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Long-term monitoring program reveals a mismatch between spatial distribution and reproductive success in an endangered raptor species in the Mediterranean area

Beatriz Martínez-Miranzo[1,2,3] | Eva I. Banda[1,4] | Andrea Gardiazábal[5] | Ernesto Ferreiro[5†] | Javier Seoane[6,7] | José I. Aguirre[1]

[1]Department of Biodiversity Ecology and Evolution, Faculty of Biology, Complutense University of Madrid, Madrid, Spain

[2]Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Universidad Nacional de La Pampa (UNLPam), Santa Rosa, Argentina

[3]Instituto de Ciencias de la Tierra y Ambientales de La Pampa (INCITAP), Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Santa Rosa, Argentina

[4]ENARA Educación Ambiental, XI, Madrid, Spain

[5]BIOMA TBC, Ceuta 10, Madrid, Spain

[6]Terrestrial Ecology Group, Department of Ecology, Universidad Autónoma de Madrid, Madrid, Spain

[7]Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain

Correspondence
Beatriz Martínez-Miranzo, Department of Biodiversity Ecology and Evolution, Faculty of Biology. Complutense University of Madrid, José Antonio Novais 12, 28040 Madrid, Spain, and Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Facultad de Ciencias Exactas y Naturales-UNLpam- Instituto de Ciencias de la

Abstract

Unmasking the ecological processes responsible for the dynamics of a population is a necessary step toward understanding its threats and viability. We examined a fitness proxy (reproductive success) of an endangered raptor in relation to its ecological niche and spatial distribution to provide insights into the dynamics and potential threats to the population. We first studied how biotic and abiotic conditions drive both the spatial distribution of Bonelli's eagle (*Aquila fasciata*) and its long-term reproductive success in a large area of northwestern Spain. We focused on the relationship between these two characteristics of the population. Our results showed that biotic factors (occurrence of competitors such as the golden eagle or prey availability) were more associated with the spatial distribution of the species than with its reproductive success. In contrast, abiotic factors describing climate were linked to reproductive success. Most interestingly, we found a mismatch between spatial suitability and reproductive success because reproduction was compromised in the areas that were more suitable for the occurrence of the species. The results suggest that productivity (less than one chick per year), measured as long-term reproductive success, may compromise the population viability and suggest the presence of an underlying mechanism in the population. Our results highlight the benefits of simultaneously considering both large-scale spatial distribution patterns and measures of fitness, which often require larger investments of time, for endangered species conservation programs.

KEYWORDS
Bonelli's eagle, breeding success, distribution pattern, ecological trap, habitat modeling

Tierra y Ambientales de la Pampa (INCITAP), CONICET, L6302 Santa Rosa, La Pampa, Argentina.
Email: bmartinez@ucm.es

1 | INTRODUCTION

The number of studies focusing on species distributions has increased over the last two decades, fostering the development of concepts and applications in a wide range of disciplines within biogeography and ecology (Peterson et al., 2011). Essentially, correlative species distribution models (SDMs; see Sillero et al., 2021) represent ecological niche hypervolumes based on species occurrence points and various environmental variables where species can exist, following the seminal concept advanced by Hutchinson (1957). However, distribution patterns are determined by ecological, evolutionary, and geographical factors, which make the study of the distribution of species a complex problem (Gaston, 2003).

A shortcoming of these studies based on the analysis of occurrence that is often mentioned is that the mere presence of a species in any area may be a misleading clue to the habitat suitability or to the favorability of that particular area. This may be due to a variety of ecological processes (Guisan & Thuiller, 2005), such as source-sink (Furrer & Pasinelli, 2016) and transient population dynamics (Pulliam & Danielson, 1991), displacement of subordinate individuals to suboptimal habitats (Fretwell & Lucas, 1970), or migration and the biogeographical context (Schick et al., 2008; Tellería, 2018). Maguire (1973) included aspects of demography in Hutchinson's niche definition, considering parameters that drive population dynamics such as measures of reproductive success. In that way, approaches based on species demographic processes would account for populations' performance and dynamics, unlike descriptions of niches based on simple observations of species presence (Pironon et al., 2018). This would improve depictions of ecological niches and insights into the conservation status of species and populations (Briscoe et al., 2019; Carrascal & Seoane, 2009).

SDMs are developed principally for characterizing distributions of species but are connected to underlying population-biological processes (Guisan & Zimmermann, 2000; Soberon, 2007). Indeed, the consideration of demographic processes (births, deaths, or migration) in models of species ranges was soon acknowledged as a desirable factor in correlative SDMs (Guisan & Thuiller, 2005) and has recently given rise to sophisticated and hybrid process-based methods, with

substantial data requirements and technical challenges (reviewed in Briscoe et al., 2019).

