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To breed or not to breed: Territory occupancy is predicted by reproductive performance and habitat heterogeneity

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Abstract

Species life history and anthropogenic influence are important drivers of population performance and viability in human-dominated ecosystems. How these factors affect habitat selection and occupancy in long-lived species is an important topic for their conservation. Long-term datasets are needed for establishing the underlying drivers of this process. In this 22 year-long study, we conducted annual surveys of Bonelli's eagle in the east of the Iberian Peninsula. During this period, 42.8% of the known territories remained unoccupied. Territories with a higher likelihood of raising two chicks over time were stable, evidenced by a lower coefficient of variation in productivity, and were more likely to remain occupied. Moreover, territories with lower habitat diversity, dominated by coniferous forest or agricultural fields, and those located further away from the coast and at higher altitudes showed lower rates of occupancy (i.e., unoccupied >3 consecutive years). To validate these associations, we monitored space use of 22 individuals equipped with Global Positioning System/Global System for Mobile (GPS/GSM) transmitters, which confirmed that eagles selected for open habitats (mainly scrublands and transitional woodland-scrubs) intermixed with forest areas within their home ranges. In contrast, individuals avoided areas dominated by agricultural, urban, and continuous forests for breeding in line with the observations for unoccupied territories. Our results highlight the important interplay between natural and anthropogenic factors, which also have important implications for other raptor species. Preservation of the most productive territories and the re-occupancy of unoccupied territories along with reducing threats in the preferred habitats are fundamental actions that should be taken immediately to sustain viable populations. Potential management actions include enhancing natural prey density through habitat restoration and conservation, mitigating threats and reducing mortality risks due to power lines, fences, poisoning, and maintaining habitat heterogeneity important to eagles' hunting activities.

KEYWORDS
Aquila fasciata, breeding ecology, conservation, GPS, landscape, telemetry, territoriality

INTRODUCTION

The central topic for conservation of endangered species is identifying the underlying causes of their population decline (Dirzo et al., 2014). Anthropogenic development driving changes in distribution and availability of natural habitats is the main cause affecting species populations and their fitness (Loss et al., 2015; McClure et al., 2018).

Life history traits of species such as low reproductive rates, body mass, and long generation time can make them more vulnerable to human-induced environmental changes (Burger & Gochfeld, 2004; Espín et al., 2016; Helander et al., 2008; Kovács et al., 2008; Movalli et al., 2019; Sergio et al., 2004, 2005, 2006). Apex predators, including raptors, are particularly susceptible to the impacts of human-induced developments, such as urbanization and intensified agriculture that affect their prey base and hunting habitats (McClure et al., 2018). Therefore, protecting these species also ensures the preservation of natural processes that promote their existence (Burger & Gochfeld, 2004; Espín et al., 2016; Helander et al., 2008; Kovács et al., 2008; Movalli et al., 2019; Sergio et al., 2005, 2006).

The establishment and maintenance of a breeding territory is a fundamental need for raptors, as it directly influences reproductive success and population persistence (Newton, 1979). Therefore, factors affecting territory maintenance and occupancy shape their fitness (Boulinier et al., 2008; Lõhmus, 2004; Tapia et al., 2007). Raptors invest substantial time and energy in securing and defending their territories, which encompass suitable foraging areas, nest sites, and resources essential for rearing their young (Orians & Wittenberger, 1991; Tapia & Zuberogoitia, 2018). Therefore, territory requirements are usually linked to prey availability, inferred often through raptors' selection for habitat types or vegetation structure, being open areas preferred by many raptor species as hunting grounds as detectability of prey is higher in them (Demerdzhiev et al., 2022; Ferrer & Donázar, 1996; Martínez et al., 2014; Ontiveros et al., 2005; Tapia et al., 2007; Whitfield et al., 2007). When the costs of holding a breeding territory outweigh the hunting success, reproduction and survival, individuals may abandon these (Adams, 2001; Gordon, 1997; Newton, 1998; Sánchez-Zapata & Calvo, 1999; Wiens et al., 1987). Occupancy is generally considered a measure of breeding territory quality (McIntyre, 2002; Rodríguez et al., 2016; Sergio & Newton, 2003). Territories may remain occupied as a consequence of site fidelity due to previous breeding experience (Forero et al., 1999; León-Ortega et al., 2017; Martínez et al., 2006; Schmidt, 2004; Sergio & Newton, 2003; Serrano et al., 2001; Whitfield et al., 2007). Territory abandonment can reflect changes in environment, mortality of territory holders, increased competition, prey populations decline, or human-induced disturbance (Tapia & Zuberogoitia, 2018).

The Bonelli's eagle (*Aquila fasciata*) is an endangered top predator in Mediterranean ecosystems (Cramp & Brooks, 1992; Ontiveros et al., 2004). Bonelli's eagle's survival and reproduction are known to be affected by intraspecific and interspecific competition, habitat quality, anthropogenic disturbance, and climatic variables such as temperature, precipitation, and incidence of sunlight (Balbontín & Ferrer, 2005; Carrete, Sanchez-Zapata, Martínez, Sánchez, et al., 2002, 2006; Carrascal & Seoane, 2009b; Gil-Sánchez et al., 2004; Hernández-Matías et al., 2011; López-López et al., 2004; López-Peinado & López-López, 2023; Martínez-Miranzo et al., 2022; Ontiveros & Pleguezuelos, 2003; Perona et al., 2019; Real & Mañosa, 1997; Real et al., 2001). In general, Bonelli's eagles have lower productivity in colder and higher areas (Gil-Sánchez, 2000; Gil-Sánchez et al., 2004; López-Peinado & López-López, 2023), whereas higher proportion of sunny days per year and milder temperatures correlate with a higher breeding performance (Carrascal & Seoane, 2009a).

The European population of Bonelli's eagle is estimated between 1100 and 1200 breeding pairs (BirdLife International, 2023). The main breeding population is established in the Iberian Peninsula, where it has decreased in recent years from 733 (2005) to 711 pairs (2018). Some small subpopulations (especially the northern ones) are extinct, and others are in decline (Del Moral & Molina, 2018).

To establish the underlying drivers of their decline, we conducted detailed annual surveys for the entire population of the Bonelli's eagle in the east of the Iberian Peninsula beginning in the year 2000 through 2021. These surveys were aimed at monitoring breeding and long-term population dynamics to inform conservation. Therefore, our main goals were to (1) analyze how the population size has changed over the last 22 years; (2) test the relationship between breeding performance and territory occupancy; (3) evaluate the role of landscape composition and habitat heterogeneity in territory occupancy; and (4) analyze habitat selection by individuals in the population to validate eagles' preference for particular habitat types. For (1), we expected a decrease in the number of occupied territories in accordance with decline observed for the overall Iberian population. For (2), we predicted that chronically unoccupied territories would be characterized by lower productivity, higher rate of breeding failure, lower rate at which two young were produced, and higher coefficient of variation of productivity than occupied territories. Because continentality may affect breeding timing and success (López-Peinado & López-López, 2023, 2024), we also hypothesized that most continental territories (i.e., those located at higher elevation above sea level (asl) and farther from the coastline) are more likely to remain consistently unoccupied. For (3), as human-driven habitat modifications (i.e., agriculture) are expected to affect breeding performance, we hypothesized that habitat composition should differ between territories that are consistently occupied versus those unoccupied. In particular, more heterogeneous territories are more likely to be occupied. For (4), we hypothesized that urban-dominated and intensive agricultural habitats will be avoided, and open natural areas will be preferred.

METHODS

Study area

Our study area is located in the Castellón province (6670 km^2, east of Spain). This is a Mediterranean region that includes elevations up to 1814 m asl, with abrupt changes in slopes across the region. The study area's ruggedness is ought to the confluence of two mountain ranges, the Iberian System (northwest-southeast orientated) and the Catalánides (east-southeast orientated), which results in an abrupt orography full of cliffs, ravines, and suitable nesting places for eagles. Mean annual temperature varies from 17°C at lower and coastal areas to 8°C at the highlands. Annual mean precipitation varies from 400 to 900 mm, with highest during autumn and spring and the lowest during summer. The landscape is composed of Mediterranean forests and scrublands where prevalent species are pine (*Pinus* spp.) and oak (*Quercus* spp.). The study area is intermingled with nonirrigated and irrigated cultivation zones. Prey species for the Bonelli's eagle include partridges (*Alectoris rufa*), pigeons (*Columba* spp.), rabbits (*Oryctolagus cuniculus*), hares (*Lepus granatensis*), and lizards (*Timon* spp.), among others (e.g., López-López & Urios, 2010; Moleón et al., 2007, Moleón, Sánchez-Zapata, et al., 2009; Ontiveros & Pleguezuelos, 2000; Ontiveros et al., 2005), and all of them are present in the different landscapes of the study area.

