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Research Article

Nests in trees are as good as or better than cliffs for two formerly persecuted, primarily cliff nesting eagles in Spain: a cautionary tale in defining the habitat of range-restricted or threatened species

Ryan Baumbusch[1], Jesus Bautista[2], Jose Rafael Garrido[2], Ian Newton[3], Miguel Ferrer[1] and Virginia Morandini[4]

[1]Estación Biológica de Doñana (CSIC), Sevilla, Spain
[2]Agencia de Medio Ambiente y Agua, Consejería de Sostenibilidad, Medio Ambiente y Economía Azul, Junta de Andalucía, Sevilla, Spain
[3]Centre for Ecology and Hydrology, Monks Wood Research Station, Abbots Ripton, Huntingdon, Cambs, UK
[4]National Museum of Natural Sciences (CSIC), Madrid, Spain

Correspondence: Miguel Ferrer (mferrer@ebd.csic.es)

In the late-20th century, golden and Bonelli's eagles suffered population declines on the Iberian Peninsula, partly due to human persecution. Habitat assessments – especially for Bonelli's eagles – always found or assumed strong associations with cliffs that provided nesting sites. However, in recent years these eagles have increasingly used trees for nests in this region. Using multi-decadal surveys of golden and Bonelli's eagle fledglings at nests across Andalusia in southern Spain, we compared the number of young fledged in tree nests to the number reared in the more numerous cliff nests. We evaluated alternative hypotheses with an Information Theoretic approach to test whether increased use of trees resulted from growing populations relying on lower quality habitat or whether trees provide equivalent or higher quality nest-sites that were previously unused. Reproductive rates of Bonelli's eagles were substantially higher in tree nests, while reproductive rates of golden eagles were similar between trees and cliffs. We found no difference in reproductive rates between trees and cliffs within territories that contained both types. Our results illustrate the difficulty in characterizing a species' habitat following a population decline or range restriction. Golden and Bonelli's eagles were intensively persecuted in Spain, which may have precluded them from nesting in trees that were easily accessed by humans. We should be cautious in making judgements about the quality or totality of habitat when we know a species no longer occupies the full extent of its former range. Overly narrow and inflexible definitions of a species' habitat in these cases may impede eventual recovery efforts for the species in question.

Keywords: *Aquila chrysaetos*, *Aquila fasciatus*, Bonelli's eagle, golden eagle, nesting habitat

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Introduction

A key component of endangered species conservation is the identification and protection of habitat. Defining the habitat of a species can be difficult (Johnson 2007), and is further complicated when considering rare species (Lomba et al. 2010). Habitat is the biotic and abiotic features of a landscape that support occupancy through survival and reproduction (Hall et al. 2006), and identifying these landscape features for a given species is unlikely to occupy that species being present in the landscape. Yet, when a species is endangered, it is likely to no longer occupy all parts of its former range that provide a variety of alternative habitats (Scheele et al. 2017). Thus, if we try to define the habitat of a range-restricted or declining species, those features that we find to be habitat, or even high-quality habitat, may not represent the full scope of what the species could use as habitat or include the highest-quality habitat. This is akin to the distinction between a fundamental and realized niche (Hutchinson 1957), yet with implications for species conservation, government policy, and industrial regulations. When the anthropogenic threats that an endangered species faces are also linked with features of the landscape, this can confound what we are able to identify and protect as habitat.

While all components of a species life cycle are important for its survival and reproduction (Culp et al. 2017), breeding habitat is often of particular concern in conservation efforts, especially for birds (Robbins et al. 1989). Nest site selection and construction can have important implications for factors such as predation risk (Lima 2009) or thermal buffering during harsh weather (Rockweit et al. 2012). Nesting behaviors evolve over time, resulting in a diverse array of strategies across avifauna (Collias 1997). Aspects of nesting include the size and shape of nest construction, placement on or above the ground, and substrate, among others, with each aspect influencing fitness (Martin 1995).

Bonelli's eagles *Aquila fasciata* and golden eagles *Aquila chrysaetos* are large raptors that live on the Iberian Peninsula in Europe. Bonelli's eagles, in particular, have received considerable research and conservation effort in this region due to a steep population decline in the late 20th century (Muñoz et al. 2005), and because they are listed as endangered in the Red Book of Birds of Spain (Madroño et al. 2004). Golden eagle populations have suffered somewhat less in Spain, but the species was listed as near-threatened in the Red Book of Birds of Spain (Madroño et al. 2004). Both species are considered to use cliffs as primary nesting sites in this region (Ontiveros 1999, Penteriani et al. 2003, Gil-Sánchez et al. 2004) and to only rarely use trees. Habitat suitability and species distribution models for Bonelli's eagles often find or assume strong associations with cliff availability for nesting (Ontiveros 1999, Muñoz et al. 2005, López-López et al. 2006, Carrascal and Seoane 2009, Hernández-Matías et al. 2010, Muñoz and Real 2013). However, it was recently noted that, in the Sierra Morena of southern Spain, the proportion of nesting attempts in trees has increased for both Bonelli's and

golden eagles (Matínez-Abraín et al. 2021), while in southern Portugal, where Bonelli's eagles have expanded their range, almost all newly established territories involved the use of trees as nest sites (Dias et al. 2017). What remains unknown, however, is the quality of habitat that trees provide as nesting substrates compared to the more frequently used cliffs.