A simpler but successful ecological framework for studying population-biological processes of interest in conservation was presented by Pulliam (1988) as the source-sink model. For many populations, individuals may regularly occur in "sink" habitats, where within-habitat reproduction is insufficient to balance local mortality; nevertheless, populations may persist in such habitats, being locally maintained by continued immigration from more productive "source" areas nearby (Pulliam, 1988). Nevertheless, sinks may seem attractive to individuals, which may prefer to settle there despite reaching lower fitness levels than in other available habitats (Pulliam, 2000; Robertson & Hutto, 2006). This is known as an ecological trap (Battin, 2004), a site with lower suitability for reproduction and survival that cannot sustain a population even though individuals prefer it to other areas of higher suitability. Ecological traps may occur because animals may make errors in habitat assessment as a result of some mismatch between the environmental cues they use to select habitats and the actual suitability (Kristan III, 2003). This is often attributed to human-induced rapid environmental changes, which may increase the gap between suitability of the environment and the cues of that suitability that animals use, making population sinks ecological traps for individuals (reviewed in Hale & Swearer, 2016). Identifying such trap systems can therefore be used to understand population declines that cannot be explained by species–environment relationships (for instance: Murphy, 2001).

Bonelli's eagle (*Aquila fasciata*) is a long-lived territorial raptor distributed in the western Palearctic from southeast Asia through the Middle East to the western Mediterranean (Orta et al., 2020). This species has suffered a general decline in the last few decades because of high levels of adult and pre-adult mortalities, mainly from electrocution and direct persecution (Hernández-Matías et al., 2015, 2020). Other factors that have had negative effects on Bonelli's eagle populations are related to the loss of suitable habitat and variations in prey population and interspecific competition with other raptors, such as the golden eagle (*Aquila chrysaetos*) (Hernández-Matías et al., 2013). Currently, Bonelli's eagle is considered to be "Near Threatened" in Europe (BirdLife International, 2019). At an estimate of 920–1100 pairs,
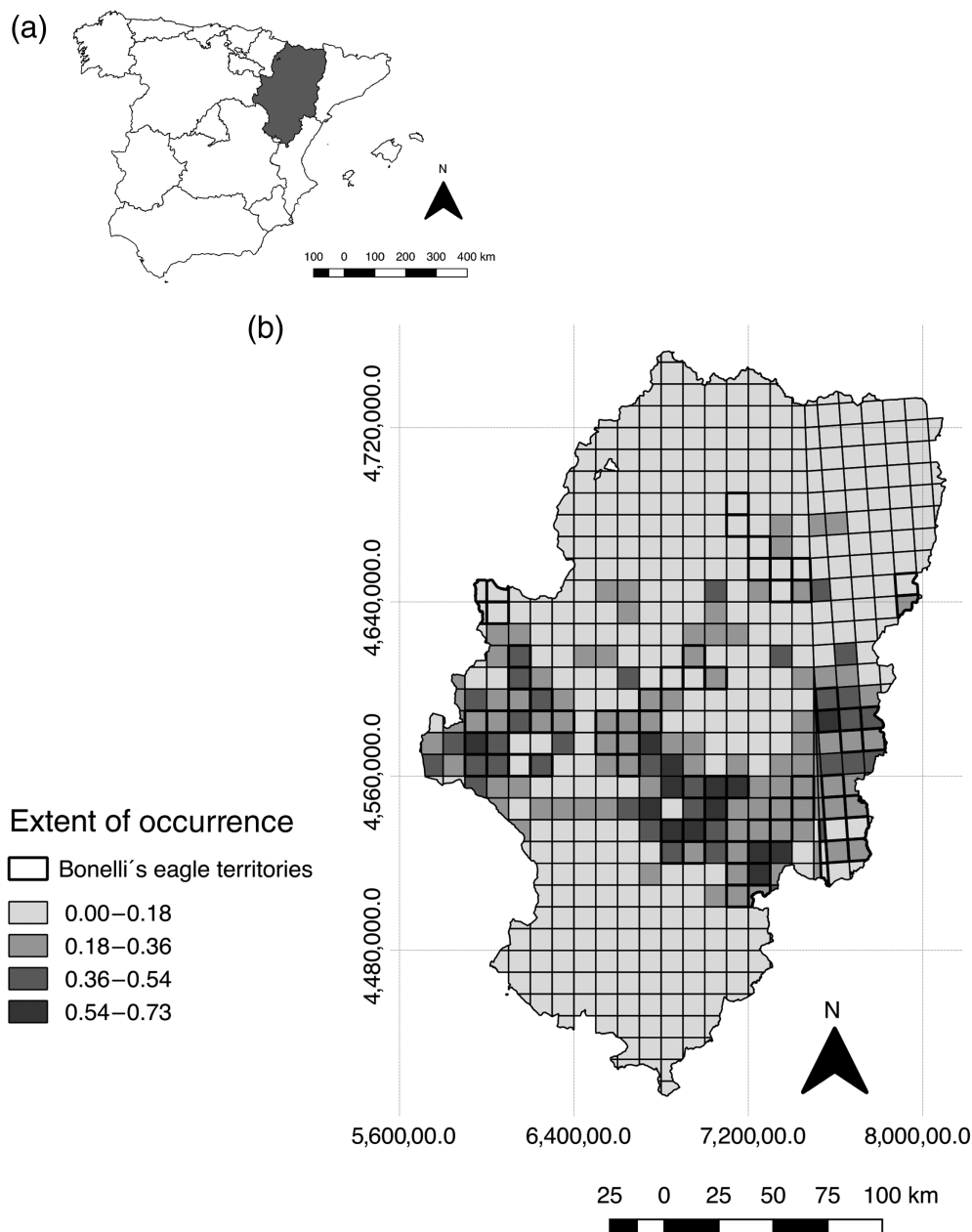
the Spanish population accounts for about 60% of the European population (BirdLife International, 2019) but is classified as "vulnerable" according to national regulations (Real Decreto, 139/2011).