Study species

The Bonelli's eagle is a long-lived raptor distributed from the European Mediterranean region to Southeast Asia (Cramp & Brooks, 1992; Orta et al., 2020). Bonelli's eagle is listed as "Least Concern" in Europe (BirdLife International, 2023; Orta et al., 2020), as "Vulnerable" in Spain (Royal Decree, 139/2011), and "Endangered" in the Valencian Region (DOGV Orden 2/2022). Bonelli's eagle usually breeds on cliffs, sometimes on trees (Arroyo et al., 1995) and, in extremely rarely cases, on electric pylons (Ontiveros, 2016). Bonelli's eagles build multiple nests that they may use alternately between years within same territories (e.g., Martínez et al., 2022). In Mediterranean Spain, the breeding season starts in October–November, with nest building and courtship behavior. By November–December, courtship flights intensify, and mating occurs usually from December to April (López-López et al., 2007; López-Peinado & López-López, 2024; Morollón et al., 2022a). Laying date varies with continentality, usually starting in January in coastal territories until the first weeks of April in some inland territories located at higher altitudes (López-Peinado & López-López, 2024). Replacement clutches after early breeding failure are usually rare (Moleón, Martín-Jaramillo, et al., 2009). Incubation period usually spans 37–41 days (Arroyo et al., 1995). Brood size usually varies from zero to two nestlings. Nests with three fledglings are extremely rare and have never been observed in the study area (López-Peinado & López-López, 2023).

Fieldwork

Between 2000 and 2021, we monitored at least once a month (from January to June) all 35 known Bonelli's eagles' territories in the study area, those occupied as well as the ones that historically had been occupied but remained consistently unoccupied even though the habitat appeared to be suitable for the species from lack of any major land modification (López-López et al., 2006; López-Peinado & López-López, 2023). Observations were made with 20–60× telescopes during clear days at >300 m from nesting cliffs to avoid disturbance to eagles (López-López et al., 2004, 2006, 2007). Every year, we recorded occupancy of each territory.

Since each territory can hold multiple nests, we ensured that a territory was unoccupied when all known nests were checked multiple times within the breeding season. Occupancy was confirmed based on observed nesting attempt, through arranged nests with green branches, typical pair behavior (i.e., eagles flying together and courtship behavior), brood rearing activity, or presence of young (López-López et al., 2007). We also recorded other variables including nest type (tree nest, covered shelf, open shelf or cave), orientation/aspect (N, NE, E, SE, S, SW, W, NW), change of used nest with respect to the nest used the previous year (yes or no), breeders' age (adult, subadult or mixed breeding pair), number of nestlings (0, 1, 2), and number of fledglings (0, 1, 2) (López-Peinado & López-López, 2023). Young were considered to have fledged when they reached 80% of the fledging age (i.e., more than 55 days old) at the last visit, provided that, at this age, nestlings were fully feathered and ready to fly (Gil-Sánchez et al., 2004; López-López, 2022; López-López et al., 2007). We identified territories as consistently unoccupied after being vacant for >3 consecutive years (i.e., no observations of any individual or any signs of breeding attempts).

Landscape composition and heterogeneity

To establish the scale of analyses for landscape composition, we used previously published Bonelli's size estimates for eagle home range (Morollón et al., 2022b). Home range can be defined as the area used year-round by individuals during their daily activities such as searching for food, mates, and perching places (Bosch et al., 2010). The average (± standard deviation) individual home-range size of the Bonelli's eagles in the study area estimated during the study period was 54.84 ± 20.78 km^2 according to Morollón et al. (2022b). Maximum home ranges were 75.62 km^2. Since we did not have detailed telemetry information of all territories in the study area over the study period, we used the same approach for all of them and assumed the existence of circular home ranges of maximum possible size centered on the most frequently used nest yielding a 4.90-km radius. Therefore, we created buffers with a 5.00-km radius around the most used nest to have a spatial estimator of the approximate available home range for the Bonelli's eagles in our study area (for a similar approach see e.g., Carrete, Sanchez-Zapata, Martínez, Sánchez, et al., 2002; Eichenwald et al., 2021). Using these buffers, we extracted the land cover diversity as an index of habitat heterogeneity, during the years 2000–2005, 2006–2011, and 2012–2018. These are the periods for which the CORINE land cover (CLC) estimates have been performed periodically (https://land.copernicus.eu/en/products/corine-land-cover) and these fell within the time period of our territory occupancy monitoring.

We recorded the presence and relative abundance of all CLC classes within each home range as an index of habitat diversity. We used the "rcorr" function from "Hmisc" R package to calculate the Pearson's correlation coefficients between classes. We combined these correlations and a principal components analysis for associations between classes based on eigenvalues (PCA, Lê et al., 2008) to select the most relevant classes for our study. We grouped the variables selected by the PCA based on their biological/habitat relevance for eagles. From the original 47 CLC classes, we obtained seven classes (Table 1): "Agriculture" (all the agricultural lands that are present in the study area), "Broad-leaf forest," "Coniferous forest", "Urban habitats" (noncontinuous urban environments), "Open natural areas" (natural non-forest habitats), "Unsuitable habitats" (paved roads and buildings), and "Water bodies" (running waters, lakes, ponds, and pools of fresh water). Primarily to match with the CLC data availability, we created the temporal comparative classes for territorial occupancy for each territory, with year 2000 as baseline and whichever relevant later CLC class when a territory became unoccupied (for >3 consecutive years) as final. We extracted the initial

TABLE 1 Grouped habitat classes obtained by the principal components analysis (PCA) of CORINE land cover (CLC).

Habitat class	CLC label
Agriculture	Nonirrigated arable land
	Permanently irrigated land
	Fruit trees and berry plantations
	Olive groves
	Pastures
	Complex cultivation patterns
	Land principally occupied by agriculture, with significant areas of natural vegetation
Broad-leaved forest	Broad-leaved forest
Coniferous forest	Coniferous forest
Urban habitats	Discontinuous urban fabric
	Industrial or commercial units
	Mineral extraction sites
	Dump sites
	Sport and leisure facilities
Open natural areas	Scattered woody vegetation
	Sclerophyllous vegetation
	Transitional woodland-shrub
	Sparsely vegetated areas
Unsuitable habitats	Continuous urban fabric
	Sea and ocean
Water bodies	Inland waters

(CLC 2000) and the final habitat composition (CLC 2006/2012/2018), for each territory according to the period they become unoccupied, and the difference between both periods. We calculated the Shannon–Wiener diversity index with the different habitat categories inside the territories and their relative frequency, to get a simplistic proxy of habitat diversity (Kallimanis & Koutsias, 2013).

We obtained the altitude (masl) of the most frequently used nest of the territory (in some cases within the same cliff) from an elevation map using QGIS 3.3 (http://www.qgis.org). To calculate the distance from each frequently used nest to the coastline, we used the function "dist2Line" from the package "geosphere" (Hijmans et al., 2017).

Trapping and tagging

We trapped 22 territorial Bonelli's eagles from 10 different territories, 12 males and 10 females, by means of a folding net between 2015 and 2017 and equipped them with 48 g solar-powered Global Positioning System/Global System for Mobile (GPS/GSM) dataloggers (e-obs GmbH, Munich, Germany). Transmitter duty cycle was programmed to record one GPS location at 5 min intervals, from 1 h before sunrise to 1 h after sunset, year-round (see details in Morollón et al., 2022a, 2022b, 2022c; Perona et al., 2019). The mass of transmitters was 1.6%–2.4% of eagles' body mass, which is within the recommended limits to avoid negative effects on behavior (Bodey et al., 2018; Kenward, 2000). Tags were fixed in a backpack configuration using a Teflon tubular harness designed to ensure that the harness would fall off at the end of the tag's life. Data were retrieved, stored, and managed through the Movebank online repository (www.movebank.org).

Handling was authorized and conducted under permissions issued by regional authorities (Generalitat Valenciana) and all efforts were made to minimize handling time to avoid capture myopathy to eagles.

Data preparation and analysis

We grouped breeding parameters and territory occupancy (accounting for multiple nests within a territory) every 6 years since 2000 to analyze them in relation to landscape variation using the CLC: 2000–2005, 2006–2011, 2012–2017. We computed the following proxies of breeding performance: (1) "productivity": number of chicks fledged/number of breeding attempts; (2) "rate of breeding failure": proportion of breeding attempts with zero fledged chicks; (3) "rate of maximum brood size": proportion of breeding attempts with two chicks fledged; and (4) "coefficient of variation" of productivity: standard deviation/average productivity. For all the territories we calculated these proxies during the last six-year period in which abandonment took place (2000–2005, 2006–2011, or 2012–2017) and for all the years we had information of the territory (since 2000 until the last occupancy).

