbits. This, in turn, directly affects the survival of some of the most endangered predators in the Mediterranean biocenosis, such as Bonelli's eagle. Our research focuses on the significance of rabbits as prey for Bonelli's eagle. In this study, we aimed to determine the abundance of rabbits in relation to habitat types and their influence on the foraging behaviour of Bonelli's eagles in territories with differences in abundances of this lagomorph.

The global aim of this study was to determine whether rabbit abundances influence spatial use by territorial Bonelli's eagles. To achieve this, we tested (i) whether there were differences in rabbit abundances between different types of habitats present in Bonelli's eagle territories; and (ii) whether eagles' territory use is determined by the rabbit abundance or the habitats they prefer. Therefore, we hypothesised that (1) there are significant differences in rabbit abundance between different habitat types in Bonelli's eagle territories, with rabbit abundance higher in open habitats and shrublands compared to dense forests; and that (2) the spatial use of territorial by Bonelli's eagles is influenced by rabbit abundances and their preferred habitats, because Bonelli's eagles will use areas with higher rabbit abundances more intensively and prefer habitats with higher rabbit abundances for foraging.

Materials and methods

Study area and target population

The study was conducted on a Bonelli's eagle population in Catalonia, Spain (Fig. 1). The landscapes are typically Mediterranean and arid, with an average annual rainfall



Fig. 1 Study area in the Catalan Costal Range (NE Iberian Peninsula). (A) Map showing Bonelli's eagle (*Aquila fasciata*) territories, including their home range (Kernel 95% and Kernel 50%) and the corresponding number of territory identifiers. Territories are labelled as NPR (Northern Pre-littoral Range), CR (Coastal Range), and SRP (Southern Pre-littoral Range). (B) Illustration of the 100% Minimum Convex Polygon (MCP) and 95% Kernel Density Estimation (KDE) home ranges, along with six transects used to assess rabbit (*Oryctolagus cuniculus*) abundance. As an example, three transects are located within the MCP and three within the 95% KDE of one of the 11 territories studied

425-664 mm. We studied 11 pairs of Bonelli's eagles from three different breeding nuclei in nesting areas situated between 300 and 1200 m a.s.l., each of which has different environmental features (Fig. 1): Northern Pre-littoral Range (NPR; four pairs), Coastal Range (CR; six pairs) and Southern Pre-littoral Range (SPR; one pairs) (Bosch et al. 2010). The NPR is characterised by steep mountain ranges at altitudes ranging from 400 to 1200 m, extensive forest cover (60-80%) of holm oak (Quercus ilex) and Aleppo pine (Pinus halepensis), and high levels of human presence (approximately 1,100 habitants per km² (Institut d'Estadística de Catalunya; https://www.idescat.cat/?l ang=en). The CR is located in coastal hills at altitudes ranging from 300 to 650 m. It enjoys a dry mild climate and its landscapes consist mainly of scrub and dry meadows, with considerable human presence (approx. 890 habitants per km²). Lastly, the inland SPR has a more continental climate and is also characterised by steep mountain ranges at altitudes ranging from 400 to 1100 m; land cover here consists mainly of scattered non-irrigated cultivation and secondary pinewoods and scrub, with little human presence (approx. 112 habitants per km²). In all cases, the home ranges of eagles were characterised by a breeding zone, usually in more abrupt areas with cliffs and rocky areas, and dense holm oak forests. By contrast, foraging areas are covered by shrublands and dry meadows surrounded by plains with scattered pine forests and cultivated areas (Real et al. 2016).

Home ranges

During 2002–2006, we radio-tagged 11 male eagles, each corresponding to a nesting territory. Nine of these birds were tracked using VHF (Very High Frequency) terrestrial transmitters with activity switch (TW-3 32–40 g, Biotrack Ltd., Wareham, Dorset, UK), and three using solar 45 g Argos/GPS PTT (Microwave Telemetry, Inc., Columbia, MD 21045, US). We monitored all eagles throughout the year, which allowed us to obtain a detailed understanding of their home ranges and associated features (see details in Bosch et al. 2010).