Previous studies have revealed that Bonelli's eagle populations in Spain belong to a single spatially structured population that exhibits source-sink dynamics. The southern populations act as sources, remain stable, and sustain the northern population that continues to decline (Hernández-Matías et al., 2013). In this context, it is important to identify the relationship between source-sink populations and habitat suitability, with the aim to ascertain whether ecological trap phenomena may be operating in these areas. We studied a population in northeastern Spain which has suffered a continuous decline in recent years, despite the fact that the environment seems suitable for the species. Consequently, the species is considered "endangered" by the regional government.

The aim of this study was to combine information on spatial distribution and reproductive performance to assess whether individuals in a population of the endangered *A. fasciata* may be subjected to an ecological trap. First, we identified how different abiotic and biotic factors determine the current spatial distribution of the model species and their effects on the species' long-term reproductive success. We then described and discussed the relationship between the estimated

probabilities of occurrence (as a proxy of environmental favorability) and fecundity (as a proxy for biological fitness). Such an approach to the study of species distribution that includes information on performance can help species conservation projects at the regional level and for the larger distribution area of the studied species in Spain.

2 | METHODS

2.1 | Study area

We focused our analyses in Spain (40°0′0″ N O 4°0′0″). Specifically on the Autonomous Community of Aragón (northeastern Spain, 47,720 km²) (Figure 1). The area is a climatically contrasting region on the Iberian Peninsula that comprises a large elevation gradient (65–3400 m) between river basins, high plateaus and mountain areas, with a corresponding large range in temperatures (−10–35°C) and precipitation (300–2000 mm, with an annual average of 800 mm across most of the region). Pine and oak forests as well as Mediterranean scrub are interspersed with crops, mostly cereals, vineyards, and olive groves (Figure 1).

2.2 | Data on species distribution and reproductive success

The regional government carried out a monitoring program of Bonelli's eagles from 2004 to 2016. This program surveyed the occurrence of breeding pairs in the study area, recording a total of 32 pairs holding territories during this period (Figure 1). Out of this total, 21 pairs had at least one member equipped with a GPS satellite telemetry device. Moreover, the regional government identified the nesting areas of each breeding pair by direct observation. We estimated territory size with 95% kernels applied to the information on animal movements for individuals equipped with satellite devices (about 48,000 locations; see Martínez-Miranzo et al., 2016 for more details). Even though territory size differed among individuals, the size and shape of the home range among years remained constant for each individual over the sampling period in this area (Martínez-Miranzo et al., 2016). Because territories remained stable, we used the entire data pool available for each marked individual to estimate their territories. We estimated the territory for the remaining 11 pairs by assuming a buffer of the average territory size for the marked individuals centered on the nesting areas. We intercepted territories and buffers with the 10 × 10-km Universal Transverse Mercator (UTM) grid and selected those that matched the buffers, identifying the territories of the unmarked individuals. We overlapped the entire study area with a 10 × 10-km (UTM) grid (Figure 1). Cells in which a Bonelli's eagle territory was present were assigned a value of 1, whereas empty cells were assigned a value of 0.