The increased use of trees for nesting by these eagles could have occurred for several reasons. The populations of both species have expanded in recent decades – Bonelli's eagles more so than golden eagles. Density-dependent regulation of productivity through habitat heterogeneity (Ferrer and Donazar 1996) would suggest that as the populations have grown, high-quality habitat (i.e. cliffs for nesting) was settled first, and with continued recruitment, new territories were established increasingly in poor-quality habitat (i.e. trees for nests). Cliffs are thought to provide better protection from nest predators and also provide better wind currents for these soaring species. However, an alternative explanation is that until recently these eagles were systematically excluded – through human persecution – from territories where they could nest in trees. Both species were persecuted during the first half of the 20th century, with support from government bounty programs in Spain (Ferrer 2001). An alternative common name for Bonelli's eagles in Spain translates to partridge eagle, and they suffered extensive persecution as a perceived threat to the important game species they were named after (Moleón et al. 2011). Cliff nests are generally on higher ground than trees, involving a difficult uphill walk for potential persecutors, and likely affording much more protection for these eagles than for tree-nesting pairs on lower ground more accessible to persecutors. The observed strong preference of these eagles to nest on cliffs may thus result from an avoidance of human disturbance or simply because those individuals nesting in trees were killed, as has been observed for Bonelli's and golden eagles – among other tree-nesting raptors – in North Africa (Garrido et al. 2021).

Here we assessed the value of trees as nesting sites for Bonelli's and golden eagles and compared alternative hypotheses to explain trends in productivity as both species have increasingly used tree nests. We utilized two long-term datasets of productivity that recorded the number of young fledged per active nest in both Bonelli's and golden eagles across the region of Andalusia in southern Spain. Particularly for the recovering Bonelli's eagle, if productivity in tree nests is substantially lower than that in cliffs, this could be an indication that the population is approaching carrying capacity with new pairs relegated to establishing territories with poor-quality nesting sites. This would also suggest that habitat conservation efforts should continue to focus on protecting areas that provide cliffs for nesting. On the other hand, if productivity in tree nests is equivalent to or better than nests on cliffs, this may indicate that these species are utilizing a part of the landscape that was previously unavailable due to persecution or from which the eagles had been eliminated in the past.

Material and methods

Study species

The Bonelli's eagle is a large long-lived bird of prey found in western Europe and North Africa, across southern Asia, and into Indonesia (Cramp and Simmons 1980). Pairs are monogamous, lay two eggs (range 1–3), and acquire full adult plumage at around 5 years of age (Ferguson-Lees and Christie 2001). This species is sedentary in Europe, and its members defend territories throughout the year. They have suffered a population decline across their entire distribution range (Real and Mañosa 1997). The European population was estimated at between 938 and 1039 breeding pairs (Real et al. 1996). The Spanish population was estimated at 658–721 pairs in 2000 (Ontiveros et al. 2004) and at 711–745 pairs in 2018 (Del Moral and Molina 2018).

The golden eagle is a long-lived monogamous raptor with a wide global distribution (Cramp and Simmons 1980). In most of the European range, pairs remain in the same area throughout the year. First breeding typically takes place when individuals are 4 to 5 years old, and pairs usually lay two eggs (Brown and Amadon 1968). In Spain, the species is mostly distributed across the main mountain systems, covering an area of about 250 000 km². In recent years, population size was estimated to be stable or increasing (Carrete et al. 2002a, Del Moral 2009, Arroyo 2017), with the most recent estimate of the Andalusian population at 348 breeding pairs (CAGPDS 2019).

Study area and data collection

To assess variation in the proportions of tree versus cliff nesters in golden and Bonelli's eagles, we selected a large and well-monitored region in southern Spain where both nest substrate types are widely available. We monitored the breeding populations of the Baetic Mountains and Sierra Morena. In the Baetic Mountains, the dominant geology is calcareous, with some siliceous outcrops. The highest elevation is Mulhacen Peak at 3482 m a.s.l. in the Sierra Nevada massif. There is a wide range of annual rainfall (300–1200 mm; Rivas-Martínez et al. 1997) and a great diversity of Mediterranean climates, from montane to subcontinental, subtropical, and sub-desert. Natural vegetation (mainly *Quercus ilex* woodland) has been highly transformed, mainly by non-irrigated cultivations (olive groves *Olea europea*, almond groves *Prunus dulcis*, and cereal crops), with scattered fragments of Mediterranean scrub and pine plantations (mainly *Pinus halepensis* and *P. pinaster*). Livestock grazing is extensive, though the recent trend is toward intensive farming. In addition, small game hunting is practiced in most of the area; big game hunting is more restricted than in the Sierra Morena range.