To assess the relationships for all our objectives we used logistic regressions and ranked different models based on Akaike's information criterion (AIC), selecting as the best model the one with lower AIC and with more than two units of AIC difference with the next one (Anderson & Burnham, 2002). Our response variable was territory consistently unoccupied (1) or occupied (0). Models were fitted using the "glm" function in R, with a binomial error distribution and the "logit" link. The explanatory variables for objective (2) were CV, rate of breeding failure, rate of maximum brood size, and productivity for the six-year period when a territory became unoccupied, and for all the years of occupancy of the territory. We also computed models for the interaction between CV and the other proxies for the six-year period and the entire history of the territory. For objective (3) explanatory variables were altitude, distance from the coastline, original composition of the territories (surfaces of CLC before it became unoccupied), habitat composition after territory became unoccupied (surfaces of CLC after occupancy ends and the composition in 2018 for occupied territories), and differences between both compositions (surfaces of CLC after-before).

For objective (4), we calculated preferences in habitat/land cover use based on Integrated Step Selection Models (Avgar et al., 2016), using the "amt" package (Signer et al., 2019), which allowed us to study the habitat selection using actual habitat use and availability. We resampled the raw data every 15 min for each individual taking into account all the relocations recorded between 2015 and 2021. Using these data, we validated the results of the other hypotheses and compared if the habitats/land cover types more relevant for periods when territories were unoccupied were avoided or less used than the other habitats available. All analyses were conducted using R version 4.1.0 (R Core Team, 2023).

RESULTS

Population trend

After 22 years of Bonelli's eagle breeding monitoring in 35 territories, 15 became unoccupied (for >3 consecutive years), that is, 42.86% reduction in the number of occupied territories. Dividing the data into periods, six territories were consistently unoccupied between 2000 and 2005 (17.14% of 35 territories), five between 2006 and 2011 (17.24% of 29 territories), and four between 2012 and 2017 (16.67% of 24 territories).

Abandoned territories and breeding performance

Territories with lower productivity (Estimate = −1.11; *Z* value = −1.51) and a lower rate of maximum brood size (Estimate = −2.38; *Z* value = −1.56) during the six-year period were more likely to became unoccupied. A higher rate of breeding failure during the six-year period also was positively related to consistent territory unoccupancy (Estimate = 1.47; *Z* value = 1.23).

The higher the CV of the productivity during the full period for all territories, the more likely they were to become unoccupied (Estimate = 1.57; *Z* value =1.50). This was, however, not observed for six-year periods, that exhibited a very moderate effect (Estimate = −0.07; Z value = −0.10). The final model based on the ranking via ΔAIC (Appendix S1: Table S1), contained the CV of productivity and the rate of maximum brood size, along with their interaction (Table 2; Figure 1).

Territory quality and continentality

Territories farther away from the coastline (Estimate = 0.03; *Z* value =1.27) and at higher altitude (Estimate = 0.00; *Z* value = 0.71) had a lower occupancy rate, with distance from the coastline showing a stronger correlation (Figure 2).

Landscape composition and territory occupancy

There were significant differences in landscape composition between consistently unoccupied and occupied territories. Territories dominated by agricultural lands or coniferous forest were more likely to become unoccupied (Table 3). A higher occurrence of human-dominated habitats affected occupancy positively (Table 3; Figure 3).

TABLE 2 Summary of the best model predicting the relationship between abandonment and proxies of breeding performance.

	Estimate	Std. error	*Z* value	Pr(>|*z*|)
Intercept	4.83	2.77	1.75	0.08
rt2	**−14.24**	**7.20**	**−1.98**	**0.05**
CV	**−4.59**	**2.43**	**−1.89**	**0.06**
rt2:CV	**14.24**	**7.57**	**1.88**	**0.06**

Note: The variables with absolute *Z* value higher than 1 are highlighted in bold.
Abbreviations: CV, coefficient of variation of the productivity; rt2, rate of maximum brood size.

Landscape heterogeneity and territory occupancy

There was a negative relationship between the land cover diversity index and probability that a territory would become unoccupied (Estimate = −2.17; *Z* value = −1.42). Habitat diversity was lower in unoccupied territories (Figure 4).

Habitat use

Among the habitat/land cover classes, eagles selected open natural areas (Estimate = 1.63; *Z* value = 86.60), coniferous forests (Estimate = 1.46; *Z* value = 68.70), water bodies (Estimate = 0.97; *Z* value = 6.24), and broad-leaved forest (Estimate = 0.30; *Z* value = 7.02) over agricultural lands (Figure 5). On the other hand, eagles avoided unsuitable habitats (Estimate = −3.31; *Z* value = −18.30) and human-dominated habitats (Estimate = −0.59; *Z* value = −8.40) more than agricultural lands (Figure 5).

DISCUSSION

Long-term field monitoring is essential to assess population trends and identify the factors affecting survival and breeding performance (Bakker et al., 2018; Oppel et al., 2022; Votier et al., 2008). Habitat selection analyses demonstrated by tracked eagles confirmed eagles' preference for open habitats (mainly scrublands and transitional woodland-scrubs) intermixed with forest areas to establish their territories and avoidance of urban habitats. Hence, tracking results combined with long-term field monitoring and patterns associated with land cover changes over time suggest habitat management is crucial for Bonelli's eagle conservation. Open and semi-open natural areas were preferred over human-dominated habitats. The habitat selection function shows a clear avoidance of urban habitats, in agreement with previous studies (Gil-Sánchez, 1996; Moreno-Rueda et al., 2009; Perona et al., 2019). Bonelli's eagle tolerates but not prefers human presence. Furthermore, satellite telemetry information confirms eagles' preference for open natural areas, mainly scrubland and transitional woodland scrub area where it is easier to detect the main prey species: rabbits, pigeons, partridges, other birds, and lizards

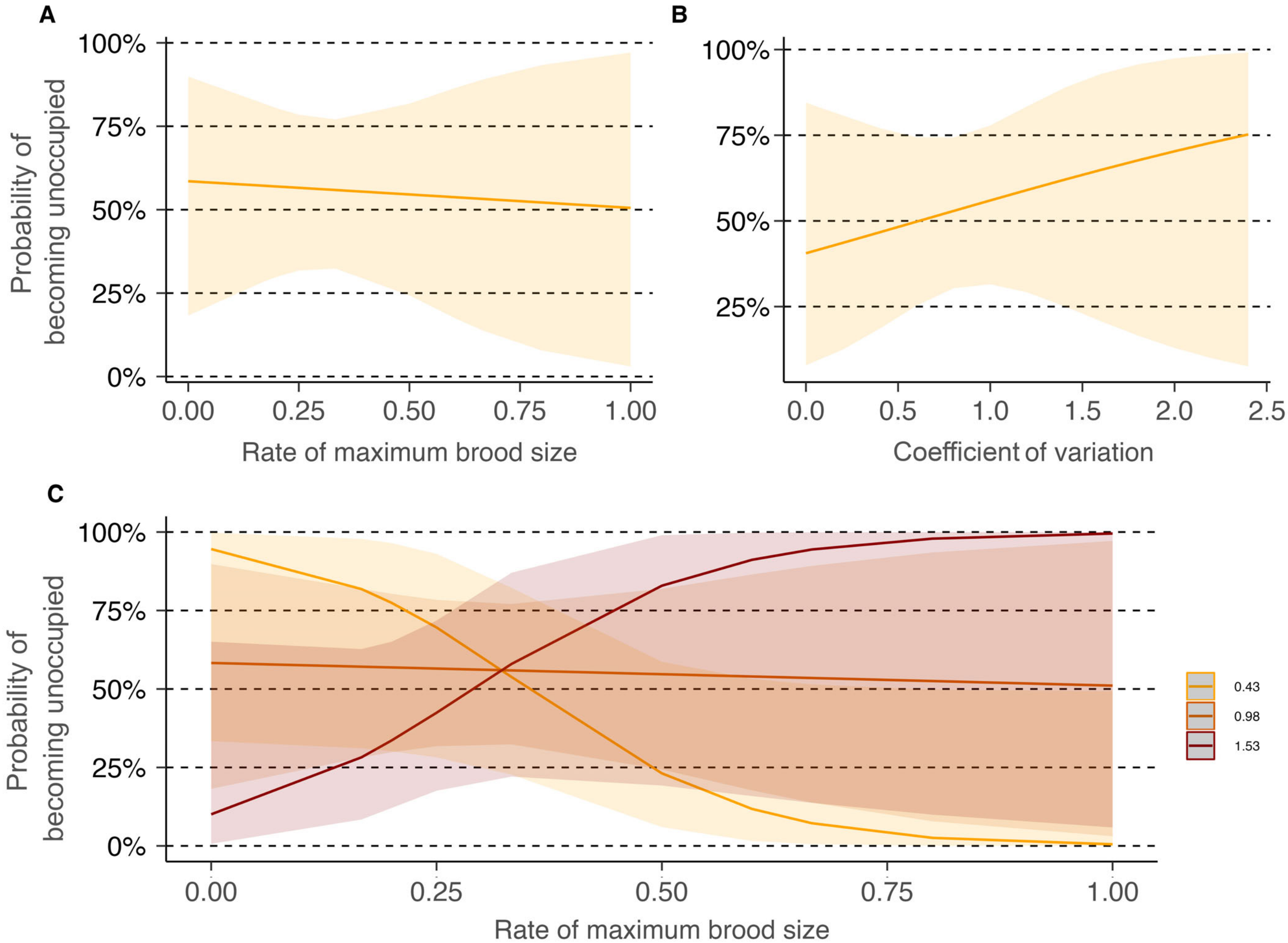

FIGURE 1 Predicted probability of territory becoming unoccupied relative to rate of maximum brood size* (A), coefficient of variation of the productivity (B), and their interaction (C) during the six-year period in which the territory was lost. Shades show the 95% confidence interval (CI) of the predicted effect. *Rate of maximum brood: Proportion of breeding attempts with two chicks fledged.