Breeding performance was also monitored. From February until July, regional government nature protection officers visited each occupied territory and monitored them throughout the entire breeding season. Each breeding pair was assigned to an officer. Monitoring was carried out throughout the year, with at least two monthly visits and provided that there was visual contact with the individuals in their territory. Also, in 2014, cameras were installed in five Bonelli's eagle nests where monitoring by officers was not as exhaustive to monitor breeding behavior (Gil-Sánchez et al., 2021). The combination of cameras and observations by officers allowed the collection of data on the numbers of fledglings produced each year and on the replacement rate in the breeding pairs. The number of fledglings produced in each territory in all monitoring years was considered as (long-term) reproductive success.

2.3 | Predictors for models of occurrence and reproductive success

We considered three sets of variables to predict the distribution and reproductive success of Bonelli's eagle and to summarize its ecological niche and its interaction with other species, each measured in the 10 × 10-km grid. First, we evaluated climatic variables to set the general limits of the distribution of the species in the study area. Mean annual temperature and precipitation (Table 1) were long-term averages obtained from WorldClim (version 1.4 with 30″ spatial resolution, processed using ArcGis 9.3). Second, we assessed the available habitat as the cover percentage of forest and scrub within the grid. Data were extracted from CORINE Land Cover 2006 (European Environmental Agency, 2006). We aggregated broad-leaved forest, coniferous forest, and mixed forest within a single forest category and transitional woodland shrub and sclerophyllous vegetation within a scrub category (Table 1). These climate and habitat variables described the scenopoetic dimension of the ecological niche.

To complete the niche description, we added a third set of biotic variables as proxies for competition pressure and food resource availability, which were the occurrence of the golden eagle (*A. chrysaetos*) and total prey biomass (Martínez-Miranzo et al., 2019) (Table 1). The golden eagle is considered the principal competitor of Bonelli's eagle (Carrete et al., 2002). We considered confirmed

TABLE 1 Predictor variables tested in the models relating the occurrence and the long-term breeding success of Bonelli's eagle in 10 × 10-km Universal Transverse Mercator (UTM) squares in Aragon (northeastern Spain)

Variable (unit)	Source	Model	Purpose
Temperature (°C)	WorldClim	Occurrence and breeding	Scenopoetic description
Precipitation (mm)	WorldClim	Occurrence and breeding	Scenopoetic description
Scrub (%)	CLC	Occurrence and breeding	Scenopoetic description
Forest (%)	CLC	Occurrence and breeding	Scenopoetic description
Occurrence of golden eagle (yes/no)	ED	Occurrence and breeding	Proxy for interspecific competence
Prey biomass (g)	ED	Occurrence and breeding	Proxy for food availability
Geographical coordinates (UTM)	Centroid of square	Occurrence	Spatial gradient
Replacement of breeders (yes/no)	ED	Breeding	Proxy for breeding mortality

Note: Shown are the source and purpose for each variable, and the model where each was tried. WorldClim from Hijmans et al. (2005). CLC from European Environmental Agency (2006; https://land.copernicus.eu/pan-european/corine-land-cover/clc-2006. ED is data from Environmental Department of the Aragón regional government.

presence of a breeding pair (1) or assumed absence (0) of golden eagles in each 10 × 10-km cell (information on golden eagle occurrence provided by the regional government). To estimate total prey biomass, we measured the densities of rabbits (*Oryctolagus cuniculus*) and red-legged partridges (*Alectoris rufa*), which are the main types of prey for this species in this area (Martínez-Miranzo et al., 2019) and account for 33% of the total potential prey in this region (Alcántara et al., 2003). The densities of rabbits and partridges were obtained by linear transects, within the species population standardized monitoring program carried out by nature protection agents of the regional government from 2004 to 2014. Surveys were adapted to each species and standardized following Tellería (1986). Rabbits were surveyed by car four times a year (corresponding to four seasons of their annual cycle), counting individuals during twilight hours while driving 30-km transects at a constant speed of 20 km/h. Partridges were surveyed by walking 3-km line transects by foot between sunrise and midday during September and October for each year. Censuses were carried out in 24 administrative areas of Aragon, which correspond to 72% of the total for the region. We estimated an index of relative abundance as biomass/length for each transect and assigned a biomass index value to the cells of the grid where data were available (Martínez-Miranzo et al., 2019). We extrapolated these indices from the transects to the complete study area by kriging (Oliver & Webster, 2007) and extracted the information aggregated at the 10 × 10-km UTM grid level. We preferred to model the local variation of prey density using a purely spatial method (kriging vs. a model based on habitat variables) to avoid considering other potentially influential environmental variables that were later included in the models for the target species as predictors. We believe that prey density varies according to

local, fine-scale factors, insufficiently represented in the regional thematic cartography. All raw data on biological variables were provided by the government's Environmental Department of Aragón (unpublished data). The GIS analyses were done with ArcGis 9.3.