Sierra Morena has a relatively steep relief on its southern slope, which corresponds to our study area. It has a low elevation, reaching an altitude of 1333 m a.s.l. Its landscape is much more homogeneous than that of the Baetic Mountains, represented almost entirely by extensive forests of holm oak *Quercus ilex* accompanied by cork oak *Quercus suber* and gall oak *Quercus faginea* in the wetter areas, and wild olive trees *Olea europea sylvestris* on the border with the Guadalquivir depression. There are also pasture areas with grassland under the holm oaks. The scrubland areas are represented by extensive rockrose *Cistus ladanifer* interspersed with mastic *Pistacia lentiscus*, kermes oak *Quercus coccifera,* and arbutus *Arbutus unedo*. In several areas of Sierra Morena there are patches of foreign species that have replaced the original native forest, such as eucalyptus plantations (*Eucalyptus* sp.) and reforestation of various species of pine (*Pinus pinaster, Pinus pinea*). Average monthly temperatures vary between 8°C in January and 28°C in July. Average annual rainfall varies between 570 and 1100 mm. Most of the area of Sierra Morena is privately owned, so access to people is very restricted. Most of its surface is mainly used for hunting, chiefly of big game, and for cattle, pigs, cattle, goats and sheep.

The Andalusian Environmental Administration, and other external entities, monitored productivity – the number of young that fledged – at golden and Bonelli's eagle territories across Andalusia and noted whether nesting took place on a tree or cliff. In the Baetic Mountains, 25–30% of populations for both eagle species were monitored annually. Periodic censuses were conducted across the region of Andalusia in 2004, 2006, 2008, 2014, and 2018 for golden eagles and in 2000, 2005, 2009, 2012, and 2018 for Bonelli's eagles. Both species may have multiple nest sites located within a territory, but only use a single nest within a breeding season. Productivity was measured by a minimum of three nest checks throughout the breeding season for each species to verify territory occupancy, incubation, and the number of fledglings. Any territories with an insufficient number of checks during a breeding season were excluded from the analysis. Territory coordinates were recorded as the approximate center of nests used within a territory. Age of breeding individuals was determined through plumage and categorized as subadult or adult. Identity of individual eagles was unknown.

Statistical analyses

To evaluate the importance of nesting substrate on productivity in golden and Bonelli's eagles we used an information-theoretic approach to compare multiple hypotheses that could explain variation in eagle productivity (Burnham and Anderson 2002). Despite reproductive values being similar for both golden and Bonelli's eagles, we modelled each species independently, as they may have different processes governing reproduction. Since most territories were monitored over multiple years, we fit generalized linear mixed-effects models (GLMMs) with a Poisson error distribution, where the response variable was the number of young fledged at a given territory in a given year. Territory was fit as a random effect because of repeated measures at this level and because variation in habitat quality between territories can affect productivity (Penteriani et al. 2003, Fielding 2024).

Each hypothesis was represented by a univariate model in the model set for each species (Table 1). One model was fitted with nesting substrate as a categorical variable. As the population of a territorial species grows in size, high-quality

Table 1. Values of all model parameters evaluated for Bonelli's eagles and golden eagles monitored in Andalusia, Spain. For numeric values, Bonelli's eagles values are listed first and values for golden eagles are listed second after the slash.

Parameter	Type	Summary
Nest substrate	Factor	2 Levels: 'Cliff' or 'Tree'
Pair age	Factor	3 Levels: 'Adult', 'Mixed', or 'Subadult'
Year of first survey	Integer	Range = 1980–2020/ 1998–2020
Year trend	Integer	Range = 1980–2020/ 1998–2020
No. of years surveyed	Integer	Range = 1–27/ 1–23
No. of known territories	Integer	Range = 2–335/ 20–204
Distance to conspecific	Continuous	Mean = 8.4/ 11.6, SD = 6.47/ 8.85, Range = 0.192–113/ 0–114
Distance to path	Continuous	Mean = 0.746/ 0.86, SD = 0.57/ 0.60, Range = 0.005–3.47/ 0.005–3.12

territories should be occupied first. Thus, we fitted a model with year of first survey to test this hypothesis, expecting that sites present in earlier surveys should have more fledglings than sites first surveyed later. Several different processes of population regulation may be captured in a year trend. We rescaled both year of first survey and the year trend such that the year of first survey for each species was set to 0. Likewise, as a population grows in size, it may experience density-dependent effects on fecundity, whereby higher density results in lower productivity. We fitted a model with the number of known territories in a given year as the predictor. We had a broad range in the number of years any given territory was surveyed. Fewer years of monitoring at a territory can introduce sampling variance. Biologically, however, low-quality territories may also be occupied less frequently than high-quality territories, resulting in lower annual productivity in less frequently occupied territories. We fitted a model with the number of years a territory was surveyed as a predictor of productivity. We did not use the number of surveyed territories in a year, knowing that not all occupied territories in a year would have been monitored. We also fitted a model using distance to the nearest conspecific territory monitored in a given year to evaluate a density-dependent effect at the territory level rather than at the population level.