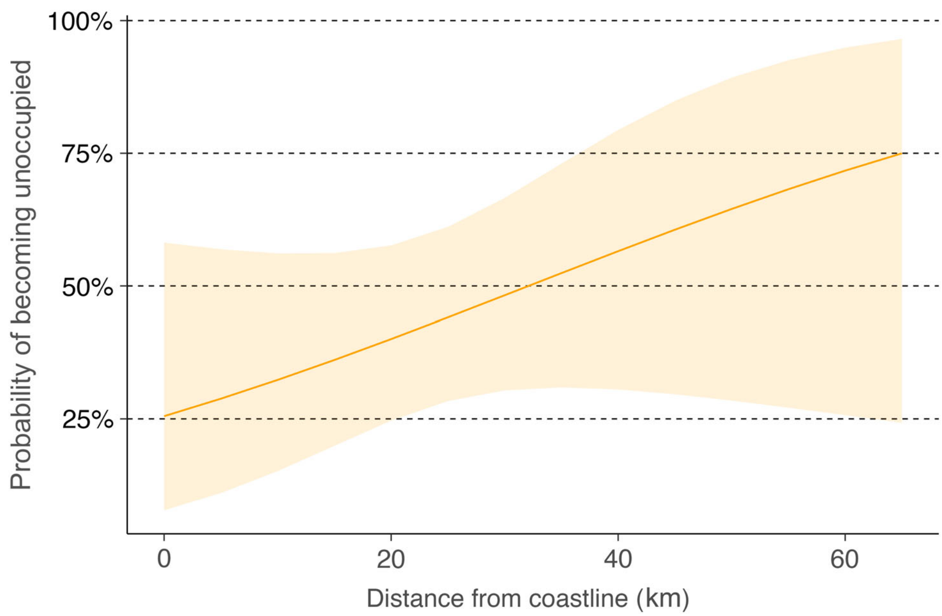

FIGURE 2 Predicted probability of territory abandonment in relation to the distance of the territory from the coastline. Shade shows the 95% CI of the predicted effect.

TABLE 3 Parameter estimates of the best model predicting the relationship between chronically unoccupied territories and landscape composition.

	Estimate	Std. error	Z value	Pr(>|z|)
Intercept	−7.47	7.44	−1.01	0.32
Agriculture	**0.00**	**0.00**	**1.98**	**0.05**
Broad-leaf forest	0.00	0.00	0.51	0.61
Coniferous forest	**0.00**	**0.00**	**1.03**	**0.30**
Urban habitats	**−0.05**	**0.02**	**−1.97**	**0.05**
Open natural area	0.00	0.00	0.84	0.40
Unsuitable habitats	−0.01	0.02	−0.44	0.66
Water bodies	0.06	8.51	0.01	0.99

Note: See Table 1 for details on how variables were aggregated. The variables with absolute *Z* value higher than 1 are highlighted in bold.

(Moleón et al., 2007; Ontiveros et al., 2005). Thereby, GPS information validated the results obtained by the approach we made to make data comparable among territories.

Population decline

The substantial decline of this subpopulation, shown in this study, follows the general trend reported in other Spanish regions according to the latest national survey (Del Moral & Molina, 2018). Furthermore, historical data suggest an existing downward trend in the whole Iberian population. By the time our study began, our subpopulation had already suffered a significant regression in the decades before as reported in nearby regions such as

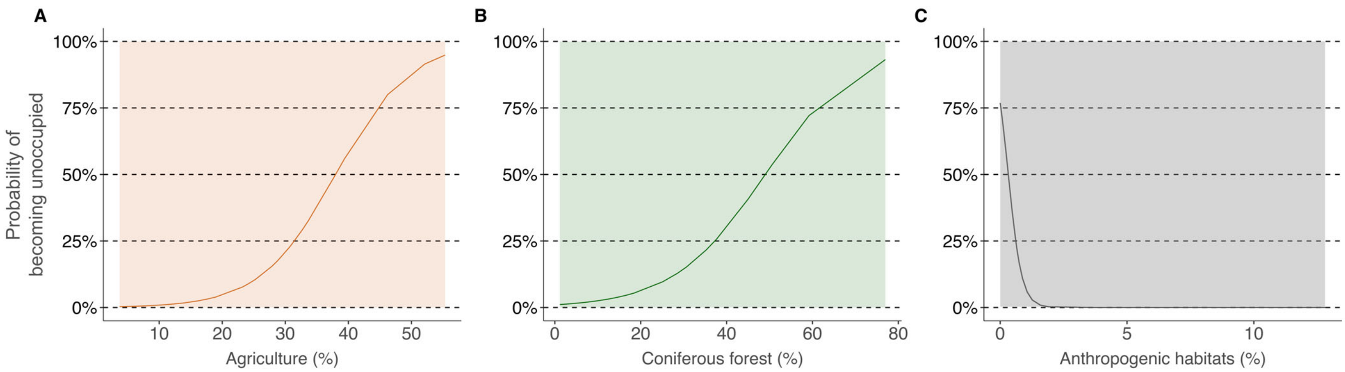

FIGURE 3 Effects of the variables with absolute *Z* value (test statistic) higher than 1 from the best model predicting abandonment in relation to landscape composition.

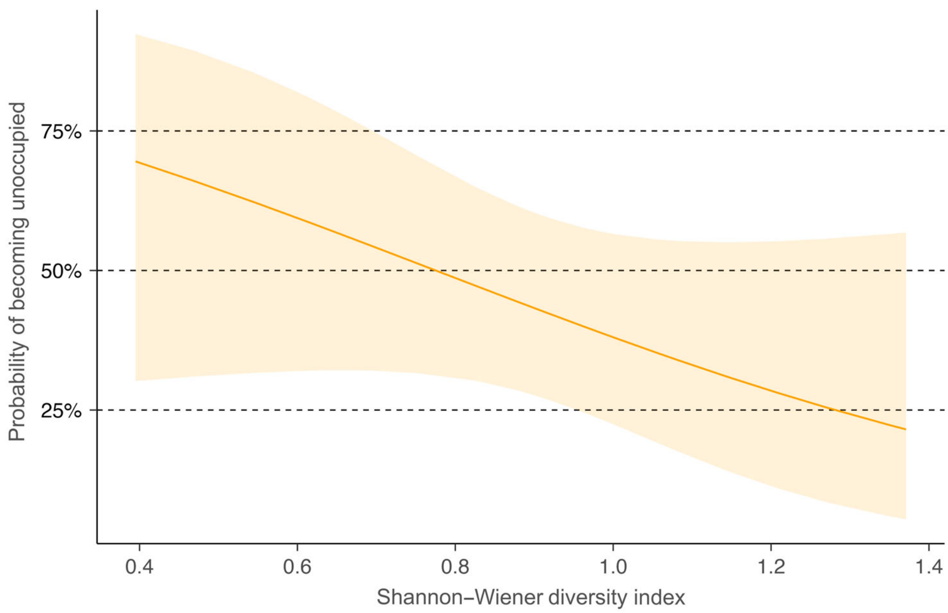

FIGURE 4 Predicted probability of territory abandonment in relation to landscape Shannon–Wiener diversity index. Shaded area shows the 95% CI of the predicted effect.

FIGURE 5 Habitat use by Bonelli's eagles tracked in Eastern Spain. Points indicate the estimates of the integrated step selection function for the logarithm of the residual sum of squares (log_rss). Error bars show 95% CI for the estimate. The model uses Agriculture habitat usage (red solid line) as reference. Colors differentiate between habitat classes. Aggregation of habitat variables explained in Table 1.

Catalonia (Real & Mañosa, 1997; Rocamora, 1994) and Murcia (Carrete, Sanchez-Zapata, Martínez, et al., 2022). Furthermore, breeding parameters for the study population have not shown any significant improvement despite reduced intraspecific competition (López-Peinado & López-López, 2023).