We defined the home range of each individual according to two metrics: the Minimum Convex Polygon 100% (MCP; Mohr 1947) and the 95% fixed kernel density estimate (KDE; Worton 1989). The MCP represents the maximum area used the eagles, while the 95% KDE represents the most used area. Home ranges were calculated with a reference smoothing factor of 1 to reveal the overall distribution of recorded locations (Seaman and Powell 1996) using RANGES VII software (South et al. 2005). Home-range sizes were constructed using independent hourly locations (Swihart and Slade 1985; Seaman and Powell 1996; Kenward et al. 2001) and excluding all consecutively repeated locations in the early morning and late evening (Bosch et al. 2010). We employed the incremental area analysis method with kernel and independent locations sorted randomly to calculate the number of locations needed to build the area of each home range (South et al. 2005). This approach produces a plot of percentage of area vs. number of locations that approaches an asymptote, thereby allowing for an approximate estimate of the number of locations required (Bosch et al. 2010).

Rabbit abundance counts and habitat characterisation

To estimate rabbit abundance, we used six 4-km long transects in each territory to count rabbit latrines, defined as areas where rabbits have deposited droppings or faces, typically forming clusters on the ground. Each latrine served as an indicator of rabbit activity and presence. This method is a proxy for estimating rabbit abundance (see Cabezas-Díaz and Virgós 2022; Delibes-Mateos et al. 2023). Three transects were performed in the area most intensively used by eagles (95% KDE) and in the MCP. The other three transects were outside the 95% KDEarea but within the MCP (Fig. 1). Rabbit counts were conducted in June and July 2004 (eagle pairs 3, 6, 8, 9, 12 and 102) and in 2007 (pairs 11, 13 and 19), coinciding with the eagle survey. Each 4-km transect had a randomly chosen starting point and direction, thereby had no predetermined routes and did not use any existing roads or trails. Along each transect, 10 sub-transects of 100 m were selected at regular intervals of 400 m, along which observers counted all the rabbit latrines within a 2 m-wide band.

To study the rabbit habitat selection, the observer also visually recorded the percentage of habitat coverage at the beginning of each sub-transect (within a radius of 100 m). Habitat categories were as follows: dense forests, open forests, dense shrublands, open shrublands, rocky areas and cultivated areas (see Supplementary Material for more details).

Statistical analysis

We used generalized linear mixed models (GLMM) to investigate whether or not rabbit abundance was related to different habitat types in the eagles' territories, with the number of latrines in each 100 m subtransect as the response variable and habitat coverage of each habitat type as the explanatory variables. Moreover, we used the interaction of territory and transect as random variable. We employed the *lme4* R package to perform Poisson-distributed GLMMs with a log link function, which is suitable for count data (Bates et al. 2015). We checked for collinearity between the variables using Variance Inflation Factors (VIF), with a restrictive threshold set at 5 or more to reject variables from other models (Quinn and Keough 2002). As none of our habitat coverage variables showed a VIF over 10, we proceeded with our analyses. Our data were analysed through a systematic model selection process. We began by comparing the null model with all possible models containing just one explanatory variable, and selecting the best-fitting model based on the smallest AICc (Akaike Information Criterion corrected for small sample sizes). We then incrementally added additional explanatory variable to this base model, guided by biologically relevant combinations of variables. Our general approach aimed to maintain a parsimonious model by including only those variables necessary to test our hypotheses. Model comparison and selection were performed using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We estimated the Akaike weights (ω i) of each model as a measurement of model plausibility, considering models to be statistically equivalent when they were within 2 AICc from the best-fitted model (Burnham and Anderson 2002).

We used GLMMs to assess whether or not the use of the Bonelli's eagle territories depends on rabbit relative abundance or on its preferred habitats. The response variable was binary: '1' within the eagle's intensive-use area (inside 95% KDE) and '0' if they were located outside this area but still within the MCP. Using this criterion, we ensured that transects outside the most intensively used areas (95%) KDE) were still within the broader territory (MCP) potentially used by territorial eagles. The explanatory variables included in the models were the rabbit relative abundance and various habitat coverages. Due to the variability in rabbit relative abundance between different territories (MCP), we defined an additional explanatory variable, "rabbit territorial richness". Then, we classified territories into 'rabbitrich territories' (>1 latrine/100 m in the entire transect) and 'rabbit-poor territories' (<1 latrine/100 m) based on these measures (see Results; Fig. 2). Subsequently, we included this variable and its interaction with rabbit abundance in the analysis of eagle territory use. The response variable was modelled using a Binomial distribution with a logit link function. Also, we added territory as a random factor to address any potential non-independence of clustered observations. We estimated the parameters of the averaged model (models with an Δ AICc value <2; Burnham and Anderson 2002) to account for model selection uncertainty and ensure robust parameter estimates and predictions (Grueber et al. 2011; Symonds and Moussalli 2011).