Human disturbance is thought to have a major effect on raptor productivity. We fitted a model with distance to human paths (including all types of paths from highways to hiking trails) as an index of disturbance, expecting those territories closer to paths to have lower productivity (Morandini et al. 2017). In Scotland, many persecuted nests are away from public rights of way (A. Fielding unpubl.). The age of individuals within a breeding pair can substantially influence that pair's reproductive success (Sánchez-Zapata et al. 2000, Balbontín et al. 2003, Ferrer and Bisson 2003). We fitted a model with pair age as a categorical variable with three levels: full adult pairs, full subadult pairs, and mixed-age pairs with one adult and one subadult. Because the age of the breeders can have a substantial impact on their productivity, if young eagles disproportionately nest in trees, this may affect our measure of the quality of nesting substrate that trees provide. To control for variation in the proportion of adult breeders within the populations, we fitted additional models with pair age as an additive effect included with each of the models listed above.

Interspecific competition between golden and Bonelli's eagles may also influence productivity, especially for Bonelli's eagles (Gil-Sánchez et al. 2004, Bautista et al. 2020), where we saw on several occasions throughout the study period that Bonelli's eagles were sometimes displaced from their territories by golden eagles. While we have data on distances between conspecific territories, golden eagle surveys began 18 years after Bonelli's eagle surveys, so we do not have these data for the first 18 years of Bonelli's eagle surveys and could not include this in the above model set.

Both species of eagles will only attempt nesting once per breeding season, but will use different nest sites within their territories in different years. Some territories contained both tree and cliff nests that were used in different years. To better understand whether any differences in productivity between tree and cliff nests were due to an intrinsic difference in the nesting substrate itself or some other extrinsic factors of the surrounding area, we performed a paired, two-sided Wilcoxon test with territories that contained both tree and cliff nests. The mean number of fledglings produced in each nesting substrate was averaged within each territory. These averages were then paired within territories to test for a difference in productivity between the nesting substrates within a territory.

Results

We monitored 2703 Bonelli's eagle nesting attempts between 1980 and 2020, and the first use of a tree nest was recorded in 1997. We monitored 1047 golden eagle nest attempts between 1998 and 2020, and the first use of a tree nest was recorded in 1998, the same year that monitoring began for this species. Among these attempts, 101 Bonelli's eagle and 70 golden eagle nest attempts were in trees. Tree nests and cliff nests were located in similar habitats (with cliff nests being at higher altitudes than tree nests). The number of golden eagles breeding attempts that contained both cliff and tree nests was 13, with a total number of breeding attempts of 977 on cliffs and 70 on trees. The number of Bonelli's eagle breeding attempts that contained both cliff and tree nesting attempts were 8, with a total number of breeding attempts on cliffs of 2602 and 101 on trees.

A total of 335 unique Bonelli's eagle territories were monitored over the study period, 20 of which contained

Table 2. The number of nest attempts made in cliffs and trees by adult, subadult, and mixed-age pairs of Bonelli's eagles and golden eagles in Andalusia, Spain.

| Pair age classes | Nest substrate | |
	Cliff	Tree
Golden eagles		
Subadults	65	1
Mixed-age	144	6
dults	768	63
Bonelli's eagles		
Subadults	18	0
Mixed-age	158	5
Adults	2426	96

Table 4. The mean and standard deviation of the number of fledglings produced per year within territories that contained both tree and cliff nests for golden and Bonelli's eagles monitored in Andalusia, Spain between 1980–2020 (Bonelli's eagles) and 1998–2020 (golden eagles), along with the number of territories for each species that contain both tree and cliff nests as well as the p-values of a two-sided Wilcoxon test comparing the average productivity of tree and cliff nests within territories.

