The expanding tree-nesting Bonelli´s eagle (*Aquila fasciata*) population of southern Portugal

Andreia Suzana Ribeiro e Cota de Pinho Dias

"Só voa quem se atreve a fazê-lo."

"Solo vuela el que se atreve a hacerlo."

"Only those who dare may fly."

Luís Sepúlveda

ANDREIA DIAS
Doctoral thesis 2020

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THE EXPANDING TREE-NESTING

BONELLI´S EAGLE
(*Aquila fasciata*)

POPULATION OF SOUTHERN PORTUGAL

Doctoral thesis 2020

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La expansión de la población arborícola del águila azor perdicera (*Aquila fasciata*) en el sur de Portugal

Memoria presentada por

Andreia Suzana Ribeiro e Costa de Pinho Dias

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Andreia Suzana Ribeiro e Costa de Pinho Dias

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DIRECTOR i TUTOR

Dr. Joan Real Ortí
Facultat de Biologia, Universitat de Barcelona
Secció de Zoologia i Antropologia.
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals

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ABSTRACT

Bonelli's eagle is considered an umbrella and flagship species in Mediterranean ecosystems.

In this thesis, we focus on the fact that the Bonelli’s eagle population in southern Portugal nests in trees – behaviour that sets it apart from the typical cliff-nesting populations that exist elsewhere in this eagle’s range – and on the ecological, demographic and conservation implications that this behaviour has for this population. The study of this phenomenon is key for providing guidelines that will assist in its conservation and in the management of species and/or populations with similar behaviour.

It terms of biometry, no differences were observed between tree-nesting Bonelli’s eagles and those from the rest of the Iberian Peninsula and France. There were no gradual size variations with environmental temperature, although there were marked differences of statistical significance in some biometric measures (larger body length, wingspan, head length and width, tarsus width and tail length). These may represent an adaptation to forest environments or be an amplification of some of the original forms present in the small group of founder birds.

Individuals in the Bonelli’s eagle tree-nesting populations prey more often on birds than birds that nest on cliffs. Taphonomy studies were conducted for the first time for Bonelli's eagle and showed that tree-nesting eagles of this species prey more often on birds. The way Bonelli's eagles consume and break up Leporidae species and birds’ bones differs from other predators, which allowed us to detect its presence at archaeological sites and discover whether former nesting sites belonged to this or another predator.

This tree-nesting population occupies a novel ecosystem containing new combinations of species and landscapes that have emerged thanks to human action, namely, the planting of eucalypt trees. Their territories and nesting areas are generally on steep slopes and may also be related to the presence of adequate trees for nests in areas that are less affected by human disturbance and forest management. Newly colonizing pairs of Bonelli's eagles chose habitats that are structurally similar to those of the initial population nucleus, which may be due to imprinting of the original habitat conditions on young birds.

Tree-nesting seems to be advantageous since this ecological novelty has permitted this species to colonize previously unoccupied areas and habitats, thereby obtaining important ecological and conservation benefits.

GENERAL INTRODUCTION

I 1. Nature's dangerous decline

Global change ranging from habitat loss and the problems posed by invasive species to anthropogenic-driven climate change are heralding the sixth great mass extinction event in the Earth's history. As species become threatened and disappear, the ecosystems and numerous benefits to human well-being that depend upon biodiversity likewise begin to recede (Mittermeier et al. 2011).

Extinction is the gravest consequence of the biodiversity crisis simply because it is irreversible. Human activities have elevated the rate of species extinctions to a thousand or more times the natural background rate (Pimm et al. 1995). The loss of species as future resources may be the most obvious consequence of this calamity (Mittermeier et al. 2011). As species are lost, we squander the origins of our crops, the genes we use to improve agricultural resilience, the inspiration for manufactured products, and the basis of the structure and functioning of the ecosystems that support humans and all life on Earth (McNeely et al. 2009).

Above and beyond material welfare and livelihoods, biodiversity contributes to our security, resiliency and freedom of choice and action (Millennium Ecosystem Assessment 2005). Less tangible – but no less important – are the cultural, spiritual and moral costs exacted by species extinctions. All societies value species for their own sake and wild plants and animals are integral to the fabric of the world's cultures (Wilson 1984). Reduced diversity may also lessen the resilience of ecosystems and the human communities that depend on them (Raymundo et al. 2009). Ending global biodiversity loss means concentrating our limited resources in the regions that need them most, that is, in the biodiversity hotspots that are defined according to the conservation planning principles of irreplaceability and vulnerability (Mittermeier et al. 2011).

A total of 35 regions now meet the hotspot criteria, each of which holds at least 1,500 endemic plant species and has lost 70% or more of its original habitat (Mittermeier et al. 2011).

The Mediterranean Basin is home to a tremendous diversity of habitats and species. The IUCN (International Union for Conservation of Nature's) has designated this region as a biodiversity hotspot owing to its rich biodiversity and in light of the threats that hang over it. Stretching eastwards from Portugal to Jordan and northwards from Cabo Verde to Italy, and covering over 2 million km^2, the Mediterranean is ranked as the second largest hotspot in the world and the third richest in terms of plant diversity (IUCN 2020). The Mediterranean Basin Biodiversity Hotspot is located at the intersection of three major landmasses – Europe, Asia and Africa – and boasts an exceptionally diverse and highly distinctive fauna and flora (IUCN 2020). The main threats to Mediterranean species are habitat loss and degradation as a consequence, for example, of the construction of dams and coastal infrastructures. Pollution, droughts, alien invasive species and overexploitation (*i.e.* over-fishing, -hunting and -harvesting) are also important elements in the decline of Mediterranean biodiversity (IUCN 2008). Two urgent conservation actions needed to ensure the future of this biodiversity are the enforcement of adequate legislation and the promotion of sustainable management of exploited species (IUCN 2008). The number of species threatened with extinction far outstrips available conservation resources and the situation looks set to worsen rapidly before it improves (Pimm 1995). We must thus conserve these special places because the unique species they contain cannot be saved by compensatory actions elsewhere as biodiversity is not evenly distributed across our planet (Mittermeier et al. 2011).

I 2. The conservation of endangered species

Although extinctions occur naturally, scientific evidence clearly suggests that the current rate of extinction is much higher than the natural or background rate of the past. The main force driving this high rate of extinction is habitat loss. Over-exploitation of wildlife for commercial purposes, the introduction of harmful exotic (non-native) organisms, environmental pollution and the spread of diseases all pose serious threats to our biological heritage. Some of the many specific reasons for investing money and efforts into actions aimed at conserving species threatened by extinction include the benefits for natural diversity, their potential contribution to medicine, the links between biodiversity and agriculture, environmental monitoring, ecosystem services and numerous other economic and intangible values (U.S. Fish and Wildlife Service Endangered Species Program. 2005).

The International Union for Conservation of Nature (IUCN) is the global authority on the state of health of the natural world and the measures needed to safeguard it. The knowledge and the tools IUCN provide are critical for ensuring that human progress, economic development and nature conservation can operate in harmony. Much of the IUCN's work in the 1960s and 1970s was devoted to the protection of species and the habitats necessary for their survival. In 1964, the IUCN established its Red List of Threatened Species™, which has since evolved into the world's most comprehensive data source on the global extinction risk of species (https://www.iucn.org/).

The IUCN Red List of Threatened Species is an easily and widely understood system for classifying species with high global extinction risks. Species are classified by the IUCN Red List into nine groups using criteria such as rate of decline, population size, range, and the fragmentation of populations and distributions. Also included are species that have gone extinct. On the IUCN Red List, the term 'Threatened' embraces three categories: Critically Endangered, Endangered and Vulnerable.

The nine IUCN Red List groups are as follows: Extinct (EX): no known living individuals; Extinct in the wild (EW): known only to survive in captivity, or as a naturalized population outside its historic range; Critically Endangered (CR): extremely high risk of extinction in the wild; Endangered (EN): great risk of extinction in the wild; Vulnerable (VU): great risk of becoming endangered in the wild; Near threatened (NT): likely to become endangered in the near future; Least concern (LC): low risk; does not qualify for a higher risk category. Widespread and abundant taxa are included in the categories Data Deficient (DD): not enough data to make an assessment of its risk of extinction; and Not Evaluated (NE): not yet been evaluated using the IUCN criteria (IUCN 2012).

The conservation status of living things is an important tool for defining priorities in species conservation and constitutes one of the most widely used indicators for assessing the state of ecosystems and their biodiversity (Cox et al. 2006).

Albeit often local in scale, field studies provide definitive evidence of particular processes; the extent to which these findings can be generalized over broader scales of space and time remains one of ecology's most contentious issues. Ecologists hesitate to make coherent generalizations regarding communities or systems given that their uniqueness and complexity make broad simplifications invalid. Paradoxically, the rejection of general theory comes at a time when robust, general principles in ecology are badly needed (Lawton 1999). The synthesis of accumulated scientific results distilled into general patterns and underlying mechanisms enables some ecological phenomena to be predicted within certain boundaries (Knapp et al. 2004). This information is useful for improving the predictive capability of ecology, as well as for identifying limits and contingencies (Kristin & Ronald, 2006).

I.3. Case study: Bonelli's eagle *Aquila fasciata*, Vieillot 1822 (identification and descriptive notes)

Bonelli's eagle (*Aquila fasciata*) is a key predator in Mediterranean ecosystems (*e.g.* Moleón et al. 2011) and is classified as Endangered in Europe (BirdLife International 2015) due to its steep population decline in Western Europe during the 1980s (Palma et al. 2009).

Yet, in the early 1990s, a hitherto completely unknown population was discovered in Portugal, which, surprisingly, consists almost completely of tree-nesters (it is usually a cliff-nesting species). This has inspired a series of scientific studies that have made this population one the best known of all Bonelli's eagle populations. Monitoring has brought to light steady population growth as birds colonise unoccupied cliffless habitats and use old trees for nesting. Genetic studies have revealed a marked differentiation from adjacent populations. These features have made this population – which is the focus of this thesis – unique from a genetic, behavioural, ecological and demographic point of view, thereby making its conservation of special national and international relevance (Palma 2013).

Research on threatened species should not be simply limited to descriptive studies of their ecology and biology; rather, it should be complemented by studies out from the perspective of conservation biology. Thus, new research models have appeared whose results aim to improve knowledge of threat factors, species´conservation status and ways of managing populations and habitats (Primack and Ros 2002).

I.3.1. Scientific classification

Kingdom: Animalia

Phylum: Chordata

Class: Aves

Order: Accipitriformes

Family: Accipitridae

Genus: Aquila

Species: *Aquila fasciata*, Vieillot 1822

Subspecies: *A. f. fasciata*/*A. f. renschi*

This species was described in 1822 by Louis Jean-Pierre Vieillot, who named it after Franco Andrea Bonelli, who first identified it in 1815 (Morvan 2010). A scientific name change has taken place in light of a decision by the French Avifauna Commission (CAF) in 2006-2007. Following phylogenic studies and decisions by several national committees on nomenclatures and classification, this eagle's scientific name was changed from *Hieraaetus fasciatus* to *Aquila fasciata* given that from a genetic point of view it is closer to the latter genus than the former (Jiguet 2007).

There are two subspecies of Bonelli's eagle:

- *Aquila fasciata fasciata* (Vieillot 1822)
- *Aquila fasciata renschi* (Stresemann 1932)

I.3.2. Conservation status

Classified as of Least Concern worldwide but Near Threatened in Europe (BirdLife International 2015), in Spain the status of Bonelli's eagle has changed from Vulnerable (Blanco & González 1992) to Endangered (Madroño et al. 2004); it has the same status in Portugal (Cabral et al. 2005).

I.3.3. Description

Body length: Males: 63–67 cm; Females: 68–74 cm (García et al. 2013)

Wingspan: Males: 143–163 cm; Females: 156–176 cm (García et al. 2013)

Weight: Males: 1,400–2,240 g; Females: 2100–3350 g (García, V. & Dias, A. Unpublished Data)

Maximum Age: 32 years in the wild (Morvan et al. 2011)

Sexual dimorphism: females are usually larger than males. In non-juvenile birds, according to García et al. (2013), males have paler underparts than females. Their undertail coverts, leg feathers and throats are whiter and have fewer brown or dark streaks or spots than females, which appear to be predominantly darker. Likewise, the extent of pale coloration on the margins of the tail feathers is greater in males than in females, males having lower mean scores.

Plumage: Four different plumages: 1) first year (juvenile); 2) second year (immature); 3) third year (subadult); and 4) fourth year or older (adult).

I.3.4. Distribution

Aquila fasciata fasciata has a wide geographical distribution that includes the Mediterranean coast from the Iberian Peninsula and Maghreb to the Middle East, and the Arabian Peninsula and southern Asia from Iran to eastern China. *Aquila fasciata renschi* is concentrated in Indonesia on the small Sunda Islands (Sumbawa, Timor, Flores, Wetar, Luang) (Ferguson-Lees & Christie 2001; Mebs & Schmidt 2006).