Territories with poor occupancy had low rates of reproduction

As per our expectations, chronically unoccupied territories were consistently less productive, produced fewer nestlings, and had a higher rate of breeding failure, as previously reported with other raptors (Forero et al., 1999; León-Ortega et al., 2017; Martínez et al., 2006; Schmidt, 2004; Sergio & Newton, 2003; Serrano et al., 2001; Whitfield et al., 2007) and with Bonelli's eagle (Carrete, Sanchez-Zapata, Martínez, Sánchez, et al., 2002). For example, Carrete, Sanchez-Zapata, Martínez, Sánchez, et al. (2002) also found that the standard deviation of productivity was higher in consistently unoccupied territories, but they did not discuss this relationship. We expected to find similarly higher values of CV for consistently unoccupied territories and found that for the overall study period, it was true, but not for the six-year periods in which we divided our dataset. Clearly, availability of yearly time series data on land cover change could be more useful to explore in this context. However, in our study, it could be explained by the fact that most territories that became eventually unoccupied exhibited no variance, primarily attributed to the fact that in the years immediately preceding the time when they became consistently unoccupied, breeding attempts were unsuccessful, resulting in zero productivity.

When the interaction between the rate of maximum brood size and the CV was taken into account the effect became more evident. Territories with a higher brood size were less likely to be consistently unoccupied. Therefore, a reduction of the yearly brood size and/or an increased variability of the productivity could be the warning signs for territories on the verge of becoming consistently vacant. Nevertheless, we cannot deny that these factors are driven by others such as annual variability in weather conditions or high turnover rate due to adult mortality (López-Peinado & López-López, 2023), which may affect these predictions. Overall, they should be taken into account too along with habitat changes.

Continentality reduces quality of territories

In our study area and generally, Bonelli's eagles prefer warm temperatures and have a higher breeding success in territories located in areas with warmer and milder winters (López-Peinado & López-López, 2023). Furthermore, Bonelli's eagle had earlier laying date in territories with milder winter weather (López-Peinado & López-López, 2024) and in those located at lower altitudes (Gil-Sánchez, 2000). Other studies have shown that areas with higher average temperatures are more suitable for eagles' reproduction resulting in larger brood sizes (Muñoz et al., 2005; Ontiveros & Pleguezuelos, 2003). In agreement with these previous studies, our results showed that more extreme territory settings (i.e., those located at higher altitude and far from the coastline) are more likely to be abandoned.

The effect of the distance from the coastline was stronger than the effect of the altitude, highlighting the effect of continentality in reducing the quality of territories. This is linked again with the declining trend in Bonelli's eagle's population observed all over Spain (Del Moral & Molina, 2018) as well as the north–south positive gradient in breeding performance described in the literature (López-López et al., 2007; Ontiveros & Pleguezuelos, 2003). This is also in agreement with the "melting range" analogy proposed by Rodríguez (2002) for a declining species that are more likely to lose territories close to the edge of its breeding range (Krüger et al., 2014).

Consistently unoccupied territories show different land cover composition

We found differences in the landscape composition between consistently occupied or unoccupied territories and before and after the territory became unoccupied. This can be attributed to the fact that large areas of some habitat classes can reduce habitat suitability and some urban habitats are positively related with Bonelli's eagle territorial occupancy. In particular, the model shows that when the territories include more than 3000 ha of agricultural lands or more than 4000 ha of coniferous forest the probability of abandonment is over 50%.

Bonelli's eagle can use agricultural lands as hunting grounds depending on the cultivation pattern in the area. In general, intensive irrigated agricultural areas have a negative effect on prey abundance (Marzluff & Ewing, 2008) and therefore on Bonelli's eagle probability of occurrence (Ferguson-Lees & Christie, 2001; Orta et al., 2020). Landscapes dominated by agriculture without other habitats show a negative effect on eagles' occupancy (Carrete, Sanchez-Zapata, Martínez, Sánchez, et al., 2002).

Coniferous forests are one of the most common habitats in the area and show positive effects on abundance of some prey populations (Moreno & Villafuerte, 1995), shelter, perching places and potential nesting places for Bonelli's eagle (Orta et al., 2020). Nonetheless, coniferous forest cover reduces prey availability and thus hunting areas available to open-country eagles (Carrete, Sanchez-Zapata, Martínez, Sánchez, et al., 2002; Marquiss et al., 1985; Ontiveros et al., 2005; Whitfield et al., 2001). Therefore, landscapes dominated by coniferous forest are less suitable for eagles that prey in open areas (Whitfield et al., 2007).

Territories where the landscape is dominated by agricultural lands and coniferous forest showed an increase in the probability of becoming unoccupied, with the opposite effect when landscape was dominated by open habitat types. Open natural areas characterized by scrublands and intermixed scrubland-woodland can be present up to more than 6000 ha within territories before the predicted probability of becoming unoccupied reaches 25%. This indicates that these habitats are preferred hunting grounds for Bonelli's eagle since these habitats are preferred by their prey (Delibes-Mateos et al., 2007, 2009a, 2009b; Delibes-Mateos & Galvez-Bravo, 2009; Moreno & Villafuerte, 1995; Palomares & Delibes, 1997), and where eagles have a higher hunting success (Martínez et al., 2014). Most research suggests that Bonelli's eagle shows a high tolerance, but no preference, for human presence (Gil-Sánchez, 1996; Muñoz et al., 2005; Carrascal & Seoane, 2009b), being human presence to be a source of disturbance that altered eagle behavior (Perona et al., 2019).

Consistently unoccupied territories show less land cover heterogeneity

Our results show that territories with higher land cover richness are less likely to become unoccupied. Habitat heterogeneity facilitates species diversity, so more prey species are expected in more habitat diverse territories (Tuanmu & Jetz, 2015). Moreover, heterogeneous landscapes showed more ecotone areas where detectability increases (Demerdzhiev et al., 2022; Ferrer & Donázar, 1996; Ontiveros et al., 2005; Whitfield et al., 2007). Abandonment of rural areas and traditional activities in the Mediterranean region, especially nonirrigated agriculture and pastoralism, have led to landscape homogenization and is a serious concern for wildlife conservation throughout the entire region (Roura-Pascual et al., 2005; Xystrakis et al., 2017; Zakkak et al., 2014). The presence of diverse habitats within eagles' home range can help to mitigate the negative effects of some of the habitats offering shelter and food for their prey (Delibes-Mateos et al., 2007, 2009a, 2009b; Delibes-Mateos & Galvez-Bravo, 2009; Moreno & Villafuerte, 1995; Palomares & Delibes, 1997). Therefore, like other studies, we also show that habitat heterogeneity favors the presence of hunting habitats for eagles (Demerdzhiev et al., 2022; Ferrer & Donázar, 1996; Ontiveros et al., 2005; Whitfield et al., 2007). As the landscape becomes more homogenized, the availability of suitable hunting habitats diminishes for the Bonelli's eagle.

Conservation implications

The Bonelli's eagle subpopulation studied in Castellón (Spain) has declined in the latest two decades. The causes affecting this population in our region do not differ from those that may be affecting other populations across the breeding range (Del Moral & Molina, 2018; Martínez-Miranzo et al., 2022). Therefore, our results are important to understand the general declining trend observed in this endangered species across its distribution range in the Mediterranean region and inform management actions.

Our results show that extant territories included urban-dominated habitats, even though eagles avoid these habitats. The convergence between humans' and Bonelli's eagles' toward lower, warmer, and coastal environments will increase human-eagle conflicts in the long term. Therefore, land protection in natural parks and maintaining natural prey populations may mitigate conflicts in coastal regions. Finally, the reduction of mortality risks in these human-dominated habitat types is necessary, including wire marking and retrofitting of power lines, the modification of irrigation ponds to prevent mortality due to drowning, as well as the implementation of measures to deter direct persecution, including both illegal hunting and poisoning (López-Peinado, Urios, et al., 2024).

Our results highlight the relevance of breeding parameters as early warning signals of reduction in territorial quality. Early detection of a consistent decrease in productivity or an increase in its variation among years could help managers to focus interventions on those territories to reduce the probability they will become consistently unoccupied. Moreover, simple approaches such as field monitoring can be useful when resources for more detailed data are scarce. Furthermore, long-term monitoring linked to landscape composition changes can be useful to understand the drivers of population trends and give as the hint for establish effective and specific management actions. Measures aimed at improving habitat heterogeneity within territories, mainly through the reduction of continuous coniferous forest and intensive agricultural surfaces in combination with an increase in open habitats will provide positive benefits.

AUTHOR CONTRIBUTIONS

Andrés López-Peinado, Navinder J. Singh, and Pascual López-López conceived the ideas, designed the methodology, wrote the manuscript, and contributed critically to the drafts. Pascual López-López collected the data. Andrés López-Peinado and Navinder J. Singh analyzed the data and wrote the first draft. Pascual López-López and Vicente Urios obtained financial support and provided the final approval for publication. All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Due to the species' endangered status in Spain and its consequent legal protection, breeding, and movement information is not publicly available. Breeding information and territorial locations are property of the University of Valencia and available to qualified researchers by contacting Cavanilles Institute of Biodiversity and Evolutionary Biology (iu.cavanilles@uv.es) and requesting Bonelli's eagles' breeding data. Telemetry data are available upon request to the data manager of the following Movebank projects: "Bonelli's eagle University of Alicante Spain" (project ID = 58923588); "Bonelli's eagle Alicante Spain" (ID = 430140799); "Bonelli's eagle University of Valencia Spain" (ID = 193515984); and "Movement ecology of large raptors in Spain" (ID = 640908212). Code (López-Peinado et al., 2024) is available in Zenodo at https://doi.org/10.5281/zenodo.13744973.