Results

The average rabbit relative abundance was 0.93 latrines/100 m (SD=0.68; n=11) per territory (range: 0.29–2.02 latrines/100 m; Table S1). We did not observe significant differences in mean rabbit abundances between territories (Kruskall-Wallis X²=13.50; df=10; p=0.197). Nevertheless, when territories were ranked, we observed a bimodal distribution of rabbit abundance: one group of territories had>1 latrine/100 m (mean=1.75; range=1.40–2.02; n=4), while another had lower abundances (mean=0.45; range: 0.29–0.6; n=7). As there were significant differences between these two groups (Kruskal-Wallis X²=12.05; df=1; p<0.01) (Fig. 2), we classified them as either 'rabbit-rich territories' or 'rabbit-poor territories,' respectively, for further analyses (Fig. 2).

Habitat selection by rabbits

To assess the effect of habitat on rabbit abundance, we initially fitted a total of 17 models. The best model (AICc=1433.13; $\omega i=0.64$) included both dense and open forests, as well as dense and open shrublands as explanatory variables (Table 1). The marginal R² (fixed effects) for this model was 0.069, while the conditional R^2 (including the random effects) was 0.146. In particular, both dense and open shrublands had a positive relationship with rabbit abundance (Estimate = 0.01; SE = 0.002; p < 0.001 and Estimate=0.01; SE=0.002; p < 0.001, respectively; Table 2). A significant difference in rabbit abundance was observed between dense and open shrublands (t =-5.53, p < 0.05), with higher abundance in open shrublands. Conversely, both dense and open forests exhibited a negative relationship with rabbit abundance (Estimate=-0.01; SE=0.003; p=0.005 and Estimate=-0.02; SE=0.004; p<0.001, respectively) (Fig. 3). Rocky areas and croplands did not have any effect on rabbit abundance since they were not selected in the best-fitted model.

Effect of rabbit abundance and habitat on eagles' territorial usen

To assess how rabbit abundance and habitat type influence the Bonelli's eagle spatial use– both within the 95% Kernel area and outside it but still within the MCP– we analysed data from 25 models (Table 3). The top three models, which had a Δ AICc values<2, were selected for further evaluation. Therefore, we averaged these models, which included rabbit relative abundance, rabbit territorial richness, their interaction and all the habitat coverage variables (Table 4). The marginal R² (fixed effects) for this model was 0.3374, while the conditional R² (including the random effects) was



Fig. 2 Rabbit (*Oryctolagus cuniculus*) latrines density (per 100 m) across Bonelli's eagle (*Aquila fasciata*) territory. The lines represent the mean latrine count for each territory, with the dashed line indicating the inflection point at 1 latrine per 100 m. Territories are grouped based on rabbit abundance, with 'rabbit-rich' territories (i.e. territo-

0.3712. Our findings showed no significant effect of rabbit abundance on eagles' spatial use within the 95% KDE area (Estimate=-0.18; SE=0.095; p>0.05). However, there was a significant negative effect of rabbit territorial richness on the spatial use of eagles (estimate=-2.071; SE=0.399; p<0.01). The interaction between rabbit abundance and

ries 3, 8, 9, and 12) and 'rabbit-poor' territories (i.e. territories 6, 10, 11, 13, 14, 19 and 102). Additionally, a difference in rabbit abundance between the inside (blue) and outside (grey) of the 95% Kernel Density Estimation (KDE) is observed only in the rabbit-rich territories

rabbit territorial richness showed a significant positive relation in rabbit-rich territories (Estimate=0.351; SE=0.110; p < 0.01), indicating that in rabbit-rich territories, the influence of rabbit abundance on eagles' spatial use was more marked than in rabbit-poor territories. Furthermore, eagles' spatial use was positively associated with open forests

Table 1 Summary of models used to analyse the effects of habitat on rabbit abundance. Models were listed in order of their difference in Akaike Information Criterion (AICc) and the Akaike weights (i). 'K' represents the number of model parameters (degrees of freedom), and AICc refers to the value of the Akaike Information Criterion corrected for small sample size. The interaction between transect and territory was treated as a random effect in all models. Habitat acronyms: dense forest (DF), spare forest (SF), dense shrublands (DS), spare shrublands (SS), Rocky Areas (RA) and cultivated areas (CA)