Figure 1 – *Aquila fasciata* world distribution (BirdLife International and Handbook of the Birds of the World (2019) 2019. *Aquila fasciata*. The IUCN Red List of Threatened Species. Version 2019-3 (Downloaded on 11 March 2020).

Despite the favourable conservation status of its southern Asian population (Bildstein et al. 1998), the European Bonelli's eagle population seems only now to be recovering from a serious decline during the 1980s (Real et al. 1996; del Moral 2006; Cadahía et al. 2008).

The European population is estimated at 1,100–1,200 pairs, which equates to 2,100-2,400 mature individuals (BirdLife International 2015). Europe forms approximately 10% of the global range, so a very rough estimate of the global population of this eagle (which requires validation) is 21,000–24,000 mature individuals (BirdLife International 2015).

Figure 2 - Bonelli's eagle distribution in Western Europe: Iberian Peninsula and southern France. Source: modified from Hernández-Matías et al. (2013) *in* Real, J. et al, 2015.

The Bonelli's eagle population in Portugal consists of at least 110 breeding pairs (Beja & Palma 2008; Palma et al. 2013).

In Spain, there are 711–745 established pairs (711 sure and 34 probables, but not confirmed) (del Moral & Molina 2018), which represent the most important European population and 63% of all European birds (BirdLife International 2017). This population appears to have declined by 25% in the period 1980–1990 (Arroyo & Ferreiro 1997).

The French population has been in sharp decline since the 1960s (the first period in which the size of this population was assessed) and 50% of birds have been lost; as of 2013, there were 32 pairs of Bonelli's eagles in France (Burger et al. 2013).

I.3.5. Movements

Breeding birds are sedentary but juvenile and immature birds wander over large distances and are frequently found in low altitude plains with high prey density that normally lack breeding pairs (Arroyo & Ferreiro 1997).

I.3.6. Habitat

Territorial adults are found in mainly warm mountainous or rough terrain, normally with crags and cliffs. Although they tend to prefer low or sparse vegetation such as garrigue, dry grassland and rocky habitats, the vegetation cover of its habitat can be highly variable and include forests and wood pasture (*dehesas*), as well as bushes and scrub. They are also often found in open habitat mosaics of non-intensive crops, vineyards, olive groves, non-irrigated orchards, copses and pastureland (Tucker & Heath 1994).

I.3.7. Dietary ecology

Bonelli´s eagles in Europe capture a wide range of prey that includes small-to-medium sized mammals (Lagomorpha and Rodentia), birds (Columbiformes, Galliformes, Passeriformes, Ardeiformes, Charadriiformes and others) and reptiles (mainly lizards) (Real 1991, Moleón et al. 2009) but show a clear preference for rabbits, red-legged partridges and pigeons (Ontiveros 2014). Nevertheless, their diet will change depending on the geographical area, habitat and the presence of prey items.

The availability and use of such a wide range of locally abundant prey is a major factor contributing to the survival rates of a raptor such as Bonelli’s eagle (Carrete et al. 2002).

I.3.8. Reproduction

The earliest breeder of all Mediterranean eagles (Cramp & Simmons 1980), the two members of a pair of Bonelli’s eagles usually remain faithful throughout their lives unless, logically, one disappears. After a period of erratism lasting at least two years, during which time they search for a territory (Balbotín 2005; Cadahía 2007), immature birds pair up, most often replacing a bird from an established pair that has disappeared (Hernández-Matías et al. 2011). Then, they settle down in a vital domain consisting of a nesting area and hunting areas.

Sexual maturity is reached at 3–5 years of age depending on the individual (Cramp & Simmons 1980).

I.3.9. Threats

The sharp decline in the Bonelli´s eagle population is due to a series of factors: direct persecution; electrocution on and collision with power lines (Carrete et al. 2002, Real 2003, Rollan et al. 2016); the use of pesticides; habitat degradation; loss of prey species (Ferguson-Lees & Christie 2001, Barov & Derhé 2011); persecution by hunters and pigeon-fanciers; declining prey availability; increasing human disturbance and poaching at nest sites; agricultural intensification (Ferguson-Lees & Christie 2001; del Hoyo et al. 1994); demographic imbalances (i.e. high mortality or low productivity rates); and competition with species such as golden eagle *Aquila chrysaetos* (Garza & Arroyo 1996; Real & Mañosa 1997).

I.4. The study population: the tree-nesting Bonelli´s eagles in southern Portugal

This thesis focuses on the peculiar tree-nesting Bonelli’s eagle population in southern Portugal.

In the Mediterranean, a significant number of pairs of Bonelli's eagles is found nesting in trees only in Cyprus and in a few North-African populations (Iezekiel et al. 2004; Bergier & Naurois 1985); nevertheless, this behaviour is frequent in Asia. (*e.g.* Zheng 1987).

The population in Cyprus was estimated at over 50 pairs in the late 1950s (Flint & Steward, 1992) but by the 1980s–early 1990s it had declined to less than 20 pairs (BirdLife International/EBCC 2000). Currently, however, the island's population probably exceeds 50 pairs. In the south of the island, 68% of pairs nest in trees, 21% on cliffs and 11% have both tree and cliff nests (Nicolaos Kassinis pers. comm.). In the north, however, the percentage of tree-nesting pairs is much lower (7.1%) (Damla Beton & Olkan Ergüler pers. comm.). According to Kassinis (2010), all tree nests are built on large Calabrian pines (*Pinus brutia*).

In Spain, Bonelli's eagles are eminently cliff-nesters (89%). In 2018, 7.48% of pairs nested in trees and 0.42% on other structures such as pylons or other water or electricity transport infrastructures (del Moral & Molina 2018).

In Portugal, it has been known since the early 1990s that practically all Portuguese Bonelli's eagle pairs are tree-nesters (Palma et al. 2013). This expanding population is the only European population that breeds almost entirely in trees.

During the 1980s and 1990s, Bonelli´s eagles underwent a serious decline and Portugal lost 15% of its pairs. Today, this eagle is still slowly declining in the north of the Iberian Peninsula, whereas in the south it is generally stable or on the increase. In Portugal, about 70% of the population is found south of the river Tagus or in Portuguese Estremadura, while the remaining 30% is located along the Portuguese and Spanish banks of the rivers Douro and Tagus (Fig. 3) (Palma et al. 2013). In the north of the country (banks of the upper river Douro and its tributaries), birds breed only on cliffs, whereas in the south they are almost all tree-nesters (Palma 1994) (Fig. 3).

The river Tagus basin is a transition zone encompassing both sides of the river near the border with Spain where cliff-nesting still predominates and tree- and mixed cliff/tree-nesting also occurs (Palma et al. 2013) (Fig. 3).

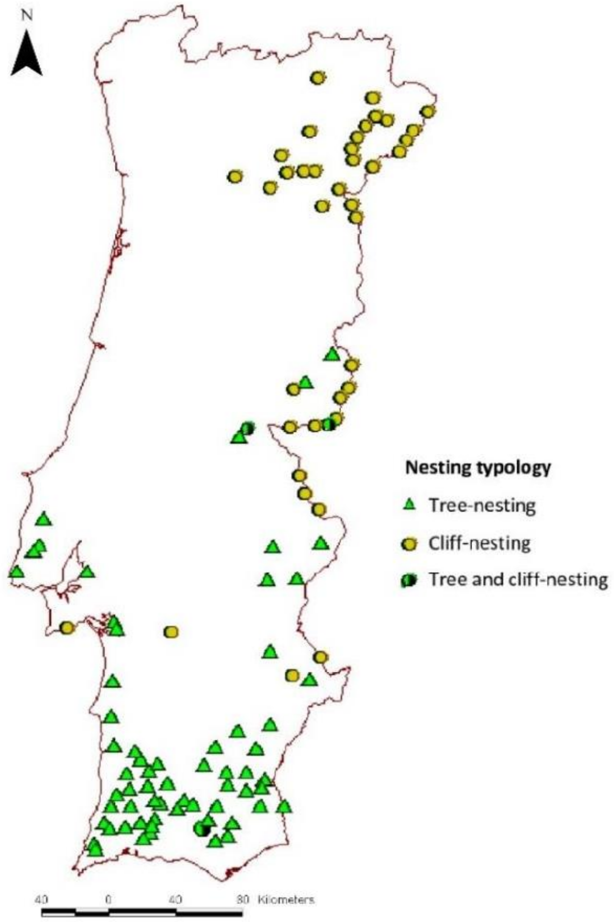

Figure 3 – The distribution of Bonelli´s eagle nesting types in Portugal. From north to south, cliff-nesting is gradually replaced by tree-nesting. Modified from Palma, L. 2010.

I.4.1. Habitat

It is possible to distinguish two main types of Bonelli´s eagle breeding habitats. In the SW uplands and hilly areas, the habitat used is native woodland and a degraded series of scrublands with low-density or scattered tree cover. Here, the dominant tree species are mainly cork oaks and, less often, holm oaks, interspersed with variable-sized eucalyptus plantations and small stands of maritime (*Pinus pinaster*) or Monterey (*Pinus* *radiata*) pines. In the SE lowlands, however, eagles nest almost exclusively in old isolated eucalyptus trees or in gallery forests along rivers and streams. The isolated trees are mainly *Eucalyptus camaldulensis* seldomly are *E. globulus* and, more rarely, maritime pines and poplars (*Populus nigra*). As well, in the heavily human-modified hilly landscape north of Lisbon these eagles breed in small patches of woodland amidst a dense network of built-up areas, motorways, secondary roads, powerlines and wind farms. Several different species of eucalypts and exotic conifers are used as nesting trees. A particular type of nesting habitat is the tall and dense maritime pinewoods that border the flatlands along the broad Tagus and Sado estuaries (Palma et al. 2013).

Palma (1995) and Pais (1996) indicate that the breeding sites of the tree-nesting population in South Portugal tend to be located in rough, relatively inaccessible, hilly terrain, with little human presence, where there are thick vegetation cover and large trees in valley bottoms.

Ferreira (2011), in a nest-site selection study of this tree-nesting population, examined 52 nest trees and concluded that the main feature of nest trees, nests and nest sites was the presence of tall dominant trees that support the large heavy nests; like Palma (1995), this author found that quiet inaccessible areas were required for the species to breed. In 1994, most occupied nests (44%) of the 16 breeding known pairs were built on cork oaks (*Quercus suber*) (Palma 1995), a finding that had been reversed by 2008 when the majority of studied occupied nests (n=32) were found in blue gum eucalyptus (*Eucaliptus sp.*). The increased use of eucalypts and pines may be related to the relative availability of suitable trees in face of the extensive morbidity and mortality occurring in cork oaks, coupled with the degradation of cork oak woods due to forestry-linked perturbation. The increase in the number of eucalypts used may, however, be due to the large limb structure and tall growth pattern of these trees compared to pines and native cork oaks. Mature eucalypts growing near water courses, of no economic interest, have their size and strength enhanced by large spreading branches (Palma 1995). These trees are selected because their physical characteristics provide better support for the large heavy nests the eagles build, and enable them to build nests at greater heights, thereby reducing the threat of access by predators. Nests are frequently built in less flexible eucalypts that are over 70 years of age (CEAI 2011).

Dias *et al.* (2017) found that nesting habitat features and selection patterns remained very similar to those of the initial population nucleus during the 25 years of population expansion, albeit with a few changes over time (see Chapter 3).

I.4.2. Expansion

This Portuguese population is closely monitored and grew from around 25 breeding pairs in1991 at least 110 in 2014 (Beja and Palma 2008; Palma et al. 2013). Since 1991, the average rate of increase has been 2.74 pairs/year, which has resulted in a threefold increase in 23 years (Palma et al. 2013).

At the start of the field monitoring, the only dense breeding cluster was restricted to the SW uplands, while just a few scattered pairs inhabited the lowlands and some isolated mountainous areas to the north as far as the international sector of the river Tagus (*i.e.* where it forms the Spanish-Portuguese border). As described in Palma et al. (2013), the range expansion consisted of three distinct stages: 1) during the initial decade up to around 2000, there was a stepwise gap-filling in the SW uplands and moderate growth in the adjoining open SE lowlands, while a few new pairs began to settle in other areas further north; 2) during the following five years, the SW uplands apparently became saturated and a northwards range extension through the adjoining coastal hilly country was observed; moderate growth and an expansion of the SE lowlands cluster and in the hilly country north of Lisbon continued; 3) from 2005 onwards, with the apparent saturation of the SW uplands, most of the subsequent expansion has occurred in the lowlands of the Guadiana Basin (and at a faster rate than before), while a few pairs have settled on the adjoining border with the uplands, where currently new pairs continue to form.