2.4 | Statistical analysis

We used a model-building strategy that combined both generalized additive models (GAM) and generalized linear models (GLM) to describe the distribution patterns, reproductive success, and the relationship between species occurrence and reproductive success in the study area.

We first performed a preliminary binomial GAM to model the occurrence of Bonelli's eagle, including the continuous variables (all except golden eagle occurrence) as regression splines. These are piecewise polynomial functions that allow for the assessment of curvilinear relationships. We also included the geographical coordinates with smooth terms to take into account any potential large-scale spatial gradient. The GAMs suggested which predictors were relevant and which could be later modeled by parametric curvilinear functions in a GLM framework. For instance, a U-shaped relationship suggested by GAM could be modeled with second-order polynomials in GLM. Geographical coordinates were approximated by a GLM with a quadratic polynomial for longitude and a cubic polynomial for latitude. Prey biomass was log-transformed and approximated by a GLM with a quadratic polynomial. We preferred building final models with GLM because this type of model is more easily interpreted (e.g., through tables of coefficients), and predicted values can more easily be plotted using the GIS software. Models for species occurrence used the
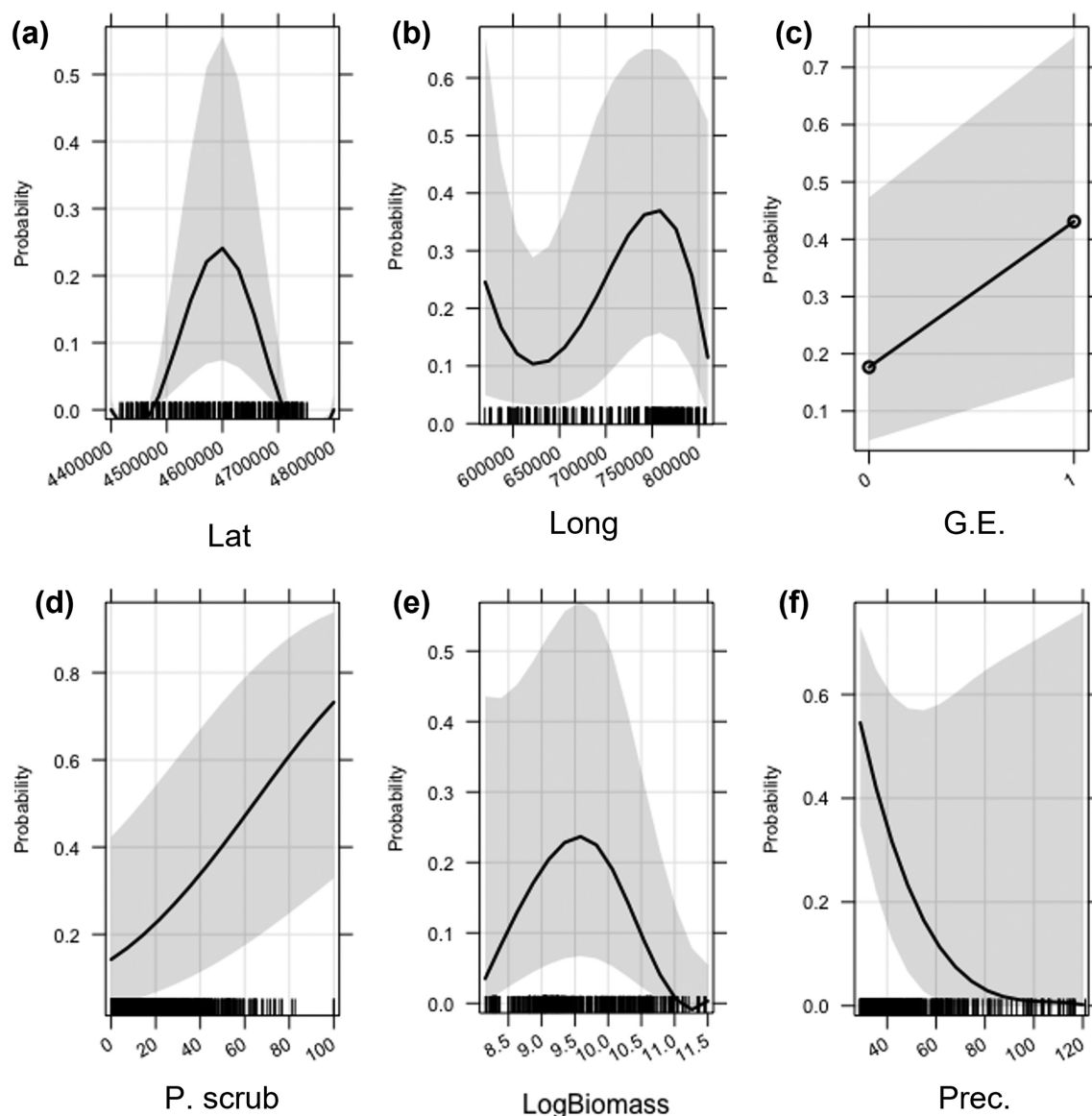
FIGURE 2 Partial residuals plots for generalized linear model. (a) Lat: latitude; (b) Long: longitude; (c) G.E.: golden eagle occurrence; (d) P. Scrub: percentage forest cover; (e) LogBiomass: logarithm of prey biomass availability; (f) Prec: precipitation. Solid lines show the marginal effect of each variable, controlling for the others, while the gray areas show the confidence interval (95%) of the effects. Note that we used algorithms that included deviation coding