Species	Tree	Cliff	n	p-value
Golden eagles	1.09 ± 0.50	1.12 ± 0.67	13	0.69
Bonelli's eagles	1.48 ± 0.64	1.12 ± 0.48	8	0.67

at least one tree nest, while 203 unique golden eagle territories were monitored, of which 16 contained at least one tree nest. Once tree nesting was started, the average percentage of nest attempts in trees each year was 4.21% (SD = 2.34%) for Bonelli's eagles, and 3.04% (SD = 1.52%) for golden eagles. While approximately one new territory with a nest tree was found each year, the proportion of monitored nesting attempts in trees across the study area remained relatively stable, with a maximum of 11 Bonelli's eagle and eight golden eagle tree nests found in any given year. The use of tree and cliff nests was relatively proportional across age classes (Table 2) for both golden eagles ($\chi^2 = 5.6307$, df = 2, p-value = 0.05988) and Bonelli's eagles ($\chi^2 = 0.93584$, df = 2, p-value = 0.6263). The first record of tree nesting within a territory almost always occurred with breeding adults, with the exception of one Bonelli's eagle and two golden eagle tree nests that were first observed with a mixed-age pair, and one golden eagle tree nest that was first observed with a subadult pair.

Productivity (the number of young fledged per nest) and nest success (whether any young fledged from a nest) were similar in golden eagles that nested in cliffs and trees, while Bonelli's eagles showed both higher productivity and nest success in tree nests compared to cliff nests (Table 3). For territories that contained both tree and cliff nests, the Wilcoxon tests indicated that there were no differences between nest types in the number of fledglings produced within a territory for either golden or Bonelli's eagles (Table 4). The average number of fledglings differed considerably between pairs comprised of two adults, an adult and a subadult, or two subadults (Table 5).

Among the models used to test alternative hypotheses to explain variation in productivity, models containing pair age as a factor essentially carried all of the model weight within each model set for both species (Table 6, 7). For Bonelli's eagle, pair age with nest substrate was the top model, with

23% of the model weight, however, the next five top models were within 2 AIC points, and all models with pair age were within 3.2 AIC points. Notably, for Bonelli's eagles, models for year of first occupancy – a common index of habitat quality – and distance to nearest human path – a common index for human disturbance – were ranked lower than the null model, and their additive models with pair age were likewise ranked the lowest among the other additive models with pair age. The effect of trees as a nest substrate in the additive model was small but positive. For golden eagles, the top model was simply pair age, and all additive models including pair age were within 2 AIC points of the top model. The univariate model for nest substrate was the lowest ranked model for golden eagles, indicating a lack of influence (both positive and negative) of nesting substrate on golden eagle productivity. Also, for golden eagles, all univariate models other than pair age (the top model) and year of first survey ranked lower than the null model, and while year of first survey ranked higher than the null model, it essentially held no model weight.

Discussion

Whether golden eagles nest in trees or cliffs appears to have little impact on the number of young the pair will fledge, suggesting that these nesting substrates are comparable in terms of reproductive value. Bonelli's eagles appear to obtain a reproductive advantage in the number of young they fledge when nesting in trees. Given that the number of young fledged did not differ between nest types within territories that had both tree and cliff nests, tree nests may not confer a reproductive advantage per se, but being able to nest in a tree may afford access to high-quality foraging habitat that otherwise lacks cliffs available for nesting. These results do not support the hypothesis that, as Bonelli's and golden eagle populations increased, new pairs established themselves in poor-quality territories and attempted to nest in trees. On the contrary, the

Table 3. Mean ± SD of the number of young fledged, and success ratio of nests that fledged at least one young for golden and Bonelli's eagles nesting in trees and cliffs in Andalusia, Spain during 1980–2020 (Bonelli's eagles) and 1998–2020 (golden eagles).

| Species | | Productivity | | | Success | | |
	n	Cliff	Tree	Total	Cliff	Tree	Total
Golden eagles	863	1.14 ± 0.76	1.17 ± 0.80	1.14 ± 0.77	0.78	0.76	0.78
Bonelli's eagles	2161	1.25 ± 0.79	1.48 ± 0.72	1.26 ± 0.79	0.79	0.87	0.79

Table 5. The mean, ± standard deviation, and sample size in parentheses of the number of eagles fledged per nesting attempt for Bonelli's and golden eagles between 1980–2020 and 1998–2020, respectively, in Andalusia, Spain. Metrics are calculated for pairs comprised of 2 adults, 1 adult and 1 subadult, and 2 subadults.

Species	Adults	Mixed-age	Subadults
Golden eagles	1.30 ± 0.70 (n = 831)	0.71 ± 0.74 (n = 150)	0.18 ± 0.49 (n = 66)
Bonelli's eagles	1.32 ± 0.75 (n = 2522)	0.34 ± 0.71 (n = 163)	0.22 ± 0.65 (n = 18)

increased productivity associated with nesting in trees among Bonelli's eagles suggests that an advantageous shift in habitat use might be underway, or that pairs are now surviving long enough to be recorded rather than being removed soon after settling.