I.4.3. Diet

The food ecology of Bonelli’s eagles in the SW uplands was studied in 1992–2001. Domestic animals played a key role in the diet of this population and domestic pigeons was the single most important prey item, although racing pigeons and domestic fowl were also frequently taken (Palma et al. 2006).

Pigeons, in particular domestic pigeons, are more important in the diet of this population than in most other European Bonelli´s eagle populations. This type of domestic prey is important at the beginning of the breeding season, although wild prey (rabbits, partridges and jays) are also relevant dietary components of its diet in most territories and become progressively more important towards the end of the breeding season as the number of pigeons captured decreases (Palma et al. 2006).

However, diets change. Within the framework of a LIFE Project (2006–2011), studies were carried out of the abundance of this eagle’s three main prey items (domestic pigeons, partridges and rabbits). A census of domestic pigeons in 2007–2008 repeated a census from 1994 and revealed a decrease by 65% in the number of pigeon lofts and 74% in pigeons, a drastic drop in prey availability. The progressive ageing and exodus of the rural human population, a process aggravated by the severe forest fires of 2003 and 2004, are probably at the root of this decline since these pigeons are domestic animals closely tied to human presence. On the other hand, in recent years hunting land in Portugal has been subject to stricter controls, which has boosted the abundance of wild prey. This evolution has also occurred in the study area and is probably the cause of the increase in the abundance of partridges. Wild rabbit populations are very unstable. It is likely that, due to the serious decrease in domestic pigeons available as prey items, these eagles currently consume a greater amount of wild prey (Life Project Internal Reports – “Conservation of Tree Nesting Bonelli´s Eagle in Portugal – LIFE06 NAT/P/000194).

I.4.4. Genetics

Historical records and genetic analysis suggested that this Portuguese tree-nesting population arose from a few founding pairs in the SW mountains and the SE steppes in the first half of the twentieth century (Mira 2006).

Mira (2006) found that the SW population has a low level of genetic diversity but a high level of genetic differentiation from other populations (in the river Douro basin in Portugal, and in Extremadura and Cadiz province in Spain), which indicates a lack of immigration and a certain degree of reproductive isolation from neighbouring Portuguese and Spanish populations. Imprinted tree-nesting behaviour causes a strong preference for these types of habitats over cliffless habitats, which may be the reason for the genetic divergence in this population (Mira 2006). Given its unique ecological, genetic and behavioural features, the SW tree-nesting population should be considered as an Evolutionary Significant Unit (ESU) of great importance, thereby warranting an independent management approach in the context of this species' conservation in the Iberian Peninsula (Mira 2006).

I.4.5. Contamination

The SW Portuguese Bonelli's eagle population is regularly spaced and distributed in a wedge-shaped area leeward of a coal-burning power station, a potential source of mercury (Hg) contamination. Palma et al. (2005) analysed total Hg concentrations in adult moult feathers and feather remains of bird prey items found at nests (collected in 1992–2001) to check this hypothesis. Great variation between territories was found, presumably reflecting differences in diet and food chain magnification. After correcting for dietary variation, the distribution of Hg levels across the study area agreed with the hypothesis that this power plant is a source of Hg contamination. The detected concentrations of Hg were particularly high and may represent a threat to this species (Palma et al. 2005).

Badry *et al.* (2019) found that the concentrations of As, Pb, Cr, Cu and Zn were relatively low and it seems that widespread contamination by these elements is unlikely to occur in SW Portugal. They did conclude, however, that emissions from a coal-fired power stations and industrial activities are the main drivers for Hg emissions, which have been shown to be biomagnified – along with Se – in the eagles' food web. They found that pollution from mining activities was more difficult to assess as it was not clearly associated with any of the investigated metals or trace elements, possibly because waste from mines does not spread far from its source.

I.4.6. Population dynamics

In 1992–2008, populations parameters for the SW Portuguese population were recorded (Beja & Palma 2008) and, in combination with data from 11 other subpopulations, a viability analysis was conducted at a Western European scale. The results showed that all subpopulations in Western Europe belong to a single, spatially structured population operating as a source-sink system, in which the populations in the south of the Iberian Peninsula act as sources that disperse and sustain all other populations and prevent the decline of this eagle in the rest of Europe (Hernández-Matías et al. 2013).

I.4.7. Threats

This population faces several conservation problems. As it is tree-nesting, it is often affected by the poor management of forestry activities. Although uncommon, the most serious impact is the felling of large trees, especially if they hold nests. The most common impact is disturbance due to forestry activities during breeding. The widespread degradation of tree cover caused, among other factors, by the decrease in rainfall, wildfires and disease outbreaks (*e.g.* maritime pines have been dying out rapidly due to wilt disease caused by an introduced nematode; as well, root pathogens are decimating native oaks, Palma et al., 2013) are a further serious threat (Palma & Alcaria 2011).

Hunting including illegal shooting and the disturbance it creates during the breeding season is another potential threat to this eagle. Predation by eagles of game species and racing pigeons is a potential source of conflict between hunters and pigeon fanciers. However, the true number of pigeons taken by eagles is only a small percentage of the total numbers involved in these activities; furthermore, the pigeons that are predated are often the weakest birds. Adult eagles and, especially, nestlings, are affected by trichomonosis, an often-lethal parasitic disease acquired through the consumption of infected domestic pigeons. Powerlines are a further danger and cause mortality, mainly due to electrocution. Of concern is the rapid spread of windfarms in breeding areas, which leads to the degradation of nesting habitat and increased risk of collision with turbine blades (Palma & Alcaria 2011).

I.4.8. Conservation measures

A LIFE Nature Project *Tree-nesting Bonelli's Eagle* (LIFE06 NAT/P/000194) was conducted from 1 October 2006 to 31 March 2011. Conservation actions included the reinforcement of fragile nests and the building of artificial nests where natural nesting conditions had deteriorated; and, for social reasons, the construction of improved pigeon lofts in collaboration with hunting associations in territories with poor food availability to lessen predation pressure on domestic pigeons. Habitat management and tree leasing agreements with landowners involving monetary compensation were implemented to ensure the preservation of current or potential nest trees and reduce disturbance in their surroundings. Non-contractual agreements were established in similar cases with paper companies, to which technical assistance was regularly provided (as it was also to electric companies and wind farm promoters). This helped reconcile economic activities and the preservation of good breeding conditions. Extensive public awareness campaigns were focussed primarily on hunting associations and rural populations in the tree-nesting range. Environmental education addressing primary and secondary schools was also widely undertaken (Palma & Alcaria 2011).

I.5. Thesis structure

In this thesis, we focus on the fact that the southern Portuguese Bonelli's eagle population has atypical nesting behaviour and is expanding do to its success.

Environmental changes have caused episodes of habitat expansion during the evolutionary history of many species. These range changes affect the dynamics of biological evolution in multiple ways. Species expand from where they first evolve, invade favourable habitats, and move in response to environmental changes such as climate warming, glacial cycles and gradients in, for example, nutrients, salinity and environmental temperature. Population expansions in space are common events in the evolutionary history of many species, ranging from biofilms to humans (Hallatschek & Nelson 2010). The southern Portuguese Bonelli's eagle population behaves somewhat differently from other populations since its numbers have increased steadily over the past two decades. This is the only population throughout the species' range in Europe that exhibits such a positive trend, which has occurred concurrently with an increase in its breeding range. Interestingly, this trend can be attributed both to high survival rates and the tendency of eagles from this population to nest in trees, which allows them to occupy new territories even in areas without cliffs (Palma et al. 2006, Beja & Palma 2008).

The study of a long-lived and slow-reproducing species such as Bonelli´s eagle can only provide solid and reliable results if it continues for a sufficiently long period of time, especially if the aim is to provide information for the management and conservation of the species.

The tree-nesting population in southern Portugal has been the target of several research (*e.g.* study of diet, ecotoxicology, population genetics and habitat) and conservation projects (*e.g.* LIFFE Nature Project; LIFE06 NAT/P/000194).

The present thesis takes advantage of pre-existing information and continues the research performed since 1991 that includes 25 years of continuous monitoring and biometric parameters of individuals from various Iberian and French populations (including the tree-nesting population from Portugal), along with multidisciplinary knowledge in such fields such as taphonomy.

In **Chapter 1**, we address *biometric parameters*. Bird biometry is a very important component of a variety of fields of study, especially those with taxonomic, physiological, ecological and evolutionary implications (Araóz et al. 2016). Studies of variations in morphometric parameters in birds mainly focus on geographical variation between populations, morphological variation in migratory groups, ecomorphological comparisons, and the descriptions of intra-populational variation (Nowakowski 2002).

Comparisons of measurements – if they have been collected over a long period time or on a large geographical scale in a standardised manner – allows inferences about the response of individuals to changes environmental factors to be drawn (Zink & Remsen 1986; Eck 2011). The study of morphological variations in species along geographical gradients can be useful for testing hypotheses regarding the factors determining their distribution and biology (Zink & Remsen 1986; Ricklefs & Miles 1994). Behavioural differences might also be associated with biometric differences in populations of a species.

We took advantage of the robustness of existing data (*i.e.* all biometric parameters had been measured by the same observers) from the past 22 years in individuals from Bonelli's eagle populations in Portugal, Spain and France.

We investigated whether the tree-nesting Bonelli’s eagle population in southern Portugal, which exhibits the above-mentioned features, differs from other populations in terms of its biometric measurements.

In **Chapter 2** we use *taphonomy,* a field never previously used in studies of Bonelli´s eagles, to assess the activity of Bonelli’s eagles at Pleistocene archaeological sites (Lloveras et al. 2014).

Here, we had the opportunity to collaborate with archaeologists by providing pellets from the tree-nesting Bonelli´s eagle population in southern Portugal. In addition to taphonomic studies, albeit with a very small sample size, we were able to investigate the current diet of these eagles via prey remains left in nests and surrounding areas, and by pellet analysis.

Archaeological assemblages are the result of events taking place over a long period of time at the same site. The factors implicated in the formation of these assemblages can also be very diverse, since hominids, raptors and mammalian carnivores all could have used the same spaces to perform their activities (*e.g.* Rufà et al. 2016a; Rufà et al. 2016b; Alonso *et al.* 2019). Attempting to understand the processes involved in the formation of an archaeological site is a challenging task, as separating the palimpsest of occupation is almost impossible during excavation. This underlines the importance of identifying the predators that could intervene in the origin of uncovered remains (Rufà & Laroulandie 2019), of gathering information for helping to understand the formation processes at archaeological and palaeontological sites, and distinguishing human and other animal agents of accumulation (Lloveras et al. 2017).

Establishing the taphonomic pattern of each predator is a basic step towards determining the origin of faunal accumulations (Alonso et al. 2019). Each predator hunts and consumes its prey in a particular way. Consequently, the traces left by predators on bones may vary according to how prey is processed (Andrews 1990). The main modifications consist of breakage and fragmentation from the mechanical action of teeth, beaks and talons before or during ingestion and corrosion during digestion. These two processes are correlated since high values of fragmentation facilitate the attack of digestive enzymes (Fernández-Jalvo & Andrews 1992).

Diurnal birds of prey produce a substantial amount of bone destruction during prey consumption (Mayhew 1977; Hoffman 1988). Eagles disarticulate prey carcasses by removing and discarding the prey’s intestines to consume the soft organs. The flesh is then stripped and eaten along with some bones, which are later regurgitated in pellets. The bones that are not consumed are discarded at the kill or at the feeding or nest site. Bone assemblages created largely by the deposition of eagle pellets differ from those created by the abandonment of unswallowed remains (Hockett 1995; Bochenski et al. 1997).

In **Chapter 3**, *Habitat selection of the tree-nesting Bonelli's eagle in southern Portugal*, we study the ecological and demographic behaviour of this population based on data acquired over more than 20 years.

The tree-nesting Bonelli’s eagle population in southern Portugal occupies a novel ecosystem containing new combinations of species and landscapes that have arisen through human action, namely, in light of the introduction of allochthonous trees (Hobbs et al. 2006) such as eucalypts, which are this eagle’s favourite nesting trees (Ferreira 2011).

Behavioural innovations are an important source of phenotypic plasticity in animals and have potentially significant ecological and evolutionary consequences (Nicolakakis et al. 2003; Reader & Laland 2003). Flexibility in behaviour lies at one end of a continuum of plastic responses that includes developmental plasticity in individual physiology and anatomy, and genetic responses to selection over generations (Dukas 1998; Pigliucci 2001; West-Eberhard 2003). Of these forms of response, behavioural changes generally occur most quickly and thus are likely to be the first responses to changes in the external environment. An organism may face changes due to naturally occurring events or to human activities that alter its native habitat. It may also face rapid changes when introduced into a novel habitat by human activities (Wright 2010).