presence (1) or absence (0) of the species in the UTM 10 × 10-km grid as the response variable and climatic, habitat, and bionomic variables as potential predictors. After an exploratory data analysis, temperature was eliminated from the set of explanatory variables because it showed a strong correlation with precipitation, which was preferred because precipitation is a known limiting factor for the reproductive success of the species in the Mediterranean area (Ontiveros, 2016). Next, we built a Poisson GLM to model long-term reproductive success, using the total number of fledglings, combining data across monitoring years for each territory as the response variable ("breeding success") and the sets of climatic, habitat, and bionomic variables as linear-term predictors. We also included a factor describing whether there had been a replacement of one of the members of the breeding pairs ("change" vs. "no change") and the number of monitoring years for each territory as an offset. In general, the mean number of follow-up years was 9.75 years (range 3–11 years) (see Table S1). Our limited sample size ($n = 32$ territories) precluded building a preliminary GAM or a polynomial GLM to explore potential curvilinear relationships between reproductive success and the predictors. We simplified the models by backward-forward stepwise selection of variables based on the Akaike information criterion.

In addition, we investigated the relationship between reproductive success and species distribution. We built a

TABLE 2 Coefficient table for the Poisson generalized linear model explaining the long-term reproductive success of the Bonelli's eagle in 10 × 10-km Universal Transverse Mercator squares in Aragon (northeastern Spain)

Variables	Estimate	SE	t-Value	p-Value
Prec	0.036	0.013	2.676	0.012
Temp	0.014	0.007	1.970	0.058

Note: Prec: mean annual precipitation; Temp: mean annual temperature. Deviance explained by the model (Nagelkerke's $R^2 = 0.326$). The *t*-values after estimation corrected for heteroscedasticity following Long and Ervin (2000). The number of monitored years differed per pair and was included as an offset in the model.

TABLE 3 Coefficient table for the linear model relating occurrence probability and predicted long-term reproductive success of the Bonelli's eagle in 10 × 10-km Universal Transverse Mercator squares in Aragon (northeastern Spain)

Variables	Estimate	SE	t-Value	p-Value
Predict	−1.072	0.433	−4.699	0.019
Change	−0.249	0.212	−1.1778	0.249
Predict × Change	1.056	0.433	2.439	0.021

Note: Predict: predicted values from the distribution model; Change: replacement of one of the members of the breeding pairs. Deviance explained by the model ($D^2 = 30\%$). The *t*-values after estimation corrected for heteroscedasticity following Long and Ervin (2000).

linear regression using the breeding index as a response variable and the mean predicted values from the distribution model as the explanatory variable. As territories overlap several cells within the UTM 10 × 10-km grids, and as some do not occupy the entire cell, we selected the cell with the highest predicted value within each territory; that is, we regressed one breeding index to one cell value per territory (by using the highest predicted value for occurrence, we assumed that the best conditions are those that limit performance). We also tested whether including "change" and its interaction with the predicted values from the distribution model improved the model. Robust sandwich estimators for standard errors were used in this model to avoid possible heteroscedasticity (Long & Ervin, 2000).

Finally, to check the relationship between habitat suitability (measured as probability of occurrence) and the probability that a member of the breeding pair changes, we performed a binomial GLM.