While the average productivity of Bonelli's eagles on cliff nests (1.25 ± 0.79 per laying pair) in our study was comparable to that found in previous research throughout western Europe (better than some but worse than others), the average productivity of Bonelli's eagles that nested in trees (1.48 ± 0.72) exceeded the average productivity of Bonelli's eagles monitored in any previous study in western Europe. The average productivity measured in 6 populations in Spain and France ranged from 0.36 to 1.24 per laying pair (Real and Mañosa 1997). A population in Castellón, Spain monitored between 2002–2006 averaged 1.12 ± 0.152 chicks fledged per laying pair (López-López et al. 2007), while a population in Alicante averaged 1.23 ± 0.05 (Martínez et al. 2008). Two studies in Granada, Spain found averages of 1.42 ± 0.38 (Ontiveros and Pleguezuelos 2000) and 1.43 ± 0.11 (Gil-Sánchez et al. 2004). Previous studies using an earlier (smaller) portion of our dataset from across Andalusia shortly after Bonelli's eagles began using tree nests found an average productivity of 1.39 ± 0.71 (Balbontín et al. 2003, Penteriani et al. 2003). There are fewer published values of productivity in golden eagles on the Iberian Peninsula, but all were below the average of both tree nesting and cliff nesting pairs in our study. During the first state census, productivity for the period between 1982–1988 was 0.81 ± 0.131 per laying pair (Arroyo et al. 1990), and values differed little from those found for a second national survey referring to 2008, 0.83 ± 0.14 (Del Moral 2009). Similarly, regional studies, such as one conducted in Murcia, also in southern Spain, found an average productivity of 0.93 in two years of breeding (Sánchez-Zapata et al. 2000), while in another population monitored between 1994–2001, an average of 0.98 ± 0.085 was obtained (Moleón et al. 2002).

The supply of sticks to cliff nests by many European raptors has been explained only as a functional means of decreasing ectoparasite loads in nests and for signaling nest occupancy. Nevertheless, facultative tree/cliff nesting species would be reproducing the nests they used to build originally on top of trees but on cliffs. Facultative species (likely evolved in forested areas) that supply their cliff nests with sticks include *Pandion haliaetus, Haliaetus albicilla, Milvus migrans, Circaetus gallicus, Buteo buteo, Aquila fasciata, A. pennata, A. chrysaetos, A. heliaca, Gypaetus barbatus, Gyps fulvus* and *Neophron percnopterus*. The supply of greenery by some large eagles to cliff nests (e.g. golden eagle, Bonelli's eagle) has been explained so far only by means of functional causes, notably the role of pine aromatic compounds used as ectoparasite repellents and for signaling nest occupancy. However, a historical explanation has never been suggested. The supply of sticks to cliff nests identifies those raptor species whose original nesting substrate was trees or large shrubs rather than cliffs. On the contrary, we suggest that cliff-nesting species that do not supply sticks to nests should be considered the only true cliff-nester species.

These kinds of findings among raptors include examples from other species. For example, the red kite in the United

Table 6. AIC$_c$ model selection results for generalized linear mixed-effects models estimating the number of Bonelli's eagle young fledged from nests during each yearly breeding attempt from 1980–2020 in Andalusia, Spain.

Model	K	AICc	ΔAICc	w	Log(L)	Cum. w
Pair age + Nest substrate	5	6827.59	0.00	0.23	−3408.78	0.23
Pair Age + No. of known territories	5	6828.08	0.50	0.18	−3409.03	0.41
Pair age + Year trend	5	6828.69	1.11	0.13	−3409.33	0.54
Pair age	4	6828.78	1.19	0.13	−3410.38	0.66
Pair age + Distance to conspecific	5	6828.88	1.30	0.12	−3409.43	0.78
Pair age + No. of years surveyed	5	6829.00	1.41	0.11	−3409.49	0.90
Pair age + Year of first survey	5	6830.33	2.74	0.06	−3410.15	0.95
Pair age + distance to path	5	6830.78	3.20	0.05	−3410.38	1
No. of known territories	3	7006.86	179.27	0.00	−3500.42	1
Nest substrate	3	7007.16	179.58	0.00	−3500.58	1
Year trend	3	7007.36	179.77	0.00	−3500.67	1
No. of years surveyed	3	7007.83	180.24	0.00	−3500.91	1
Distance to conspecific	3	7007.97	180.39	0.00	−3500.98	1
Null model	2	7008.98	181.39	0.00	−3502.49	1
Distance to path	3	7010.88	183.30	0.00	−3502.44	1
Year of first survey	3	7010.98	183.40	0.00	−3502.49	1

Table 7. AIC$_c$ model selection results for generalized linear mixed-effects models estimating the number of golden eagle young fledged from nests during each yearly breeding attempt from 1998–2020 in Andalusia, Spain.