Ecological innovation – *i.e.* the adoption of behaviours that allow individuals in a population to exploit newly available, previously unused, or familiar resources in a new way (Greenberg 2003) – is not a new topic of study. Lloyd Morgan in 1896 argued that behavioural plasticity paved the way for major, genetically based adaptations to new environments, while Baldwin in 1896 noted that these plastic responses may be critical to population establishment and persistence.

The ability of an organism to selectively modify behaviour in response to changing circumstances may arise from several sources. Innate behaviour – *i.e.* that which is independent of experience – may enable individuals to respond to a variety of different stimuli, even though these reactions, potentially highly tuned, are non-modifiable. Such flexibility is predicted to be beneficial to the degree that either the cues for – or the timing of – changes such as diurnal or seasonal changes in the environment, or developmental changes in the animal itself, are predictable over generations (Stephens 1991; Dukas 1998; Shettleworth 1998). These advantages may vary with social context, individual state and the external environment, thereby suggesting that the expression of flexibility might vary over time even within an individual (Wright 2010). Learned behaviour that might be expected to show adaptive flexibility include foraging strategies, diet choice, nesting or burrowing site choice, roosting or sleeping site, choice, anti-predator responses, preferred group sizes, mate choice and anti-parasite strategies (Wright 2010).

This peculiar tree-nesting Bonelli´s eagle population arose due to its ability to colonise formerly unoccupied habitats where cliffs are scarce or even non-existent. The main population must have originated from a few pairs during the first half of the twentieth century, when most of the land had been cleared for cereal production, leaving little space for breeding (Acácio et al. 2009). However, the extensive rural abandonment that followed, coupled subsequently with renaturalization, less disturbance and the growth of tall trees, encouraged a steady range expansion (Palma et al. 2013). Many of the huge eucalyptus trees isolated in stream bottoms may be the product of seed dispersal from trees planted beside houses on the tops of hills to provide geographical markers of human dwellings at the time when access was very limited. Due to the scarcity of these trees and the difficulty in reaching them, they had no economic interest and were seldom cut down. This permitted them to grow unchecked over the years, thereby providing appropriate and fairly secure nest sites for large eagles such as Bonelli´s eagle. These are novel habitats as old trees of exotic species introduced by humans are the major factor determining this colonisation process (Ferreira 2011).

The Portuguese tree-nesting Bonelli´s eagle population demonstrate that this species, typically cliff-nesting in absence of tall trees, can successfully adapt to a novel ecosystem. It is thus very important to know and study the requirements of this particular population, which bucks the unfavourable global trend in this species' numbers.

This has motivated a set of thematic studies at both local and regional scales and has also provided data for wider research across the Mediterranean region.

In this chapter, we compare factors influencing nesting choice at different scales with random locations. Although space use and habitat selection have been studied extensively for cliff-nesting Bonelli´s eagles (*e.g.* Ontiveros 1999; Carrete et al. 2002; Gil-Sánchez et al. 2004), there is little information about space use and habitat selection patterns in a tree-nesting population.

Our findings are potentially significant for Mediterranean forest management aimed at favouring the availability of nesting sites at several scales for Bonelli's eagles and other similar species. It may be also used in projections of this eagle's adaptation to habitat alterations driven by climate change.

Besides furthering knowledge and the conservation of this species, the study of this particular population serves as an example for research into species with similar behaviour and requirements.

Based on the results obtained and considering the current state of the tree-nesting population, we here present information that can be applied to the conservation of this threatened eagle species.

OBJECTIVES

The main objective of the present thesis was thus centred on understanding the conditions that have facilitated the expansion of the tree-nesting Bonelli's eagle population in southern Portugal over the past 25 years.

We had three initial objectives that are discussed in three chapters:

(1) To investigate whether there are biometric parameters that distinguish the tree-nesting population in southern Portugal from the rest of the Bonelli’s eagles in the Iberian Peninsula and France; and to study at the same time whether or not these parameters vary with geographical and temperature gradients.

(2) To use a taphonomic study to determine whether or not it is possible to identify how this species breaks and consumes the bones of its prey items (*i.e.* in comparison with other predators); and to study archaeological nesting sites to study whether there are differences between the diet of cliff and tree-nesting Bonelli’s eagles.

(3) Species’ ranges often change due to alterations in environmental and demographic factors. Innovative behaviour may assist these changes by facilitating adaption to novel habitats. We aimed to study the importance of behaviour during range change, using 25 years of data from the population expansion of Bonelli’s eagle in southern Portugal, during which time this eagle had to confront new environmental conditions. We investigated whether this expansion was associated with innovation in terms of the occupancy of new habitats and an increased tolerance of human activities or whether, rather, it was a conservative change that largely retained the characteristics of the original population nucleus in terms of nesting substrate and breeding habitats.

SUPERVISOR REPORT

Dr. Joan Real Ortí, supervisor of the doctoral thesis entitled: “The expanding tree-nesting Bonelli´s eagle (*Aquila fasciata*) population of southern Portugal” certify that the dissertation presented here has been carried out by Andreia Suzana Ribeiro e Costa de Pinho Dias in its totality and grants her the right to defend her thesis in front of a scientific panel. The dissertation work comprises two articles published and one submitted to a highly ranked scientific peer review journals included in the Science Citation Index. As a supervisor, I have participated in the design, guidance and correction of earlier drafts of the thesis written by the candidate. The contribution of the doctoral candidate to each manuscript and the impact factor (Thomson Institute for the Scientific Information) is detailed below:

Capítulo 1

Dias, A., García, V., Barbosa, A. Márcia, Mayoral, H. and Real, J. 2020. Biometric differences between cliff-nesting and tree-nesting Bonelli’s eagles *Aquila fasciata*. Bird Study.

Submitted to *Bird Study*

Andreia Dias has contributed to the study design, the analysis of the data and the scientific writing.

Capítulo 2

Lloveras, L., Thomas, R., Lourenço, L., Caro, J. and Dias, A. 2014. Understanding the taphonomic signature of Bonelli's Eagle (*Aquila fasciata*) on small prey remains obtained from modern nests and pellets. Journal of Archaeological Science 49, 455-471. http://dx.doi.org/10.1016/j.jas.2014.06.005

Impact factor (2018): 3.030

Andreia Dias has participated in the collection and sample analysis and in the Scientific writing.

Capítulo 3

Dias A, Palma L, Carvalho F, Neto D, Real J, Beja P. The role of conservative versus innovative nesting behaviour on the 25-year population expansion of an avian predator. Ecology and Evolution. 2017;7:4241–4253. https://doi. org/10.1002/ece3.3007

Impact factor (2018): 2.34

Andreia Dias has contributed to the study design, the sampling collection, the analysis of the data and the scientific writing.

Likewise, it is stated that the co-authors participating in the articles that make up this thesis have not used either implicitly or explicitly any of these works for the preparation of other doctoral theses.

Barcelona, 12 de diciembre de 2020

Dr. Joan Real Ortí

CHAPTER 1

Bonelli´s eagles' biometry

Biometric differences between cliff-nesting and tree-nesting Bonelli's eagles *Aquila fasciata*

Andreia Dias[1], Víctor García[2], A. Márcia Barbosa[3], Hernán Mayoral[4] and Joan Real[1]

1 Equip de Biologia de la Conservació, Departament de Biologia Evolutiv, Ecologia i Ciències Ambientals and Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Catalonia, Spain.

2 Deputy General Directorate on Nature. Ministry of Agriculture, Food and Environment. Pza. San Juan de la Cruz s/n., E-28071 Madrid, Spain.

3 Spatial Biology Lab, CICGE – Centro de Investigação em Ciências Geo-Espaciais, Faculdade de Ciências da Universidade do Porto, Vila Nova de Gaia, Portugal.

4 Calle los Álamos, 1 40197. San Cristóbal de Segovia, Spain.

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ABSTRACT

Capsule -Tree-nesting Bonelli´s eagle from Southern Portugal have different biometric measurements when compared to the cliff-nesting populations from the rest of the Iberian Peninsula and France.

Aims **-** Test if biometric variance within populations of a species could be associated with behavioural differences.

Methods **-** Between 1998 and 2020, several biometric variables were measured (by the same observer) from 256 Bonelli's eagles captured across Spain, Portugal and southern France

Results **-** Bonelli´s eagles did not show gradual size variations in space (latitudinally, longitudinally or diagonally), but the tree-nesting population from southern Portugal showed larger body length, wingspan, head length and width, tarsus width, and tail length than the remaining, cliff-nesting populations.

Conclusion – This could indicate a difference in flight morphology, most probably dictated by a combination of different factors. Longer tails in tree-nesting Bonelli’s eagles could be an adaptive feature related to habitat and prey selection. Our results corroborate that, in the geographic area considered, Bonelli's eagle’ populations are largely homogeneous, also concerning biometric parameters, but show significant regional variations, such as a differentiation of the south-western tree-nesting population. Along with previously shown behavioural and genetic differences, this supports the notion that this population could be a distinct evolutionary unit.

1. INTRODUCTION

Biometric measurements such as lengths, weights or proportions are basic tools in ornithology (Eck et al. 2011). Some applications of biometry in the study of birds can be sex determination, differences in size among populations, wing morphology and body mass/body size relationship (Hernández et al. 2011). These measurements can be useful in conservation, ecology, biology, taxonomy and phylogenetic studies (Araóz et al. 2016).

Body size variation is one of the most used biometric parameters in endothermic animals, and it has been the subject of many studies (Hernández, et al. 2011). A hypothesis put forward to explain this variation is Bergmann’s rule, which establishes that body size varies inversely with ambient temperature, so that body size increases with latitude on a global scale. This has been supported by some studies (Ashton 2002; Meiri & Dayan 2003), but not by others (Yom-Tov & Yom-Tov 2005; Rodríguez et al. 2008). Global warming experienced over the last decades may also influence the variation in body size of birds, through changes in factors such as environmental variability (Jakober & Stauber 2000). However, some studies also show the difficulty of finding a relationship between global warming and body size variation (Guillemain et al. 2005; Moreno-Rueda & Rivas, 2007), which seems to be influenced by other factors apart from climate, such as feeding ecology (Toïgo et al. 2006).

It is not uncommon, within a single species, for the size of individuals within populations to vary along their geographical distribution. The analysis of biometric differences between populations enables to relate them to environmental parameters and infer possible causes that may explain them (Hernández et al. 2011).

Comparison of measurements, if they have been collected over a long time or on a large geographical scale in a standardised manner, allows inferences about the response of individuals to changes environmental factors (Zink & Remsen 1986; Eck 2011). The study of morphological variation of species along geographical gradients can be useful for testing hypotheses about the factors determining their distribution and biology (Zink & Remsen 1986; Ricklefs & Miles 1994). Nonetheless, biometric differences within a single species can be found in more reduced geographical areas, such as the Iberian Peninsula and the British Isles (Wyllie & Newton 1994).

Bonelli´s eagle (*Aquila fasciata*) provides a good opportunity to explore species' biometry variations, due to its wide geographical distribution and available data concerning biometric measurements. It is a large resident bird of prey, whose most important numbers in Europe are found in the Iberian Peninsula and on the Mediterranean coast of France (Cramp & Simmons 1980). In Europe, the species is considered "Near Threatened", and it has a population estimated with 1100 – 1200 pairs (BirdLife International 2015).

In the Iberian Peninsula, the species was in decline in the mid-1980s (Real & Mañosa 1997; Real 2004). Nowadays, the population size remains stable or is increasing lightly in some areas, although some populations at the northern and western extremes of the distribution range, continue to show some decline (Del Moral 2018).

In a study which showed that Bonelli's eagle females were generally larger than males, García et al. (2013) also noted that individuals from Portugal were generally larger than those from Spain and France. While this analysis did not fit biogeographical patterns, as

Bonelli's eagle populations are not divided by national borders (fig. 1), it hinted on biometric differences among western Mediterranean populations of this species.

In western Europe, Bonelli's Eagles most frequently nest in cliffs (Arroyo et al. 1995), except in south-western Portugal, where the population is almost exclusively tree-nesting (Dias et al., 2017). It is not known whether this population, which shows both genetic and behavioural differences (Mira et al. 2013; Palma et al. 2013, Dias et al. 2017), also has biometric differences. If these differences are found with this study, it would reinforce the notion that this population could represent a distinct evolutionary unit. The study area, which includes de Iberian Peninsula and southwestern France, provides an interesting biogeographic scenario for the study of morphological variation in Bonelli´s eagle.