ETHICS STATEMENT

Ethical review and approval were waived for this study because it does not include animals used for experimentation.

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REFERENCES

Adams, E. S. 2001. "Approaches to the Study of Territory Size and Shape." *Annual Review of Ecology, Evolution, and Systematics* 32: 277–303.

Anderson, D. R., and K. P. Burnham. 2002. "Avoiding Pitfalls when Using Information-Theoretic Methods." *The Journal of Wildlife Management* 66: 912–18.

Arroyo, B., E. Ferreiro, and V. Garza. 1995. *Bonelli's eagle (Hieraaetus fasciatus) in Spain. Census, reproduction and conservation*. Technical Report. Madrid: Technical Collection ICONA.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. "Integrated Step Selection Analysis: Bridging the Gap between Resource Selection and Animal Movement." *Methods in Ecology and Evolution* 7: 619–630.

Bakker, V. J., M. E. Finkelstein, D. F. Doak, E. A. VanderWerf, L. C. Young, J. A. Arata, P. R. Sievert, and C. Vanderlip. 2018. "The Albatross of Assessing and Managing Risk for Long-Lived Pelagic Seabirds." *Biological Conservation* 217: 83–95.

Balbontín, J., and M. Ferrer. 2005. "Condition of Large Brood in Bonelli's Eagle *Hieraaetus fasciatus*." *Bird Study* 52: 37–41.

BirdLife International. 2023. "BirdLife Species Factsheet." http://datazone.birdlife.org/species/factsheet/bonellis-eagle-aquila-fasciata.

Bodey, T. W., I. R. Cleasby, F. Bell, N. Parr, A. Schultz, S. C. Votier, and S. Bearhop. 2018. "A Phylogenetically Controlled Meta-Analysis of Biologging Device Effects on Birds: Deleterious Effects and a Call for More Standardized Reporting of Study Data." *Methods in Ecology and Evolution* 9(4): 946–955.

Bosch, R., J. Real, A. Tinto, E. L. Zozaya, and C. Castell. 2010. "Home-Ranges and Patterns of Spatial Use in Territorial Bonelli's Eagles *Aquila fasciata*." *Ibis* 152: 105–117.

Boulinier, T., M. Mariette, B. Dolige, and E. Danchin. 2008. "Choosing where to Breed-Breeding Habitat Choice." In *Behavioural Ecology*, edited by E. Danchin, L. A. Giraldeau, and F. Cézzilly. Oxford: Oxford University Press.

Burger, J., and M. Gochfeld. 2004. "Metal Levels in Eggs of Common Terns (*Sterna hirundo*) in New Jersey: Temporal Trends from 1971 to 2002." *Environmental Research* 94: 336–343.

Carrascal, L. M., and J. Seoane. 2009a. "Linking Density, Productivity and Trends of an Endangered Species: The Bonelli's Eagle in Spain." *Acta Oecologica* 35: 341–48.

Carrascal, L. M., and J. Seoane. 2009b. "Factors Affecting Large-Scale Distribution of the Bonelli's Eagle *Aquila fasciata* in Spain." *Ecological Research* 24: 565–573.

Carrete, M., J. Sánchez-Zapata, J. Martínez, M. Sánchez, and J. Calvo. 2002. "Factors Influencing the Decline of a Bonelli's Eagle *Hieraaetus fasciatus* Population in Southeastern Spain: Demography, Habitat or Competition?" *Biodiversity and Conservation* 11: 975–985.

Carrete, M., J. Sánchez-Zapata, J. Tella, J. Gil-Sánchez, and M. Moleón. 2006. "Components of Breeding Performance in Two Competing Species: Habitat Heterogeneity, Individual Quality and Density-Dependence." *Oikos* 112: 680–690.

Carrete, M., J. A. Sanchez-Zapata, J. E. Martínez, and J. F. Calvo. 2002. "Predicting the Implications of Conservation Management: A Territorial Occupancy Model of Bonelli's Eagle in Murcia, Spain." *Oryx* 36(4): 349–356.

Cramp, S., D. Brooks, 1992. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic*. Oxford: Oxford university Press.

Del Moral, J., and B. Molina. 2018. *El águila perdicera en España, población reproductora en 2018 y método de censo*. SEO/BirdLife: Madrid.

Delibes-Mateos, M., P. Ferreras, and R. Villafuerte. 2009a. "Rabbit (*Oryctolagus cuniculus*) Abundance and Protected Areas in Central-Southern Spain: Why they Do Not Match?" *European Journal of Wildlife Research* 55: 65–69.

Delibes-Mateos, M., P. Ferreras, and R. Villafuerte. 2009b. "European Rabbit Population Trends and Associated Factors: A Review of the Situation in the Iberian Peninsula." *Mammal Review* 39: 124–140.

Delibes-Mateos, M., and L. Galvez-Bravo. 2009. "A Review of the Multifunctional Key Role of European Rabbits in the Iberian Mediterranean Scrubland." *Ecosistemas: Revista Cietifica y Tecnica de Ecologia y Medio Ambiente* 18: 14–25.

Delibes-Mateos, M., S. M. Redpath, E. Angulo, P. Ferreras, and R. Villafuerte. 2007. "Rabbits as a Keystone Species in Southern Europe." *Biological Conservation* 137: 149–156.

Demerdzhiev, D., D. Dobrev, G. Popgeorgiev, and S. Stoychev. 2022. "Landscape Alteration Affects the Demography of an Endangered Avian Predator by Reducing the Habitat Quality." *Avian Research* 13: 100030.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. "Defaunation in the Anthropocene." *Science* 345: 401–6.

Eichenwald, A. J., A. Amar, P. Tyrrell, E. R. Buechley, and M. Z. Virani. 2021. "Declines in an Augur Buzzard Buteo Augur Population in a Region of Increasing Human Development." *Frontiers in Ecology and Evolution* 9: 590073.

Espín, S., A. J. García-Fernández, D. Herzke, R. F. Shore, B. van Hattum, E. Martínez-López, M. Coeurdassier, I. Eulaers, C. Fritsch, and P. Gómez-Ramírez. 2016. "Tracking Pan-Continental Trends in Environmental Contamination Using Sentinel Raptors-What Types of Samples Should we Use?" *Ecotoxicology* 25: 777–801.

Ferguson-Lees, J., and D. A. Christie. 2001. *Raptors of the World*. London: Christopher Helm.

Ferrer, M., and J. A. Donázar. 1996. "Density-Dependent Fecundity by Habitat Heterogeneity in an Increasing Population of Spanish Imperial Eagles." *Ecology* 77: 69–74.

Forero, M. G., J. A. Donázar, J. Blas, and F. Hiraldo. 1999. "Causes and Consequences of Territory Change and Breeding Dispersal Distance in the Black Kite." *Ecology* 80: 1298–1310.

Gil-Sánchez, J. M. 1996. "Selección de hábitat de nidificación por el Aguila Perdicera (*Hieraaetus fasciatus*) en Granada (SE de España)." *Ardeola* 43: 189–197.

Gil-Sánchez, J. M. 2000. "Effects of Altitude and Prey Availability on the Laying Date of Bonelli's Eagles (*Hieraaetus fasciatus*) in Granada (SE Spain)." *Ardeola* 47: 1–8.

Gil-Sánchez, J. M., M. Moleón, M. Otero, and J. Bautista. 2004. "A Nine-Year Study of Successful Breeding in a Bonelli's Eagle Population in Southeast Spain: A Basis for Conservation." *Biological Conservation* 118: 685–694.

Gordon, D. M. 1997. "The Population Consequences of Territorial Behaviour." *Trends in Ecology & Evolution* 12: 63–66.

Helander, B., A. Bignert, and L. Asplund. 2008. "Using Raptors as Environmental Sentinels: Monitoring the White-Tailed Sea Eagle *Haliaeetus albicilla* in Sweden." *Ambio: A Journal of the Human Environment* 37: 425–431.

Hernández-Matías, A., J. Real, R. Pradel, A. Ravayrol, and N. Vincent-Martin. 2011. "Effects of Age, Territoriality and

Breeding on Survival of Bonelli's Eagle *Aquila fasciata*." *Ibis* 153: 846–857.

Hijmans, R. J., E. Williams, C. Vennes, and M. R. J. Hijmans. 2017. "Package 'geosphere'." *Spherical Trigonometry* 1(7): 1–45.