3 | RESULTS

3.1 | Species distribution

The habitat suitability model (GAM) suggested that the occurrence of Bonelli's eagles is positively and linearly related to scrub cover for most of its range, is negatively and linearly related to precipitation and has a relationship to prey biomass availability that could be roughly summarized with a quadratic shape (Figure S1). Contrary to what we expected, the model suggested that the occurrence of Bonelli's eagle is also positively correlated to that of the golden eagle. The final approximating model (GLM), fitted with geographical coordinates as quadratic terms, prey biomass availability as a quadratic term and scrub cover, precipitation and golden eagle occurrence as linear terms (Figure 2), had a significant but moderate discrimination and a predictive capacity (respectively, Tjur's pseudo $R^2 = 0.15$ and area under the curve = 0.79).
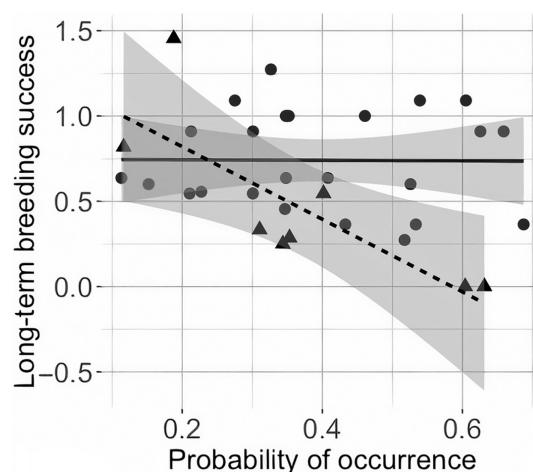

FIGURE 3 Relationship between breeding success and occurrence probability for territories with (dashed line) or without (continuous line) a replacement of any of the members of the breeding pair during the study period. Triangles represent the pairs that had a replacement of one of the members. Circles represent each pair that did not have a replacement of one of the members

The models showed that Bonelli's eagles prefer areas with a continuous prey availability biomass, with larger scrub cover and lower precipitation. Model residuals showed a weak nonsignificant spatial autocorrelation among adjacent squares (Moran's I test for distance-based autocorrelation based on simulated residuals: observed = 0.007, expected = −0.002, p-value = 0.063).

3.2 | Reproductive success

The Poisson GLM showed that only precipitation was positively and significantly associated with the number of fledglings in each territory (Nagelkerke's $R^2 = 0.32$; Table 2). Habitat and bionomic variables were not related to reproductive success at the 10 × 10-km scale in this population.

3.3 │ Relationship between species occurrence and reproductive success

The model relating the predictions of reproductive success and the species distribution was significant. It achieved a moderate explanatory capacity ($R^2 = 41.8\%$) and showed an interaction between the probability of occurrence and the replacement of any of the breeders ($p = 0.0122$; Table 3). This means that the relationship between reproductive success and the probability of occurrence was different for territories that experienced a replacement of any of the breeders compared to territories that kept the same breeders throughout the study period. Reproductive success and occurrence probabilities were negatively correlated for pairs with replacements, whereas there was no correlation for pairs that kept their members (Figure 3). Contrary to our expectation, reproductive success was lower in territories with a high occurrence probability (presumably high-suitability areas) than in territories with a low occurrence probability, and this was most apparent for territories that experienced a replacement of any of the breeders (Figure 3). We did not find a significant relationship between the probability of a replacement and habitat suitability (measured as probability of occurrence; $\beta \pm SE = -1.06 \pm 2.93$, $t = -0.36$, $p = 0.72$).

4 │ DISCUSSION

Our study shows that the spatial distribution of the study species is limited by a different set of factors than those that explain its reproductive success. This agrees with a few previous examples (Crandall et al., 2015; Mcintyre & Schmidt, 2012) that highlighted that the different dimensions of life cycles (survival, growth, and reproduction) may be determined by different factors (Begon et al., 2006; Levin, 2009). The biotic environment determined the regional distribution of the studied species, whereas the abiotic conditions, particularly climatic conditions, limited its reproduction. Most interestingly, these relationships among environment, habitat, and reproductive success differed among breeding pairs because there were replacements in the members of the pair when one individual died, decreasing long-term productivity and endangering population viability.