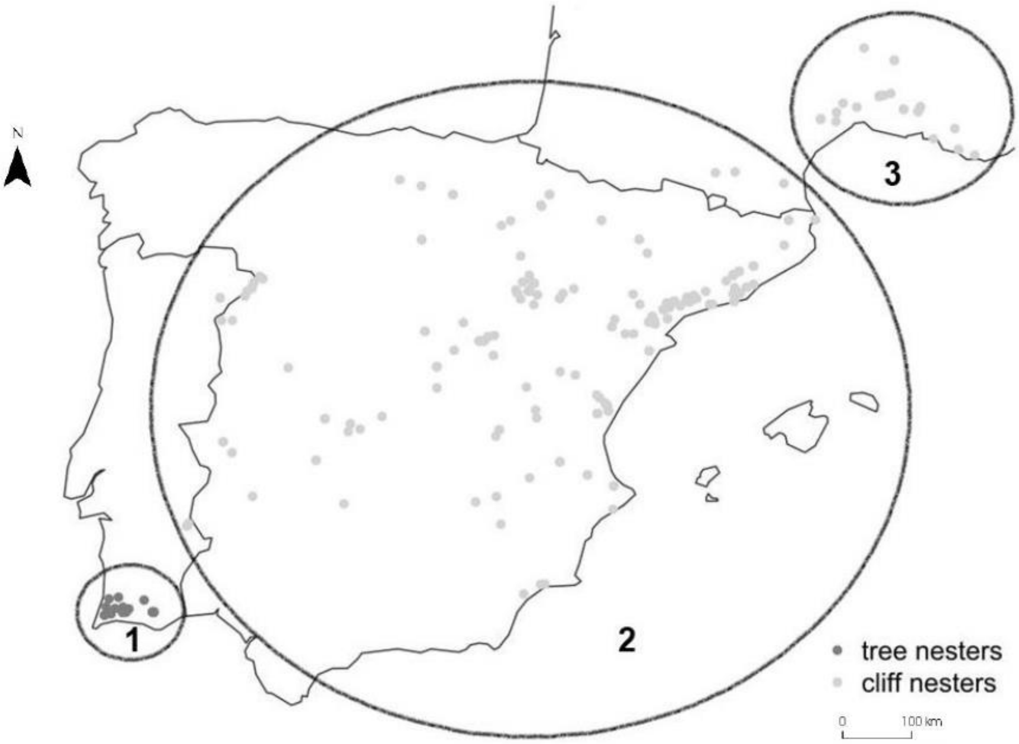

Figure 1. Locations of collected samples distributed in the six study areas: 1 - Southern Portugal; 2 - Center; 3 - SE France. Dots represent locations where samples were taken.

In this context, we aimed to test two alternative hypotheses: 1) Bonelli's eagle individual size varies with annual mean temperature; 2) the size of Bonelli's eagles differs between the tree-nesting and cliff-nesting populations.

If significant differences are found, this information can provide a useful tool for researchers and conservation workers, for example with regard to the decision to reintroduce or translocate individuals within reintroduction/conservation projects.

2. METHODS

The study area spanned de Iberian Peninsula (which comprises the mainland territories of Portugal and Spain) and south-western France (fig. 1). Across this region, 256 wild Bonelli´s eagles were live-trapped and measured, encompassing three representative population areas of the species: 1) *Southern Portugal* (n = 19 individuals) (Baixo Alentejo and Algarve); 2) *Center* (n = 208) (provinces of Badajoz, Cáceres, Ciudad Real, Salamanca, Toledo and Zamora in Spain, and Trás-os-Montes e Alto Douro, Alto Alentejo and Alqueva region in Portugal); Mediterranean area, which includes Languedoc Roussillon (France) and the Spanish provinces of Girona, Barcelona, Tarragona, Teruel, Castellon, Valencia, Alicante, Albacete and Cuenca; Aragón and inland central Spain, including Cuenca, Guadalajara, Madrid, Toledo and Zaragoza; and Upper Ebro river, located in the provinces of Álava, Burgos, Huesca, La Rioja, Navarra and part of Zaragoza and 3*) SE France* (n = 29) in Provence and Languedoc Roussillon, Côte d´Azur and Rhone – Alpes.

This population nuclei were defined according to species distribution, considering the two marginal populations (southwest Portugal (Palma et al. 2013) and north-western of the French Mediterranean area (Lieury et al. 2015) and the rest of the population.

This work was performed within the framework of different research and conservation projects for which technical assistance from the Spanish Ministry of the Environment was required. The trapping of Bonelli's eagles was carried out in areas occupied by territorial pairs but avoided the period, generally from February to April, when the birds were incubating and chicks were not yet well feathered (García et al. 2013). Baits were used along with remote-controlled floor net traps, built and patented by Víctor García Matarranz (patent number: ES2355778B1) activated by a field technician.

Birds were handled always with falconry hoods to reduce stress. Claws were wrapped with veterinary bandaging tape to prevent accidents for both the bird and the handler. All measures were gathered as quickly as possible before the birds were released back into the wild, and they were taken always by one of the authors, Víctor García, between 1998 and 2020, using a Pesola© scale, tape meter (accuracy 0.5 cm) and digital callipers (± 0.01 mm). After biometric measurements were recorded, all individuals were released in perfect condition.

2.1. Biometric variables

Body mass (weight) - was determined using a 5000g Pesola© scale. Whether the individual had a full or empty crop was taken into account. In those cases in which there was a large amount of food in the crop, 100g were subtracted; **tarsus** (Tarsus_DV - dorsoventral width of tarsus-metatarsus; Tarsus_L - Lateral width of tarsus-metatarsus (L – Left leg and D - right leg) - to measure both the lateral and the dorsoventral width, we have looked for the bulge presented by the tarsometatarsus on the proximal edge of the metatarsal fossa, taking the measurement at the point located in the narrowing that follows this protuberance; **wing chord** - measured from the carpal joint to the tip of the 7th primary, which is the longest in this species, following the natural curvature of the wing by its upper or dorsal part; **wing ventral** – the same as "wing chord", but for the ventral part of the wing, in this case, the contour is not followed but the shortest distance is taken between the two mentioned points; **7th primary** – has been named the fourth feather, if we start to count the feathers from the outermost wing part. If instead we numbered the wingtip feather as number one, we would have measured the 4th primary. It is measured from the calamus insertion to the end of the feather. For this, the end of the tape measure is inserted between the calamus of the 7th and 8th primaries until it touches the base of the feather, and from there the measurement is taken to the end of the 7th primary; **forearm** – measured from the junction of the proximal ends of the ulna and the radius with the distal end of the humerus, to the distal ends of the ulna and the radius at their junction with the carpus; **tail length** – from the uropygial gland to the end of the central rectrix; **rectrix** – from the base of the central rectrix to its end; **wingspan** – the distance between the column and the end of the longest feather, taken with the wing fully extended. Since it is a manoeuvre that requires violent manipulation for the bird, it has been preferred to do it this way instead of opening the two wings, which would place more stress on the bird; **body length** – birds were placed ventrally on a tape measure, lengthening the neck with their head stretched. The distance between the rectrices is measured, with the tail together, to the end of the bill; **bill length** - from the end of the bill to the junction of the bill with the skull, on the cranial suture; **bill height** – the perpendicular is measured from the distal edge of the wax to the point at the base of the mandible below it; **bill width** – the line between the two points where the wax of the bill ends at the edge of the upper mandible; **head length** - the distance between the end of the beak and the cerebellar prominence of the skull; **head width** – the distance in the widest part of the skull behind the orbicular zone; **claw** - the distance between the point where the upper surface of the claw emerges from the skin at the tip of the toe to the end of the claw as measured across its arc.

2.2. Statistical analysis

To test the first hypothesis (biometric variation with ambient temperature), we performed bivariate general linear regressions, using the 'lm' function in R version 4.0 (R Core Team, 2020), between each of the biometric variables (across individuals) and annual mean temperature. The latter was obtained from the WorldClim 2.0 database on a ~1 km^2 resolution (Fick & Hijmans 2017), using the 'extract' function of the 'raster' R package (Hijmans 2020). The coefficients of determination (R-squared values) of these regression models were used for assessing the extent to which ambient temperature could account for the variation in biometric variables.

To test the second hypothesis (biometric differentiation between tree-nesting and cliff-nesting populations), we compared the biometric variables of the individuals of Southern Portuguese (tree-nesting) population against those of the remaining (cliff-nesting) populations combined. For this propose, we used box plots with notches; if the notches of two boxplots do not overlap, this is considered strong evidence that the two medians are different (Chambers et al. 1983). We also performed Mann-Whitney-Wilcoxon tests of the differences in each variable. This non-parametric test is appropriate when the variables are not normally distributed. Given that Bonelli's eagle shows sexual dimorphism (García et al. 2013), we also performed these analyses separately for males and females. We also used box plots for a visual comparison of the biometric variables among all six populations, although the generally small samples sizes prevented more detailed statistical tests.

3. RESULTS

According to moult patterns and general coloration (Forsman 2007; Caro 2010), among the 256 live-trapped Bonelli´s eagles, there were 5 juveniles (first-second calendar year), 15 subadults (third-fourth calendar year) and 236 adults (fifth or more than fifth calendar year). Since all these age classes have the same biometry, all individuals were included in the analysis.

None of the biometric variables showed a gradual variation with temperature, which accounted for only 0 to 6.6% of the biometric variation (Supplementary Figure S1). However, when comparing the tree-nesting ("southern Portugal") population with the remaining (cliff-nesting) populations, both boxplot notches and one-tailed Mann-Whitney-Wilcoxon tests showed that these differences were significant for several biometric variables (Table 1; Figure 2). These included total body length, wingspan, and measurements of the head (length and width), tarsus (lateral width), and tail (length and rectrix size).

Table 1. One-tailed Mann-Whitney-Wilcoxon tests assessing if each biometric variable had larger values in tree-nesting than in cliff-nesting populations of Bonelli's eagle. Variables are described in the text. W: test statistic; *p*: significance.

Variable	**W**	***p* value**
Body mass	1896.5	0.144
Body length	426.5	0.000
Head length	627.5	0.024
Head width	389	0.000
Bill length	762.5	0.288
Bill width	866.5	0.352
Bill height	843	0.294
Claw	907.5	0.481
Tarsus L width L	1380.5	0.024
Tarsus L width R	1614.5	0.121
Tarsus DV width L	1617	0.128
Tarsus DV width R	1482.5	0.056
Wingspan	1254	0.032
Wing width	43	0.598
Wing length D	1187.5	0.103
Wing length V	1414	0.077
Primary 7	1401.5	0.354
Forearm	1326	0.128
Tail length	1041	0.001
Rectrix	1168	0.022

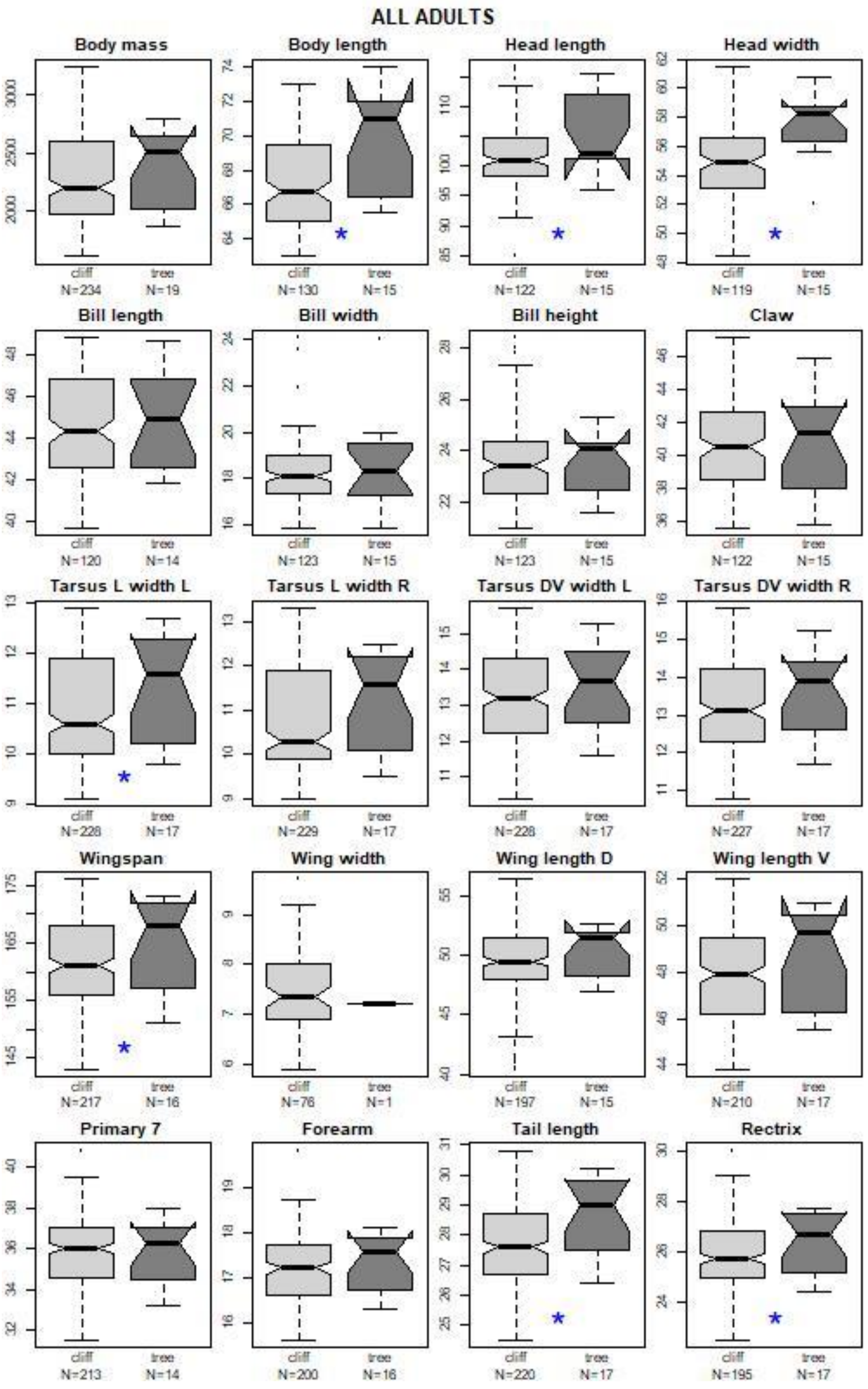

Figure - 2 Box plots comparing the values of each biometric variable between tree-nesting and cliff-nesting populations of Bonelli's eagle. Asterisks indicate variables for which the Mann-Whitney-Wilcoxon test result was significant (Table 1).