Models	k	AICc	ΔΑΙСс	ωi
DF+SF+DS+SS	6	1433.13	0	0.635
DF+SF+DS+SS+RA	7	1435.18	2.05	0.229
DF+SF+DS+SS+RA+CA	8	1436.23	3.10	0.135
DF+SF+DS	5	1447.09	13.96	5.9E-4
DS+SS+RA	5	1447.09	13.96	5.9E-4
DS+SS	4	1449.06	15.93	2.2E-4
DF+SF	4	1457.06	23.93	4.04E-6
DF+SF+SS	5	1459.09	25.96	1.46E-6
DF	3	1480.04	46.91	4.14E-11
SF	3	1488.04	54.91	7.59E-13
DS	3	1488.04	54.91	7.59E-13
SS	3	1503.04	69.91	4.2E-16
СА	3	1504.04	70.91	2.54E-16
SS+RA	4	1504.06	70.93	2.51E-16
RA	3	1505.04	71.91	1.54E-16
RA+CA	4	1505.06	71.93	1.52E-16
SS+RA+CA	5	1505.09	71.96	1.5E-16

 Table 2 Effects of the parameters selected in the best model on rabbit abundance. The table shows the estimated value, their associated standard error (SE), the upper and lower confidence interval (CI) at 95%, and the p-value for each parameter

Parameter	Estimate	SE	95% CI		<i>p</i> -value
			Upper	Lower	
Intercept	-1.09	0.21	-0.71	-1.47	< 0.001
Dense Forest	-0.01	0.003	0.006	-0.02	0.005
Spare Forest	-0.02	0.004	-0.01	-0.03	< 0.001
Dense Shrublands	0.013	0.002	0.02	0.009	< 0.001
Spare Shrublands	0.01	0.002	0.01	0.006	< 0.001

(Estimate=0.014; SE=0.006; p<0.05), dense and open shrublands (Estimate=0.036; SE=0.006; p<0.01 and Estimate=0.044; SE=0.006; p<0.01) and rocky areas (Estimate=0.025; SE=0.007; p<0.01; Fig. 4). In contrast, the relationship between eagles' spatial use and dense forests or cultivated areas were positive but not significant (Estimate=0.006; SE=0.006; p>0.05 and Estimate=0.33; SE=0.449; p>0.05, respectively).

Discussion

In Mediterranean habitats, European rabbits are crucial to maintain a complex food web, serving as key prey for predators like the Spanish imperial eagle and Iberian lynx (Palomares et al. 2001; Ferrer and Negro 2004). Rabbits also constitute a significant proportion of Bonelli's eagle diet, often more than half, affecting this endangered raptor both numerically and functionally (Moleón et al. 2012; Monterroso et al. 2016; Resano-Mayor et al. 2016), highlighting their ecological and conservation importance. Studies on Bonelli's eagle diet and habitat use emphasize a preference for shrublands during foraging, probably due to the presence of rabbits and red-legged partridges (Real 1991; Moleón et al. 2009; Monterroso et al. 2016). Even when partridges are scarce, shrublands remain the favourite foraging grounds (Moleón et al. 2011, 2012; Real et al. 2016), suggesting the relevance of rabbits. Some have attributed this preference to the abundance of rabbits in these habitats (Palma et al. 2006; Moleón et al. 2012), while others suggested it is due to prey accessibility in open areas, regardless of its abundance (Ontiveros et al. 2005). This issue may have broader implications for other prey species in which the importance of abundance versus accessibility remains an open question.

Our results indicate that rabbits are more abundant in shrubland and scarce in forests, consistent with their general biology (Fa et al. 1999; Beja et al. 2007; Rollan and Real 2011). Open shrublands, which provide food and shelter, host more rabbits than dense shrubland (Beja et al. 2007; Rollan and Real 2011; Delibes-Mateos et al. 2022) and forests, which offer fewer resources and restrict movement (Fa et al. 1999; Rollan and Real 2011). Additionally, the abundance of latrines served as an indicator of rabbit activity and presence, and is correlated with rabbit abundance (Cabezas-Díaz and Virgós 2022). As our results indicate the eagle's most-used areas are primarily covered by shrublands (dense and open), open forests and rocky areas. Rocky areas are linked to breeding (Real et al. 2016), while shrublands are



Fig. 3 Relationship between the average rabbit relative abundance and the percentage of habitat cover type in Bonelli's eagle (*Aquila fasciata*) territories. Each dot represents the mean number of rabbit latrines for a given eagle territory, with habitat cover types indicated for each territory

preferred in large-scale distributions (Carrascal and Seoane 2009a, b) especially for foraging (Real et al. 2016; López-Peinado et al. 2023).