Prey biomass availability and habitat structure influenced Bonelli's eagle distribution patterns at this scale. Territorial species establish their territory based on different factors that allow them to minimize energy expenditure and maximize fitness (Börger et al., 2008). Trophic resources are some of the most limiting factors for

organisms (Aragón et al., 2018; Benson et al., 2005; Ontiveros & Pleguezuelos, 2000). Food distribution is conditioned by habitat structure, and this structure will limit prey abundance and accessibility (Ontiveros et al., 2005). Our results show that Bonelli's Eagles occur frequently in areas with relatively low prey availability. In a previous study in the area, Martínez-Miranzo et al. (2019) found that Bonelli's eagles establish their territory based on a low prey threshold but presumably stable biomass availability over the entire annual cycle. Eagles probably select these areas rather than those with higher, unstable prey densities (Martínez-Miranzo et al., 2019). Generalist top predators may establish their territories based on average prey biomass availability, a threshold that remains stable throughout the year (Lourenço et al., 2015). These areas also include middle altitudes, where they find suitable places for nesting, with Mediterranean forest habitats being preferred by this species (Carrascal & Seoane, 2009; Muñoz et al., 2005). This overlaps with the occurrence of other species, such as the golden eagle, with which it shares an ecological niche in the area (Amarasekare, 2003).

Even though the species is distributed along a thermophilic climate gradient, factors such as temperature and precipitation did not determine the occurrence of the species. However, our results show a relationship between reproductive success and climatic factors. Variables related to weather conditions are a limiting factor in many species. Extreme conditions related to temperature and precipitation might involve brood losses and, therefore, a decrease in reproductive success (Balbontín & Ferrer, 2005).

SDMs assume positive relationships among species occurrence, habitat suitability, and fitness (Araujo & Guisan, 2006; Weber et al., 2017). Normally, SDM simplifies the niche concept and assumes this relationship, without sound ecological evidence that this is truly the case for the modeled species (Guisan & Thuiller, 2005). In this context, presence at a given location indicates that individuals have selected the site as potentially suitable to settle, survive, and reproduce. However, the probability of presence may be a poor indicator of habitat suitability, and other parameters, such as long-term reproductive success, may be considered. In fact, we found that the probability of occurrence, measured as niche performance, is unrelated to long-term reproductive success in territories where there is a change in any member of the breeding pair. The sites that are assumed to be favorable (with adequate habitat suitability for the species) and that are selected by individuals to establish their territories are associated with low reproductive success (Pellissier et al., 2013; Thuiller et al., 2014). In addition, we verified that the productivity of the population decreases, causing the population viability in the long term to be compromised in the best territories in terms of habitat

suitability. This pattern of lower reproductive output in presumably suitable habitats due the change of individuals in the breeding pairs may suggest the presence of an ecological trap (Battin, 2004).

A trap arises when environments that have been altered are selected by organisms based on previous cues that have been correlated with good habitat suitability (Schlaepfer et al., 2002). Human activities often result in rapid conversion of landscapes, climate change, novel resources in food webs, or human infrastructure such as powerlines or roads, which create new habitat types that may be positively selected but are actually poor in terms of reproduction and survival (Hernández-Matías et al., 2020; Pärt et al., 2007). There is a lack of data about changes associated with human activities, such as electric infrastructures, considered along with poison and illegal hunting (Hernández-Matías et al., 2015, 2020), the main reasons for the decline of this species in the area. Nonetheless, we found an important rate of mortality in the studied population. A third of the deaths causing replacement of individuals in areas of arguably good suitability for the species (those with predicted probabilities of presence >30%) were due to human activities, in particular illegal hunting and electrocutions in power lines. In contrast, we have no records of non-natural mortality in areas of poorer suitability where a replacement of individuals also took place. This high human-induced mortality and the fact that dead individuals are replaced by young immature ones unable to maintain the previous reproduction rate (unpublished data) may compromise the population viability of Bonelli's eagle in the study area. In fact, the long-term reproductive success of this population is less than one chick per year (see Figure 3), which indicates that some underlying process is acting to risk its long-term viability and makes us belief an ecological trap mechanism might be at work.

Our results highlight the importance of identifying problems at the population level, considering that local populations can play a role in the population network, supporting viable metapopulations (Furrer & Pasinelli, 2016; Hernández-Matías et al., 2020). At this scale, we found that the factors affecting distribution and reproductive success are different. The inclusion of long-term reproductive parameters in SDMs is rarely used and will be the key in future conservation programs for endangered species (Guisan & Thuiller, 2005). In addition, we underline the usefulness of combining spatial distribution, habitat selection, and fitness cues that may be involved in some ecological processes that are not identified a priori. Finally, when designing conservation strategies for endangered species, the underlying mechanisms that represent a mismatch between preference and fitness should be taken into account.

CONFLICT OF INTEREST

All authors declare no conflict of interest.

ORCID

Beatriz Martínez-Miranzo https://orcid.org/0000-0002-0348-5459

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