Model	K	AICc	ΔAICc	w	Log(L)	Cum. w
Pair age	4	2487.63	0.00	0.21	−1239.80	0.21
Pair age + No. of years surveyed	5	2488.17	0.54	0.16	−1239.06	0.37
Pair age + Distance to conspecific	5	2488.61	0.99	0.13	−1239.28	0.50
Pair age + No. of known territories	5	2488.89	1.26	0.11	−1239.41	0.61
Pair age + Year of first survey	5	2489.03	1.40	0.10	−1239.48	0.72
Pair age + Distance to path	5	2489.08	1.46	0.10	−1239.51	0.82
Pair age + Nest substrate	5	2489.10	1.47	0.10	−1239.52	0.92
Pair age + Year trend	5	2489.56	1.93	0.08	−1239.75	1
Year of first survey	3	2608.71	121.09	0.00	−1301.35	1
Null model	2	2611.87	124.24	0.00	−1303.93	1
No. of years surveyed	3	2611.92	124.29	0.00	−1302.95	1
Distance to path	3	2613.60	125.97	0.00	−1303.79	1
Year trend	3	2613.71	126.08	0.00	−1303.84	1
Distance to conspecific	3	2613.73	126.11	0.00	−1303.86	1
No. of known territories	3	2613.84	126.21	0.00	−1303.91	1
Nest substrate	3	2613.86	126.23	0.00	−1303.92	1

Kingdom survived in very sub-optimal habitat (an escape from persecution), so species-distribution models based on this habitat would have been very misleading (Newton et al. 1994). Also, peregrines in the English Lake District exhibited a spectacular recovery from DDT and falconry thefts with big changes in nest sites (Horne and Fielding 2002). It has been suggested (Ferrer 2019) that having the plasticity to be a tree- or cliff-facultative nester must have been a critical conservation factor in responding to human disturbance during the 20th century, as obligate tree-nesters may have been more vulnerable to human persecution than facultative tree/ cliff nesters.

It is difficult to say why we observed higher productivity in tree nests or what exactly is prompting the increasing use of tree nests, but we suspect that reduced human persecution may be a factor. Until recently, many large raptors were intensively persecuted in Spain (Villafuerte et al. 1998), as in other parts of the world (Madden et al. 2019, Newton 2020). Across all of Spain throughout most of the 1990s, persecution accounted for 60% of reported adult Bonelli's eagle deaths (Real et al. 2001). During the past two decades in Andalusia, mortality from gunshot accounted for 6% of known Bonelli's eagle deaths, and 0.4% of golden eagle deaths (CAGPDS 2019). There are several mechanisms by which this persecution would have reduced and discouraged nesting in trees by large raptors that could otherwise nest on cliffs. At the most basic level, eagles nesting in trees are much easier to kill and their nests are much easier to destroy. Breeding individuals who are not killed may be harassed and may abandon their territories, eventually settling and remaining on a cliff with better protection from humans. Nesting behavior can be a highly conserved genetic trait within avian species (Collias 1997), and if genetic variation can lead an individual to prefer one type of substrate over another, perhaps killing individuals with preferences for trees changed intrinsic substrate preferences at a genetic level within the population. Similarly, if early experience of nestlings born on trees makes them more prone to breed on this substrate, intensive human persecution would reduce the proportion of eagles with this learned preference for trees. Shifting attitudes towards large raptors with an accompanying reduction in persecution may be facilitating the ability of Bonelli's and golden eagles to make use of trees for nesting, as shootings only made up approximately 6% of the dead or injured golden and Bonelli's over the past two decades (Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible–Junta de Andalucía unpubl.).

Additionally, some discussion about the previous origin of these species can be inferred from current nesting habits. For example, large eagles like golden eagle, Spanish imperial eagle *A. adalberti*, Bonelli's eagle and others that supply nests on cliffs – or do not breed on cliffs at all – may have evolved in forests. Nesting on trees or cliffs is not the only possibility for diurnal raptors. Even though it is true that most of them breed on trees or cliffs, several species of diurnal raptors also nest on the ground. Some are frequently or totally ground-nesters, like the tawny eagle *Aquila rapax*, hen harrier *C. cyaneus* (Volchanetskii and Yal'tsev 1934, Volchanetskii 1937). In other species, ground-nesting occurs less frequently, as in the cases of the Pallas' fish eagle *Haliaeetus leucoryphus*, the bald eagle *H. leucocephalus*, the ferruginous hawk *Buteo regalis*, the black-chested buzzard-eagle *Geranoaetus melanoleucus*, the osprey *Pandion haliaetus*, the golden eagle, the Egyptian vultures *Neophron percnopterus* and the peregrine falcon *Falco peregrinus*, among others (Lokemoen and Duebbert 1976, Newton 2010, Monson 2001, Katzner et al. 2003, Gangoso and Palacios 2005, Martin 2005, Oparin 2008, Ellis et al. 2009, Pagel et al. 2010, Ratcliffe 2010). Ground nests are generally found in remote areas without a large presence of either humans or terrestrial predators. Typically, they are more frequent – but not exclusively – on islands (Del Hoyo et al. 1994, Ferguson-Lees and Christie 2001, Ellis et al. 2009). Nevertheless, ground nesting among raptors continues to be a confounding nesting behavior, especially in areas where there are potential terrestrial predators and elevated substrates available.