A significant interaction between rabbit abundance and territorial richness of this species indicates that in rabbitrich territories there is a clear positive relationship between prey abundance and the most-used areas by eagles (95% KDE). However, this relationship disappeared in rabbitpoor territories. Both types of territories showed a positive relationship with shrublands presence in the most-used areas by eagles. Nevertheless, eagles in both types of territories tend to forage in open shrublands within the 95% KDE.

In rabbit-rich territories, eagles focus their foraging within the 95% KDE on open shrublands where rabbits are more abundant, avoiding forests where rabbits are absent or scarce. In rabbit-poor territories eagles broaden their foraging habitats to include dense shrublands and open forests where alternative prey such as corvids, wood pigeons

Table 3 Summary of the models used to analyse the effects of habitat, rabbit abundance (ab), rabbit territorial richness (Rich) and their interaction (Ab*Rich) on Bonelli's eagles (Aquila fasciata) territory use. Models were listed in order of their difference in Akaike Information Criterion (AICc) and Akaike weights (i). 'K' represents the number of model parameters (degrees of freedom), and AICc refers to the Akaike Information Criterion corrected for small sample size. Territory was treated as a random factor in all models. Habitat acronyms. Habitat acronyms: dense forest (DF), spare forest (SF), dense shrublands (DS), spare shrublands (SS), Rocky Areas (RA) and cultivated areas (CA)

Models	k	AICc	ΔΑΙСс	ωi
Ab+Rich+Ab*Rich+DF+SF+DS+SS+RA	10	752.77	0.00	0.51
Ab+Rich+Ab*Rich+DS+SS+RA	8	754.24	1.47	0.25
Ab+Rich+Ab*Rich+DF+SF+DS+SS+RA+CA	11	754.30	1.53	0.24
Ab+Rich+Ab*Rich+DS+SS	7	769.86	17.09	9.9E-5
Ab+Rich+Ab*Rich+DF+SF+DS+SS	9	770.30	17.52	8.0E-5
Ab+Rich+Ab*Rich+SS+RA+CA	8	796.63	43.85	1.5E-10
Ab+Rich+Ab*Rich+SS+RA	7	812.99	60.21	4.3E-14
Ab+Rich+Ab*Rich+DF+SF+SS	8	817.38	64.61	4.8E-15
Ab+Rich+Ab*Rich+SS	6	820.50	67.73	1.0E-15
Ab+Rich+Ab*Rich+RA+CA	7	834.98	82.21	7.2E-19
Ab+Rich+Ab*Rich+CA	6	838.06	85.29	1.5E-19
SS	3	846.63	93.86	2.1E-21
Ab+Rich+Ab*Rich+DF+SF+DS	8	856.84	104.07	1.29-23
CA	3	857.01	104.24	1.2e-23
Ab+Rich+Ab*Rich+DF	6	867.82	115.05	5.4e-26
Ab+Rich+Ab*Rich+DF+SF	7	869.25	116.48	2.6e-26
Ab+Rich+Ab*Rich+DS	6	872.11	119.34	6.3e-27
Ab+Rich+Ab*Rich+RA	6	873.69	120.92	2.8e-27
DF	3	876.47	123.70	7.1e-28
DS	3	880.10	127.33	1.1e-28
RA	3	887.19	134.42	3.3e-30
Ab+Rich+Ab*Rich	5	891.68	138.91	3.5e-31
Ab+Rich+Ab*Rich+SF	6	893.21	140.44	1.6e-31
Ab	3	894.44	141.67	8.9e-32
SF	3	903.41	150.64	1.0e-33

Table 4 Effects on eagle's territory use of the parameters selected in the averaged model. The table shows the estimated value, their associated standard error (SE), the upper and lower confidence interval (CI) at 95%, and the p-value

Parameter	Estimate	SE	95% CI		<i>p</i> -value
			Upper	Lower	
Intercept	-1.36	0.27	-0.83	-1.90	< 0.001
Rabbit abundance	-0.18	0.09	0.01	-0.37	0.06
Rabbit territorial richness	-2.06	0.39	-1.28	-2.83	< 0.001
Abundance*Richness	0.35	0.11	0.57	0.13	0.002
Dense Forest	0.004	0.005	0.01	-0.005	0.34
Spare Forest	0.01	0.005	0.02	0.002	0.03
Dense Shrublands	0.03	0.005	0.04	0.03	< 0.001
Spare Shrublands	0.04	0.005	0.05	0.03	< 0.001
Rocky Areas	0.02	0.006	0.03	0.01	< 0.001
Cultivated Areas	0.33	0.45	1.21	-0.55	0.46