The differences in body length, head width, wingspan, tail length and rectrix remained significant when comparing only females among tree-nesting and cliff-nesting populations (Supplementary Figure S2). For males only, the small sample size of the tree-nesting population prevented the detection of significant differences (Supplementary Figure S3).

When visually comparing the values of each biometric variable among the south-western Portuguese, the central (Spanish and Portuguese border) populations, and the easternmost French population, the results were similar to when comparing the tree-nesting nucleus against all cliff-nesting nuclei together: body length, head width and tail length, in both females and males, are visibly higher in tree-nesters (Supplementary Figure S3 and S4).

Wingspan and head length are also larger in Southern Portuguese females (Supplementary Figure S3). Males from Southern Portugal have the smallest measurement for claw and 7th primary; however, we have to take into account that to evaluate this measurement, we had a very small number of samples (n = 5 and n = 6, respectively) (Supplementary Figure S5).

4. DISCUSSION

Biometry has seen many interesting applications in the field of ornithology, and it has important potential applications in biology, ecology, taxonomy, phylogeny and conservation (*e.g*. Hernández et al. 2011; Araóz et al. 2016). Biometric variation has been related to factors such as environmental variability, including global warming (Jakober & Stauber 2000), or to ecological aspects such as feeding habits (Toïgo et al. 2006). Our study revealed biometric differences between Bonelli's eagle populations with different nesting habitats, however, it does not have enough data to assess the effect of global warming.

It is well known that in birds of prey in general (Newton 2010), and Bonelli´s eagles in particular (Forsman 2007; García et al. 2013), females are larger than males. In a previous study that involved some of the same individuals used in this paper, García et al. (2013), found not only that females were larger than males regarding most variables analysed, but also that individuals from Portugal were also generally larger than those from Spain and France, which pointed to biometric differences among western Mediterranean populations of Bonellis' eagles. However, this analysis by country did not fit biogeographical patterns, as northern and eastern Portuguese populations are continuous with Spanish populations (see fig. 1).

The present study took a more ecologically meaningful approach by comparing biometrics among populations rather than among countries – particularly, among the tree-nesting population from Southern Portugal and the cliff-nesting populations from the remaining study area (Fig. 1). Size differences between populations could reflect adaptive variation in response to conditions in their habitats and/or nesting sites (Laiolo & Rolando 2001; Tieleman et al. 2003).

The tree-nesting Bonelli´s eagle population showed generally larger body length, wingspan, head length and width, tarsus width, and tail length. This could indicate a difference in flight morphology, most probably dictated by a combination of different factors such as flight behaviour, habitat selection, size of prey and display flight. It is known that even small morphological variations can reflect different behaviour and ecology (*e.g.* Norberg 1990, Chapter 12).

The relative importance of these different functions will, in turn, determine both the size and shape favored by natural selection. For example, tails act as control devices maintaining stability and as lifting surfaces to enhance manoeuvrability, agility, and low-speed flight. Birds that need high manoeuvrability, for instance, to avoid collisions in cluttered environments, generally have longer tails (Thomas & Balmford 1995). This means that wing and tail structures may also be related to vegetation density (Norberg 1990). This seems to be supported by the tree-nesting Bonelli´s eagle population, where longer tails could be an adaptive feature related to habitat and prey selection (Palma et al. 2006; García et al. 2013).

Body mass increase favours the resistance to adverse environmental conditions and to food unpredictability, especially when birds face a reduction in prey numbers (Hernández et al. 2011). Usually, Bonelli´s eagles prey on European rabbits (*Oryctolagus cuniculus*) in Spain (Moleón et al. 2009, 2012; Caro et al. 2011) and France (Morvan 2010; Resano et al. 2012), where populations are mostly cliff-nesters. In the peculiar population of SW Portugal, Bonelli´s eagles had to adapt to the decline of their staple prey (Palma et al. 2013), like in the Cyprus population, where they nest in Calabrian Pine *Pinus brutia* forests and use birds as their main prey (Iezekiel et al. 2010). The Southern Portuguese population feeds about 70% on Rural Pigeons *Columba livia*. Racing Pigeons *Columba livia* and Domestic Fowl *Gallus gallus* are also consumed frequently (Palma et al. 2006).

As well related to body size, geographical and temporal variations are common phenomena among organisms and may evolve within a few years. Yom-Tov and Geffen (2010) argue that body size acts much like a barometer, fluctuating in parallel with changes in the relevant key predictors, and that geographical and temporal changes in body size are actually manifestations of the same drivers. Commonly, the principal predictors of body size are food availability during the period of growth, and ambient temperature, which often affects food availability. It is a challenge to find which particular environmental factors determine food availability and, in turn, changes in animal body size. It is possible that recent changes in body size are phenotypic, but in some cases, they are partly genetic (Yom-Tov & Geffen 2010). Other environmental factors besides temperature, such as humidity, seasonality and precipitation, have been proposed as contributing to geographic variations in body size (Fan et al. 2019).

Globally, animals that live at higher latitudes/elevations (*i.e.*, at lower average temperatures) tend to have a larger body size (Bergmann's rule) and a smaller appendage size (Allen's rule) for thermoregulatory reasons. According to the heat conservation hypothesis, large body size and small appendage size help animals retain heat under cold ambient temperatures, while small body size and large appendage size help them dissipate heat under warm temperatures (Fan et al. 2019). There is no agreement about whether Bergmann's rule is general or valid. Empirical studies have found the predicted pattern at both the intraspecific and interspecific levels in mammals and birds, although animals that do not follow Bergmann's rule have also been reported (Fan et al. 2019). Within our study area, while latitudinal variation is insufficient to test Bergmann's rule directly, Bonelli´s eagles do not show gradual size variations with annual mean temperature (see Figures S1 in Supplementary Information).

In our study, although French Bonelli´s eagles (males and females) are heaviest and have larger claws (see also García et al. 2013), Bonelli´s eagles from Southern Portugal contradict Bergmann's latitudinal rule, presenting the highest values of most of the analysed biometric variables. These different biometrics could stem from adaptation to the forest environments where this population nests.

Climate warming has also been linked with changes in the spatiotemporal distribution of species and the body size structure of ecological communities (Evans et al. 2019). It may influence the variation in body size of birds through changes in factors such as environmental variability (Jakober & Stauber 2000). Body size is a major factor influencing animal morphology, physiology, ecology, evolution and extinction probability (Schmidt-Nielsen 1984; Cardillo et al. 2005).

In general, our study found significant though not very strong differences between the biometric measurements of tree-nesting versus cliff-nesting Bonellis´s eagles. The relatively small sample sizes of some populations, particularly the tree-nesting population of SW Portugal, likely hampered the detection of stronger biometric differences. Some values may also be underestimated – for example, males from SW Portugal showed the smallest sizes for claw and 7th primary, but with reduced sample sizes of n = 5 and n = 6, respectively. Further analysis including larger numbers of individuals might add strength to the observed patterns. However, it must be taken into account that the current sample size already implied countless hours (across years) of fieldwork, including the capture, meticulous measurement and release of hundreds of individual specimens, plus thousands of kilometres travelled to cover all the studied populations (fig. 1).

Despite the necessarily limited sample size, the current data show significant differences for several biometric measurements between tree-nesting and cliff-nesting Bonelli's eagles. Furthermore, this differentiation is matched by the previously described differences in diet (Palma et al. 2006, 2013), genetic structure (Mira et al. 2013) and nesting behaviour (Dias et al. 2017). All of this points to a distinctive character of the SW Portuguese population of Bonelli's eagles, which should consequently be treated as a distinct biogeographic and evolutionary unit.

The observed expansion of tree-nesting Bonelli's eagles from southern Portugal, possibly was facilitated by the tree-nesting behaviour, which allowed the colonization of areas without cliffs (Dias et al. 2017). This idea is reinforced by genetic studies which showed that these population had the lowest genetic diversity but a marked differentiation from others (Mira et al. 2013). This is also corroborated with demographic modelling where it was likely the main source of colonists throughout the expansion process. This population, like the ones from south of Iberian Peninsula, act as sources that thanks to dispersal sustain all populations (Hernández- Matías et al. 2013).

It should be noted that this study did not include biometric data on the Bonelli's eagle population from Andalusia, which serves as the main source of the species in the Iberian Peninsula (Muñoz et al. 2005; De las Heras & Garrido R. 2018). In addition, the Andalusian population has been supplying specimens in recent years to reinforce other Spanish populations, likely causing a mixture of individuals in the studied populations (Life Bonelli 2017).

Our results help corroborate the fact that Bonelli's eagle populations are largely homogeneous in the geographic area considered, also with regard to biometrics, but there are potentially important regional variations, such as a differentiation of the south-western tree-nesting population. This must be taken into account when making decisions about research, conservation and management of this endangered species, for example with regard to the decision to reintroduce or translocate individuals within reintroduction/conservation projects. In European Mediterranean ecosystems, Bonelli's eagle is regarded as an umbrella species, as it is one of the top avian predators found in these natural systems (Real 1991, Moleón et al. 2009) and moreover plays a key role in shaping the structure of the endangered biotic communities that these systems contain.

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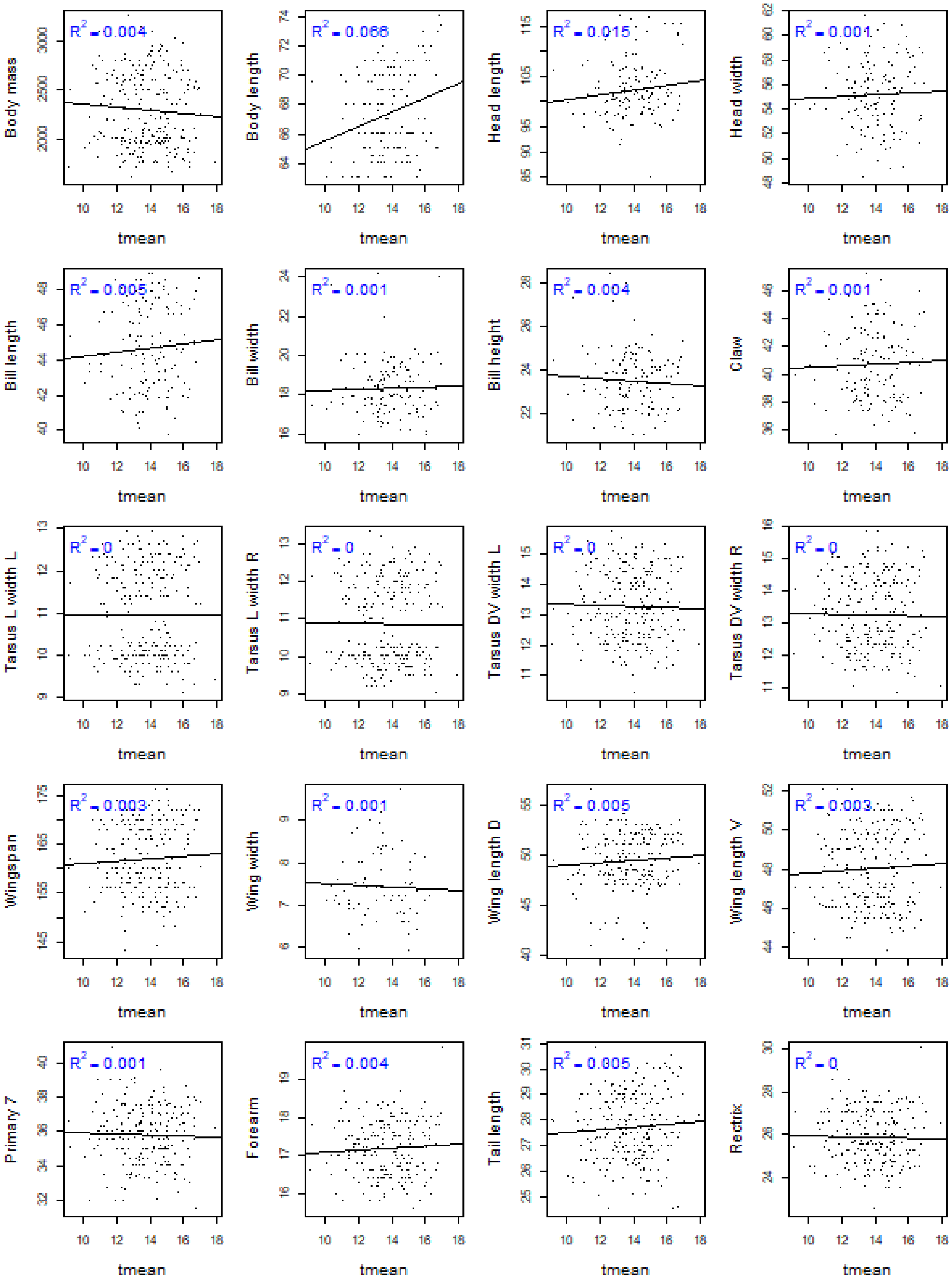

Figure S1 - Bonelli's eagle biometric differentiation variation depending on the mean spatial trend for ambient temperature (tmean).