Kallimanis, A. S., and N. Koutsias. 2013. "Geographical Patterns of Corine Land Cover Diversity across Europe: The Effect of Grain Size and Thematic Resolution." *Progress in Physical Geography* 37: 161–177.

Kenward, R. E. 2000. *A Manual for Wildlife Radio Tagging*. London: Academic Press.

Kovács, A., U. C. Mammen, and C. V. Wernham. 2008. "European Monitoring for Raptors and Owls: State of the Art and Future Needs." *Ambio: A Journal of the Human Environment* 37: 408–412.

Krüger, S. C., D. G. Allan, A. R. Jenkins, and A. Amar. 2014. "Trends in Territory Occupancy, Distribution and Density of the Bearded Vulture *Gypaetus barbatus meridionalis* in Southern Africa." *Bird Conservation International* 24: 162–177.

León-Ortega, M., M. V. Jiménez-Franco, J. E. Martínez, and J. F. Calvo. 2017. "Factors Influencing Territorial Occupancy and Reproductive Success in a Eurasian Eagle-Owl (*Bubo bubo*) Population." *PLoS One* 12: e0175597.

Lê, S., J. Josse, and F. Husson. 2008. "FactoMineR: An R Package for Multivariate Analysis." *Journal of Statistical Software* 25: 1–18.

Lõhmus, A. 2004. "Raptor Habitat Studies – The State of the Art." In *Raptors Worldwide*, edited by R. D. Chancellor and B.-U. Meyburg, 279–296. Budapest: WWGBP/MME.

López-Peinado, A., N. Singh, V. Urios, and P. López-López. 2024. "To Breed or Not to Breed: Supplementary Material, Code 1.0 (Research)." Zenodo. https://doi.org/10.5281/zenodo.13744973.

López-López, P. 2022. "Potential Negative Effects of the Installation of Video Surveillance Cameras in raptors' Nests." *Scientific Reports* 12: 21969.

López-López, P., and V. Urios. 2010. "Use of Digital Trail Cameras to Study Bonelli's Eagle's Diet during the Nestling Season." *Italian Journal of Zoology* 77: 289–295.

López-López, P., C. García-Ripollés, J. M. Aguilar, F. Garcia-López, and J. Verdejo. 2006. "Modelling Breeding Habitat Preferences of Bonelli's Eagle (*Hieraaetus fasciatus*) in Relation to Topography, Disturbance, Climate and Land Use at Different Spatial Scales." *Journal of Ornithology* 147: 97–106.

López-López, P., C. García-Ripollés, F. García-López, J. M. Aguilar, and J. Verdejo. 2004. "Patrón de distribución del águila real *Aquila chrysaetos* y del águila-azor perdicera *Hieraaetus fasciatus* en la provincia de Castellón." *Ardeola* 51: 275–283.

López-López, P., C. García-Ripollés, and V. Urios. 2007. "Population Size, Breeding Performance and Territory Quality of Bonelli's Eagle *Hieraaetus fasciatus* in Eastern Spain." *Bird Study* 54: 335–342.

López-Peinado, A., and P. López-López. 2023. "Breeders' Age, Nest-Site Characteristics and Climatic Conditions but Not Density-Dependent Effects Determine Bonelli's Eagle Breeding Performance: A Long-Term Study (2002–2021)." *Ornithological Applications* 126: duad048. https://doi.org/10.1093/ornithapp/duad048.

López-Peinado, A., and P. López-López. 2024. "Laying Date Depends on Territorial breeders' Age, Climatic Conditions and Previous Breeding Success: A Long-Term Study (2004–2021) with Bonelli's Eagle in Spain." *Journal of Ornithology* 165: 725–735. https://doi.org/10.1007/s10336-024-02165-0.

López-Peinado, A., V. Urios, and P. López-López. 2024. "A Comprehensive Analysis of Spatial and Temporal Patterns of Anthropogenic Adult Mortality of Bonelli's Eagles in Eastern Spain." *The Journal of Wildlife Management* 88: e22643.

Loss, S. R., T. Will, and P. P. Marra. 2015. "Direct Mortality of Birds from Anthropogenic Causes." *Annual Review of Ecology, Evolution, and Systematics* 46: 99–120.

Madders, M., and D. P. Whitfield. 2006. "Upland Raptors and the Assessment of Wind Farm Impacts." *Ibis* 148: 43–56.

Marquiss, M., D. A. Ratcliffe, and R. Roxburgh. 1985. "The Numbers, Breeding Success and Diet of Golden Eagles in Southern Scotland in Relation to Changes in Land Use." *Biological Conservation* 34: 121–140.

Martínez, J. E., I. Pagán, and J. F. Calvo. 2006. "Factors Influencing Territorial Occupancy and Reproductive Output in the Booted Eagle." *Ibis* 148: 807–819.

Martínez, J. E., I. Zuberogoitia, G. Gómez, J. M. Escarabajal, E. Cerezo, M. V. Jiménez-Franco, and J. F. Calvo. 2014. "Attack Success in Bonelli's Eagle *Aquila fasciata*." *Ornis Fennica* 91: 67–78.

Martínez, J. E., Í. Zuberogoitia, J. F. Calvo, M. Álvarez, and A. Margalida. 2022. "Effect of Nest Composition, Experience and Nest Quality on Nest-Building Behaviour in the Bonelli's Eagle." *Scientific Reports* 12: 4146.

Martínez-Miranzo, B., E. I Banda, A. Gardiazábal, E. Ferreiro, J. Seoane, and J. I. Aguirre. 2022. "Long-Term Monitoring Program Reveals a Mismatch between Spatial Distribution and Reproductive Success in an Endangered Raptor Species in the Mediterranean Area." *Ecological Research* 37: 421–431.

Marzluff, J. M., and K. Ewing. 2008. "Restoration of Fragmented Landscapes for the Conservation of Birds: A General Framework and Specific Recommendations for Urbanizing Landscapes." In *Urban Ecology: An International Perspective on the Interaction between Humans and Nature*, edited by J. M. Marzluff, E. Shulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, U. Simon, and C. ZumBrunnen, 739–755. Boston: Springer US.

McClure, C. J. W., J. R. S. Westrip, J. A. Johnson, S. E. Schulwitz, M. Z. Virani, R. Davies, A. Symes, et al. 2018. "State of the World's Raptors: Distributions, Threats, and Conservation Recommendations." *Biological Conservation* 227: 390–402.

McIntyre, C. L. 2002. "Patterns in Nesting Area Occupancy and Reproductive Success of Golden Eagles (*Aquila chrysaetos*) in Denali Nacional Park and Preserve, Alaska, 1988–1999." *The Journal of Raptor Research* 36: 50–54.

Moleón, M., J. M. Gil-Sánchez, J. Real, J. A. Sánchez-Zapata, J. Bautista, and J. F. Sánchez-Clemot. 2007. "Non-breeding Feeding Ecology of Territorial Bonellis Eagles *Hieraaetus fasciatus* in the Iberian Peninsula." *Ardeola* 54(1): 135–143.

Moleón, M., J. A. Sánchez-Zapata, J. Real, J. A. García-Charton, J. M. Gil-Sánchez, L. Palma, J. Bautista, and P. Bayle. 2009. "Large-Scale Spatio-Temporal Shifts in the Diet of a Predator Mediated by an Emerging Infectious Disease of its Main Prey." *Journal of Biogeography* 36(8): 1502–15.

Moleón, M., J. Martín-Jaramillo, J. Nieto, J. R. Benítez, J. Bautista, A. Madero, and O. del Junco. 2009. "Successful Replacement Clutches in European Bonelli's Eagles (*Hieraaetus fasciatus*)." *Journal of Raptor Research* 43: 164–65.

Moreno, S., and R. Villafuerte. 1995. "Traditional Management of Scrubland for the Conservation of Rabbits *Oryctolagus* *cuniculus* and their Predators in Doñana National Park, Spain." *Biological Conservation* 73: 81–85.

Moreno-Rueda, G., M. Pizarro, D. Ontiveros, and J. M. Pleguezuelos. 2009. "The Coexistence of the Eagles *Aquila chrysaetos* and *Hieraaetus fasciatus* Increases with Low Human Population Density, Intermediate Temperature, and High Prey Diversity." *Annales Zoologici Fennici* 46: 283–290.

Morollón, S., V. Urios, and P. López-López. 2022a. "Home-Range Size and Space Use of Territorial Bonelli's Eagles (*Aquila fasciata*) Tracked by High-Resolution GPS/GSM Telemetry." *Diversity* 14: 1082.

Morollón, S., V. Urios, and P. López-López. 2022b. "Fifteen Days Are Enough to Estimate Home-Range Size in Some Long-Lived Resident Eagles." *Journal of Ornithology* 163: 849–854.

Morollón, S., J. G. Pausas, V. Urios, and P. López-López. 2022c. "Wildfire Response of GPS-Tracked Bonelli's Eagles in Eastern Spain." *International Journal of Wildland Fire* 31(9): 901–8.