(*Columba palumbus*), and red squirrels (*Sciurus vulgaris*), are present (Real 1991, 1996; Moleón et al. 2009), similar to other Mediterranean predators (Fedriani et al. 1998; Lozano et al. 2006). Greater habitat diversity in the most-used areas by eagles is higher in rabbit-poor territories, suggesting that eagles expend more effort and time foraging there. This also suggests that eagles obliged to adopt a more generalist diet use and foraging areas that have more diverse habitats (Bosch et al. 2010; Navarro-Lopez and Fargallo 2015; Real

et al. 2016). The preference for rabbit-shrubland habitats by eagles can be observed when territories with more proportion of shrublands tend to be smaller so indicating an optimal relationship (Bosch et al. 2010).

Optimal foraging theory suggests that predators select prey to maximize energy gain while minimizing energy expenditure (Stephens and Krebs 1986). Bonelli's eagles, though potentially facultative specialists (Glasser 1982; Moleón et al. 2007), likely rely on rabbits due to their



Fig. 4 Relationship between Bonelli's eagle (*Aquila fasciata*) territory use and the variables selected in the averaged model. Each dot represents the value of a variable for a specific sub-transect. The lines

show the linear model predictions for rabbit-poor territories (blue) and rabbit-rich territories (red)

high biomass (average mass of 740 g) and relative ease of capture in open areas (Real 1991). Some studies indicate that Bonelli's eagle exhibit a Holling's Type II functional response (Holling 1959) when rabbits are abundant in southern Spain, where rabbits constitute a major portion of their diet (mean=34%; Moleón et al. 2012). In our studied area, however, rabbits contributed less to the eagle diet (mean=22%; range=9-56%) and vary significantly between territories (unpublished data). In low-rabbit areas, eagles may switch to alternative prey, such as Columbidae (mean=31%; range=0-55% of their diet), which can become an important food source when rabbit availability declines (see Resano et al. 2016). Therefore, our results suggest a Holling's Type III functional response whereby predators shift to alternative prev when rabbit abundance drops below a threshold (Murdoch 1969; Akre and Johnson 1979). This frequency-dependent response highlights the eagles' behavioural flexibility in response to fluctuations in prey densities, particularly in low rabbit areas. While the correlation between rabbit abundance and consumption in Bonelli's eagles should be interpreted cautiously, our results suggest a preference for areas with higher rabbit densities. Understanding the functional responses is crucial for designing effective conservation strategies, particularly in prioritising areas with high rabbit abundance (López-Peinado et al. 2023). Further research is still needed to better comprehend these intricate relationships and their implications for both predator and prey populations.

Open habitats provide eagles with more opportunities for prey detection and successful captures, as well as contain microhabitats for prey species. Consequently, prey distribution is a relevant factor driving the selection of eagle foraging habitats (Hebblewhite et al. 2005; Ontiveros et al. 2005; Courbin et al. 2013). Our results show that Bonelli's eagles actively selected habitats for foraging and, in rabbit-rich territories, avoid closed habitats for hunting (Cadahía et al. 2010; Real et al. 2016). Recognising the role of rabbits as key prey for Bonelli's eagles in western Europe and their impact on eagle breeding success, survival rates and population dynamics (Real and Mañosa 1997; Hernández-Matías et al. 2013; Resano-Mayor et al. 2016; Martínez-Miranzo et al. 2019) highlights the importance of improving rabbit populations for conservation. Given that importance of open habitats for rabbits and other species on which Bonelli's eagles depend, these habitats must be safeguarded. Maintaining traditional livestock grazing, utilizing wildfires and prescribed burns, and implementing effective management strategies are crucial for favouring rabbit populations (Rollan and Real 2011; Rollan et al. 2021; Puig-Gironès et al. 2022, 2023) and thus essential for conserving this endangered raptor.

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Author contributions JR contributed to the study conception and, with the support RPG, designed the paper. RB and JR collected the data. JR, RB, RPG and AHM conducted the analysis. JR and RPG wrote the first draft, while RB, MA, and AHM contributed to earlier versions. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the first author on reasonable request.

Declarations

Ethics approval Approval of research ethics committees of the University of Barcelona and Generalitat de Catalunya was required to accomplish the goals of this study because the work involve capture, handling or experimentation on any animal.

Competing interests The authors declare no competing interests.

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