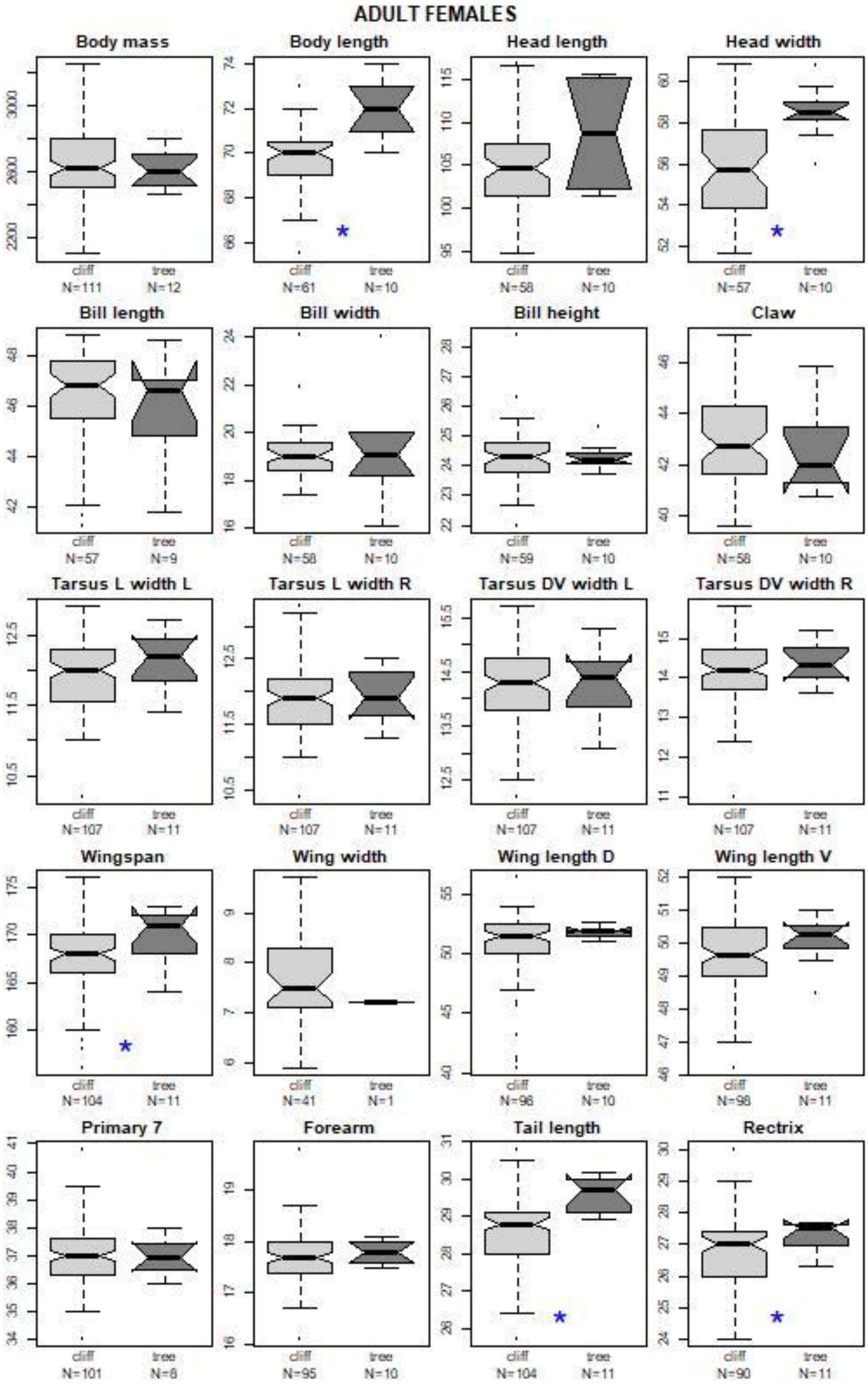

Figure S2 - Bonelli's eagle biometric differentiation between cliff or tree-nesting birds – boxplot females.

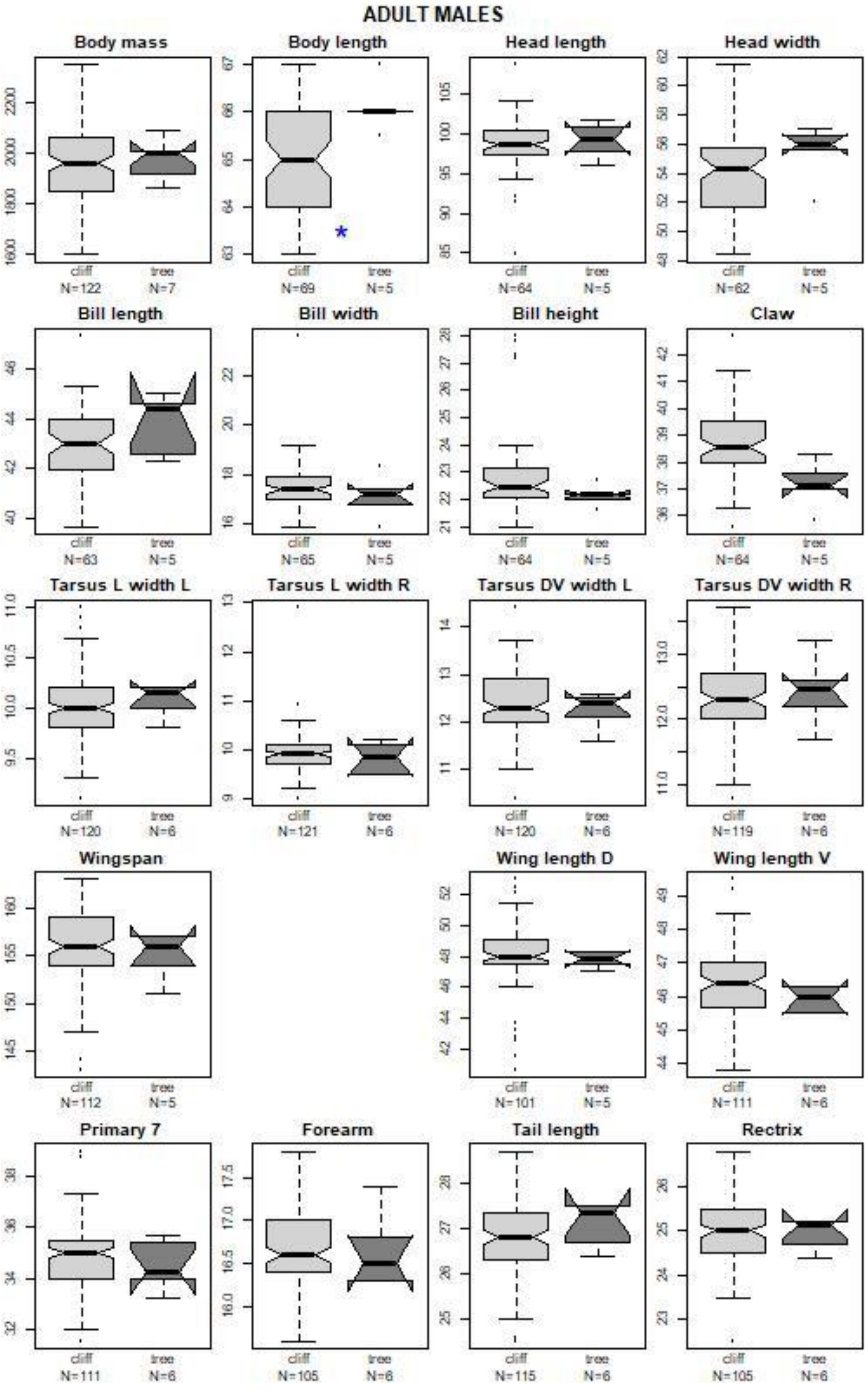

Figure S3 - Bonelli's eagle biometric differentiation between cliff or tree-nesting birds – boxplot males.

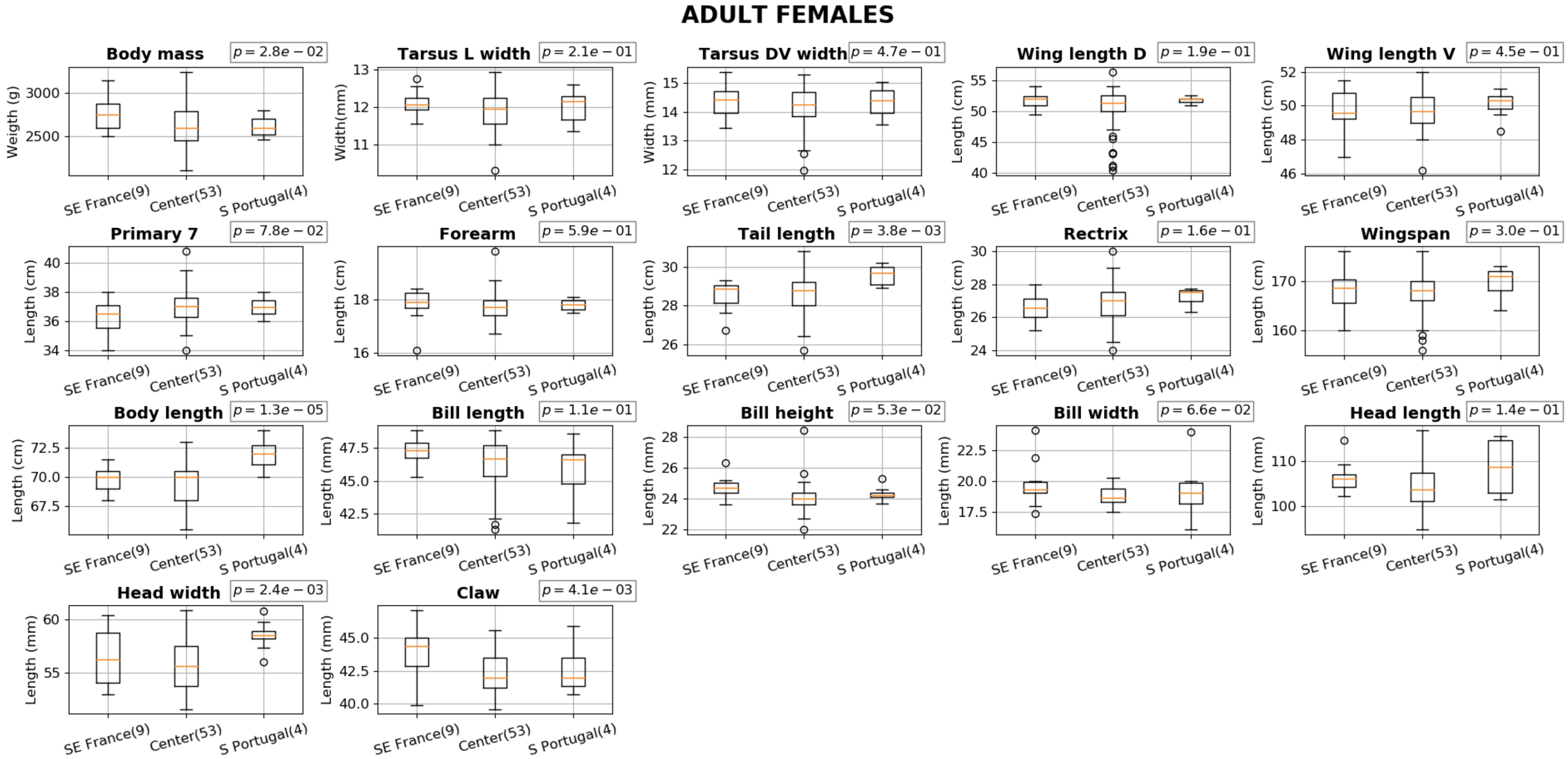

Figure S4 - Boxplots comparing values of each Bonelli's eagle´s (females) biometric variable, between geographic nuclei (1 - Southern Portugal; 2 - Center; 3 - SE France).