Movalli, P., G. Duke, G. Ramello, R. Dekker, A. Vrezec, R. F. Shore, A. García-Fernández, C. Wernham, O. Krone, and N. Alygizakis. 2019. "Progress on Bringing Together Raptor Collections in Europe for Contaminant Research and Monitoring in Relation to Chemicals Regulation." *Environmental Science and Pollution Research* 26: 20132–36.

Muñoz, A. R., R. Real, A. M. Barbosa, and J. M. Vargas. 2005. "Modelling the Distribution of Bonelli's Eagle in Spain: Implications for Conservation Planning." *Diversity and Distributions* 11: 477–486.

Newton, I. 1979. *Population Ecology of Raptors*. London: Poyser.

Newton, I. 1998. *Population Limitation in Birds*. London: Academic Press.

Ontiveros, D. 2016. "Águila perdicera – Aquila fasciata." In *Enciclopedia Virtual de los Vertebrados Españoles*, edited by A. Salvador and M. B. Morales. Madrid: Museo Nacional de Ciencias Naturales http://www.vertebradosibericos.org/aves/aqufas.html.

Ontiveros, D., and J. M. Pleguezuelos. 2000. "Influence of Prey Densities in the Distribution and Breeding Success of Bonelli's Eagle (*Hieraaetus fasciatus*): Management Implications." *Biological Conservation* 93(1): 19–25.

Ontiveros, D., and J. Pleguezuelos. 2003. "Influence of Climate on Bonelli's eagle's (*Hieraaetus fasciatus* V. 1822) Breeding Success through the Western Mediterranean." *Journal of Biogeography* 30: 755–760.

Ontiveros, D., J. M. Pleguezuelos, and J. Caro. 2005. "Prey Density, Prey Detectability and Food Habits: The Case of Bonelli's Eagle and the Conservation Measures." *Biological Conservation* 123: 19–25.

Ontiveros, D., J. Real, J. Balbontín, M. Carrete, E. Ferreiro, M. Ferrer, S. Mañosa, J. Pleguezuelos, and J. Sánchez-Zapata. 2004. "Conservation Biology of the Bonelli's Eagle in Spain: Research and Management." *Ardeola* 51: 461–470.

Oppel, S., B. L. Clark, M. M. Risi, C. Horswill, S. J. Converse, C. W. Jones, A. M. Osborne, K. Stevens, V. Perold, and A. L. Bond. 2022. "Cryptic Population Decrease Due to Invasive Species Predation in a Long-Lived Seabird Supports Need for Eradication." *Journal of Applied Ecology* 59: 2059–70.

Orians, G. H., and J. F. Wittenberger. 1991. "Spatial and Temporal Scales in Habitat Selection." *The American Naturalist* 137: 29–49.

Orta, J., G. M. Kirwan, D. Christie, P. F. D. Boesman, J. S. Marks, and E. Garcia. 2020. "Bonelli's Eagle (*Aquila fasciata*), version 1.0. Birds of the World."

Palomares, F., and M. Delibes. 1997. "Predation upon European Rabbits and their Use of Open and Closed Patches in Mediterranean Habitats." *Oikos* 80: 407–410.

Perona, A. M., V. Urios, and P. López-López. 2019. "Holidays? Not for all. Eagles Have Larger Home Ranges on Holidays as a Consequence of Human Disturbance." *Biological Conservation* 231: 59–66.

R Core Team. 2023. "R: The R Project for Statistical Computing." https://www.r-project.org/.

Real, J., and S. Mañosa. 1997. "Demography and Conservation of Western European Bonelli's Eagle *Hieraaetus fasciatus* Populations." *Biological Conservation* 79: 59–66.

Real, J., J. M. Grande, S. Mañosa, and J. A. Sánchez-Zapata. 2001. "Causes of Death in Different Areas for Bonelli's Eagle *Hieraaetus fasciatus* in Spain." *Bird Study* 48: 221–28.

Rocamora, G. 1994. "Bonelli's Eagle Hieraaetus fasciatus." In *Birds in Europe, their Conservation Status*, edited by G. M. Tucker and M. F. Heath. https://ec.europa.eu/environment/nature/conservation/wildbirds/action_plans/docs/hieraaetus_fasciatus.pdf.

Rodríguez, J. P. 2002. "Range Contraction in Declining North American Bird Populations." *Ecological Applications* 12: 238–248.

Rodríguez, S. A., P. L. Kennedy, and P. H. Parker. 2016. "Timber Harvest and Tree Size near Nests Explains Variation in Nest Site Occupancy but Not Productivity in Northern Goshawks (*Accipiter gentilis*)." *Forest Ecology and Management* 374: 220–29.

Roura-Pascual, N., P. Pons, M. Etienne, and B. Lambert. 2005. "Transformation of a Rural Landscape in the Eastern Pyrenees between 1953 and 2000." *Mountain Research and Development* 25: 252–261.

Sánchez-Zapata, J. A., and J. F. Calvo. 1999. "Raptor Distribution in Relation to Landscape Composition in Semi-Arid Mediterranean Habitats." *Journal of Applied Ecology* 36: 254–262.

Schmidt, K. A. 2004. "Site Fidelity in Temporally Correlated Environments Enhances Population Persistence." *Ecology Letters* 7: 176–184.

Sergio, F., L. Marchesi, P. Pedrini, M. Ferrer, and V. Penteriani. 2004. "Electrocution Alters the Distribution and Density of a Top Predator, the Eagle Owl *Bubo bubo*: Effects of Electrocution on Eagle Owls." *Journal of Applied Ecology* 41: 836–845.

Sergio, F., and I. Newton. 2003. "Occupancy as a Measure of Territory Quality." *Journal of Animal Ecology* 72: 857–865.

Sergio, F., I. Newton, and L. Marchesi. 2005. "Top Predators and Biodiversity." *Nature* 436: 192.

Sergio, F., I. Newton, L. Marchesi, and P. Pedrini. 2006. "Ecologically Justified Charisma: Preservation of Top Predators Delivers Biodiversity Conservation." *Journal of Applied Ecology* 43: 1049–55.

Serrano, D., J. L. Tella, M. G. Forero, and J. A. Donázar. 2001. "Factors Affecting Breeding Dispersal in the Facultatively Colonial Lesser Kestrel: Individual Experience vs. Conspecific Cues." *Journal of Animal Ecology* 70: 568–578.

Signer, J., J. Fieberg, and T. Avgar. 2019. "Animal Movement Tools (Amt): R Package for Managing Tracking Data and Conducting Habitat Selection Analyses." *Ecology and Evolution* 9: 880–890.

Tapia, L., P. Kennedy, and B. Mannan. 2007. “Habitat Sampling.” In *Raptor Research and Management Techniques Manual. Raptor Research Foundation*, edited by D. Bird and K. Bildstein, 153–169. Surrey: Hancock House Publishers.

Tapia, L., and I. Zuberogoitia. 2018. “Breeding and Nesting Biology in Raptors.” In *Birds of Prey: Biology and Conservation in the XXI Century* 63–94. Cham: Springer International Publishing AG, part of Springer Nature.

Tuanmu, M.-N., and W. Jetz. 2015. “A Global, Remote Sensing-Based Characterization of Terrestrial Habitat Heterogeneity for Biodiversity and Ecosystem Modelling.” *Global Ecology and Biogeography* 24: 1329–39.

Votier, S. C., T. R. Birkhead, D. Oro, M. Trinder, M. Grantham, J. A. Clark, R. H. McCleery, and B. J. Hatchwell. 2008. “Recruitment and Survival of Immature Seabirds in Relation to Oil Spills and Climate Variability.” *Journal of Animal Ecology* 77: 974–983.

Whitfield, D., D. Mcleod, A. Fielding, R. Broad, R. Evans, and P. Haworth. 2001. “The Effects of Forestry on Golden Eagles on the Island of Mull, Western Scotland.” *Journal of Applied Ecology* 38: 1208–20.

Whitfield, D. P., A. H. Fielding, M. J. P. Gregory, A. G. Gordon, D. R. A. McLeod, and P. F. Haworth. 2007. “Complex Effects of Habitat Loss on Golden Eagles *Aquila chrysaetos*.” *Ibis* 149: 26–36.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. “Habitat Occupancy Patterns of North American Shrubsteppe Birds: The Effects of Spatial Scale.” *Oikos* 48: 132–147.

Xystrakis, F., T. Psarras, and N. Koutsias. 2017. “A Process-Based Land Use/Land Cover Change Assessment on a Mountainous Area of Greece during 1945–2009: Signs of Socio-Economic Drivers.” *Science of the Total Environment* 587: 360–370.

Zakkak, S., E. Kakalis, A. Radović, J. M. Halley, and V. Kati. 2014. “The Impact of Forest Encroachment after Agricultural Land Abandonment on Passerine Bird Communities: The Case of Greece.” *Journal for Nature Conservation* 22: 157–165.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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