Whatever the reason for this behavior, there is a clear difference among true cliff nesters and true tree nesters (sensu Martínez-Abraín and Jiménez 2019) because the supply or lack thereof or sticks follows the same pattern observed by these authors when breeding occurs on cliffs, i.e. true tree-breeders nesting on the ground still use sticks and build a real nest on the ground, which is not the case with true cliff-breeders. This point, in our opinion, reinforces the hypothesis of Martínez-Abraín and Jiménez, showing that some evolutionary load is working on true tree-nesters and that they tend to supply sticks even on cliffs and/or the ground when they breed.

Several suggestions can be made about how this flexible behavior of selecting where to breed has evolved, and why some raptor species seem much more flexible than others. From a conservation point of view, being able to breed on trees or alternatively cliffs must have been a critical factor in responding to human interference during the 20th century. On the other hand, we have to consider the possibility of surveyor bias, as it is possible that numerous tree nests were not recorded because surveyors were not checking there. We acknowledge that within the Andalusian populations of these eagles studied here, there still appear to be a strong preference for nesting on cliffs. Yet, given the extreme rarity of tree nests in the past, especially by Bonelli's eagles, we suggest this pattern warrants further attention. Areas with few or no cliffs available for nesting may still afford high-quality nesting habitat for these eagles. This could provide increased flexibility to conservation planning in the future if regions with few or no cliffs could be used as protected areas or release sites for Bonelli's eagles. If substrate preference is heritable in Bonelli's eagles, then given the reproductive advantage we found in using trees, the future use of tree nests may become more common.

Reproduction is also just one demographic parameter relevant to recovering and sustaining a population. Survival, and especially adult survival, is the other major component, and one that is of particular importance to long-lived species with relatively low fecundity such as the eagles considered here (Real and Mañosa 1997, Real et al. 2001, Carrete et al. 2002a, Carrete et al. 2002b). Anthropogenic sources of mortality that can be managed and avoided – such as designing and retrofitting electrical distribution lines to reduce electrocution or siting wind turbines to minimize collision risk – should still be pursued (Real and Mañosa 1997, Real et al. 2001, Rollan et al. 2010, Chevallier et al. 2015, Hernández-Matías et al. 2015). While population growth rates in these k-selected species are more sensitive to changes in their survival rates (López-López et al. 2012), these eagles still need to reproduce and find habitats within which they can achieve and maintain population viability.

The case that we have presented here illustrates the paradox that wildlife managers and conservationists face in trying to recover endangered species and protect their habitats: we cannot be certain what the full range of a species' habitat is if we are trying to characterize habitat after a population has declined and its distribution has been reduced. Fundamentally, this is a difficulty in how we generate knowledge, and was described in the 18th century as the 'problem of induction' (Hume 1739). We base our inferences on what we can observe, but this is no guarantee that what has happened in the past will happen again in the future. Clearly, we can only base management decisions on the knowledge we have, and we can only study populations where they exist. We emphasize here that we do not believe previous studies of productivity in these eagles were wrong, only that they inevitably came from areas where the eagles existed at the time. Even the most statistically robust methods to characterize a species' habitat requirements would provide misleading results if the species in question is systematically excluded from some potential parts of its habitat. There should an acknowledgement of the limitations inherent in habitat studies of range-restricted species, and the results of such studies should be treated as minimal known habitat requirements as opposed to exclusive necessary habitat. Identification of habitat attributes outside of a species contemporary use or range would require moving beyond the most sophisticated geospatial analytical techniques in favor of historical resources (Rick and Lockwood 2013) or Traditional Ecological Knowledge (Huntington 2000). Similarly, government policies and regulations aimed at protecting habitat should be cautious in how they define critical habitat. Limiting protection to only those parts of the range and habitat that are in current use may appear to offer regulatory stability and avoid excessive and unneeded regulations (USFWS and NOAA 2020). Yet, such policies may, in the long run, inhibit species recovery and perpetuate regulatory burdens on industries if the habitat of a species is too narrowly defined, limiting protection that could be afforded to areas from which an endangered species has been extirpated. When it comes to the conservation of habitat for endangered species, we must move forward with the knowledge that we have in hand, but explicitly recognize that the knowledge we have may be limited.

Author contributions

Ryan Baumbusch: Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jesus Bautista**: Data curation (equal); Supervision (equal); Writing – review and editing (equal). **Jose Rafael Garrido**: Data curation (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal). **Ian Newton**: Conceptualization (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Miguel Ferrer**: Supervision (equal); Writing – original draft (equal). **Virginia Morandini**: Conceptualization (equal); Supervision (equal); Validation (equal).

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Data availability statement

Data are available in the Zenodo repository at https://doi.org/10.5281/zenodo.18703613 (Baumbusch et al. 2026).

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