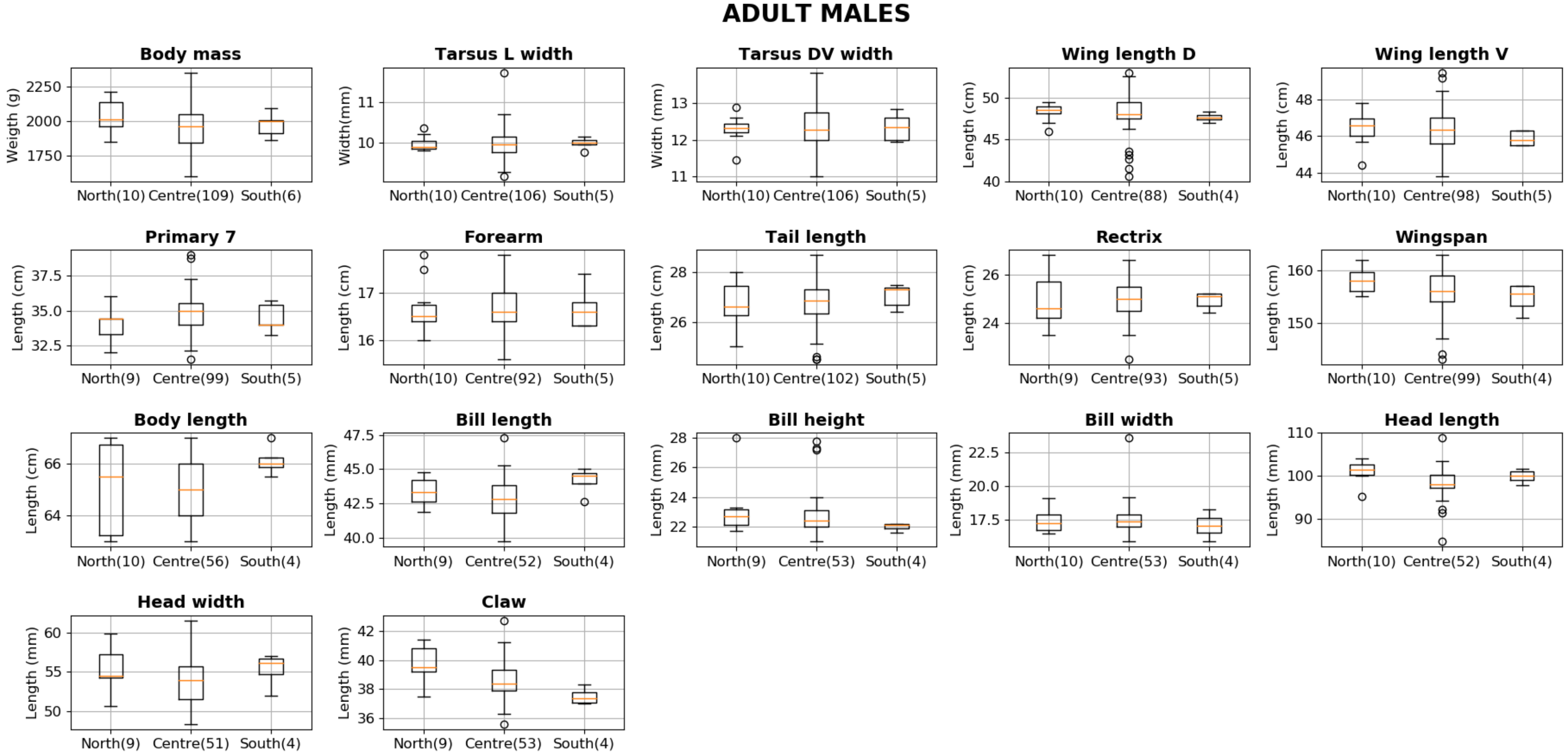

Figure S5 - Boxplots comparing values of each Benelli's eagle´s (males) biometric variable, between geographic nuclei (1 - Southern Portugal; 2 - Center; 3 - SE France).

CHAPTER 2

Bonelli´s eagles´taphonomy

Understanding the taphonomic signature of Bonelli´s Eagle (*Aquila fasciata*)

Lluís Lloveras [a, b, *], Richard Thomas [a], Rui Lourenço [c], Jesús Caro [d, e], Andreia Dias [f]

[a] School of Archaeology and Ancient History, University of Leicester, University Road, Leicester LE1 7RH, UK

[b] SERP, Departament de Prehistòria, Història Antiga i Arqueologia, Universitat de Barcelona, Montalegre 6-8, 08001 Barcelona, Spain

[c] ICAAM- Instituto de Ciências Agrárias e Ambientais Mediterrânicas, LabOr - Laboratório de Ornitologia, Universidade de Évora, Núcleo da Mitra, Ap. 94, 7002-554 Évora, Portugal

[d] Departmento de Zoología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

[e] Instituto de Investigación en Recursos Cinegéticos - IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, 13071, Ciudad Real, Spain

[f] Departament de Biologia Animal, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Catalonia, Spain

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ABSTRACT

Bonelli's eagle (*Aquila fasciata*) is a large bird of prey that breeds in warm regions of the Palearctic. In Europe, it is mainly found in the Mediterranean region, in open or partially-open landscapes in mountainous areas. They normally feed on mammals, up to the size of a hare, medium-sized birds and large reptiles.

The remains of Bonelli's eagles have been found at Pleistocene archaeological sites, raising the possibility that they were active bone accumulating agents in caves and shelters, a practice evidenced by contemporary studies that show their nests are usually located on rocky cliffs.

Taphonomic studies on prey remains consumed by these raptors do not exist and their role in bone accumulations at archaeological sites is not understood. We analyse non-ingested bone remains and pellets recovered at well-known Bonelli's eagle nests situated in the south of Spain and Portugal with the aim of characterising their accumulations. Specifically, we detail taxonomic and anatomical representation, bone breakage, beak marks and digestion damage. Results show that European wild rabbit (Oryctolagus cuniculus), red-legged partridge (*Alectoris rufa*) and pigeons (Columba spp.) are the dominant prey. The taphonomic pattern varies depending on the type of prey and the origin of skeletal materials (non-ingested versus pellets). Comparisons with other agents of bone accumulation (birds of prey and terrestrial carnivores) suggest that the taphonomic signature of Bonelli's eagle differs from most other predators.

1. INTRODUCTION

Bonelli's eagles (*Aquila fasciata*) are widespread raptors, with a range extending from the Iberian Peninsula and NW Africa across southern Europe, the Middle East and the Arabian Peninsula through Afghanistan to India, south China and Indonesia. Western Palaearctic populations are distributed mainly in the Mediterranean area, generally in fairly warm and dry regions (Cramp & Simmons 1980; Ferguson-Lees & Christie 2001;

Real 2003).

They inhabit open or partially-open landscapes often in hilly areas and prefer short or sparse vegetation, such as garrigue, dry grassland and rocky habitats; however, its habitat can be highly variable including forests and parkland as well as bushes and scrub. It is also often found in open habitats with non-intensive crops, vineyards, olive groves, small woodlands and pastures (Cramp & Simmons 1980; Tucker & Heath 1994).

Despite a marked decline in numbers since the early 1980s, Bonelli's eagle is still present in most of the Iberian Peninsula with the exception of the Cantabrian region and in the north-western quarter of Spain (Cabral 2008; Del Moral 2006). Pairs are primarily distributed in the Mediterranean regions (from southern Portugal to Catalonia), in the mountainous areas with a Mediterranean climate characterized by hot summers and low precipitation (Muñoz et al. 2005; Ontiveros & Pleguezuelos 2003; Palma et al. 1996; Real & Mañosa 1997).

Bonelli's eagles are large birds of prey (55 - 67cm in length and a mass of 1.5 - 2.5kg [Cramp & Simmons 1980]) that feed on medium-sized mammals, birds and reptiles. Previous feeding studies have shown that rabbits, partridges and pigeons are the preferred game but they also take hares, squirrels, rodents, corvids and lizards among others (Caro et al. 2011; Del Amo et al. 2008; Ontiveros & Pleguezuelos 2000; Ontiveros et al. 2005; Palma et al. 2006; Real 1996; Valkama et al. 2005). Rabbits seems to be the favourite prey of the eagle in terms of weight and energetic value, but when they are scarce, the eagle preys upon a wider range of species that are more difficult to capture and offer lower calorific returns (Arroyo & Ferreiro 1997; Moleón et al. 2009).

While Bonelli's eagles do nest in trees (particularly in south Portugal, although less than 4% of the Spanish population do it), breeding is normally in holes in cliffs rock shelters of variable size (Del Moral 2006; Palma et al. 2006). Pellets and leftover prey re- mains accumulate on the surface of the nest and under roosting sites and perches of the surrounding area (Real 1996). Pleistocene- aged remains of Bonelli's eagles have been found in archaeological deposits at Gruta da Figueira Brava (Portugal), Brechas de la Cantera de l'Altissent (Spain) and Devil's Tower and Gorham's Cave (Gibraltar) (Tyrberg 2008), raising the possibility that they were active bone-accumulating agents in prehistoric caves and shelters. Their nests can therefore occur in the same spaces frequented by prehistoric hunter-gatherers populations and the food remains of both may become intermingled. Establishing the taphonomic signature of this diurnal raptor is necessary to distinguish between human and eagle accumulations.

In recent years, assessment of the origin of small prey bone accumulations from archaeological sites has become an important line of taphonomic research. In order to identify the agent responsible for accumulations of small prey, several actualistic studies have been conducted for terrestrial carnivores (e.g. Alvarez et al. 2012; Cochard 2004a; Lloveras et al. 2008a, 2012a; Mallye et al. 2008; Mondini 2002; Rodríguez-Hidalgo et al. 2013; Sanchis 2000; Sanchis Serra & Pascual Benito 2011; Schmitt & Juell 1994; Stiner et al. 2012) and nocturnal and diurnal raptors (Bochenski 2005; Bochenski et al. 1997, 1999, 2009; Cochard 2004b; Hockett 1989, 1991, 1995; 1996; Laroulandie 2002; Lloveras et al. 2008b, 2009, 2012b, 2014a; Sanchis 2000; Sanchis et al. 2013; Schmitt 1995; among others). Information provided by these taphonomic studies is necessary to understand the formation processes at archaeological and palaeontological sites, and distinguish human and other animal agents of accumulation. The aim of our study is to elucidate the taphonomic patterns of prey remains recovered from modern nests and pellets of Bonelli's eagles and to establish diagnostic features that can be used to evaluate their role as contributors of bone accumulations in archaeological assemblages.

2. MATERIALS AND METHODS

We analysed osteological remains of prey from nine Bonelli's eagle nests located in two areas in the south of the Iberian Peninsula (Fig. 1): six nests from the Algarve and Alentejo regions (south of Portugal) and three nests from the Sistema Bético (south of

Spain).

All materials were collected by the authors (AD, RL and JC) be- tween 2007 and 2012 after the breeding season to avoid disturbing the birds. Each sample comprises non-ingested remains and pellets collected on the surface of nests and in the surrounding areas beneath them (Fig. 2). Feeding behaviour studies of Bonelli's eagles show that these raptors usually remove uneaten prey remains from the nest; only a low proportion of remains are left on the surface (Real 1996). For this reason, most non-ingested bones can be found on perches or on the floor around nests.

Pellets were disaggregated while dry to separate the osteological material and bones and teeth were sorted under a magnifying glass to prepare for analysis. Skeletal remains were anatomically determined, sided, and identified to taxon whenever possible.

Identifications were carried out using the animal bone reference collection of the School of Archaeology and Ancient History Bone Laboratory, University of Leicester. The Number of skeletal elements (N), Number of Identified Specimens Present (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were calculated as well as relative frequencies.

Determination of the age at death of the prey mammals was only possible for rabbits and was estimated taking into account the epiphyseal fusion state of long bones (humeri, femora and tibiae), metapodials, scapulae, calcanei and innominates (Rogers 1982; Taylor 1959). Only two age categories were considered, adult and immature. To facilitate comparison of the taphocoenosis of Bonelli's eagle with other predators, the analytical methodology follows the same criteria applied in previous works (Lloveras et al. 2008a, 2008b, 2009, 2012a, 2014a):

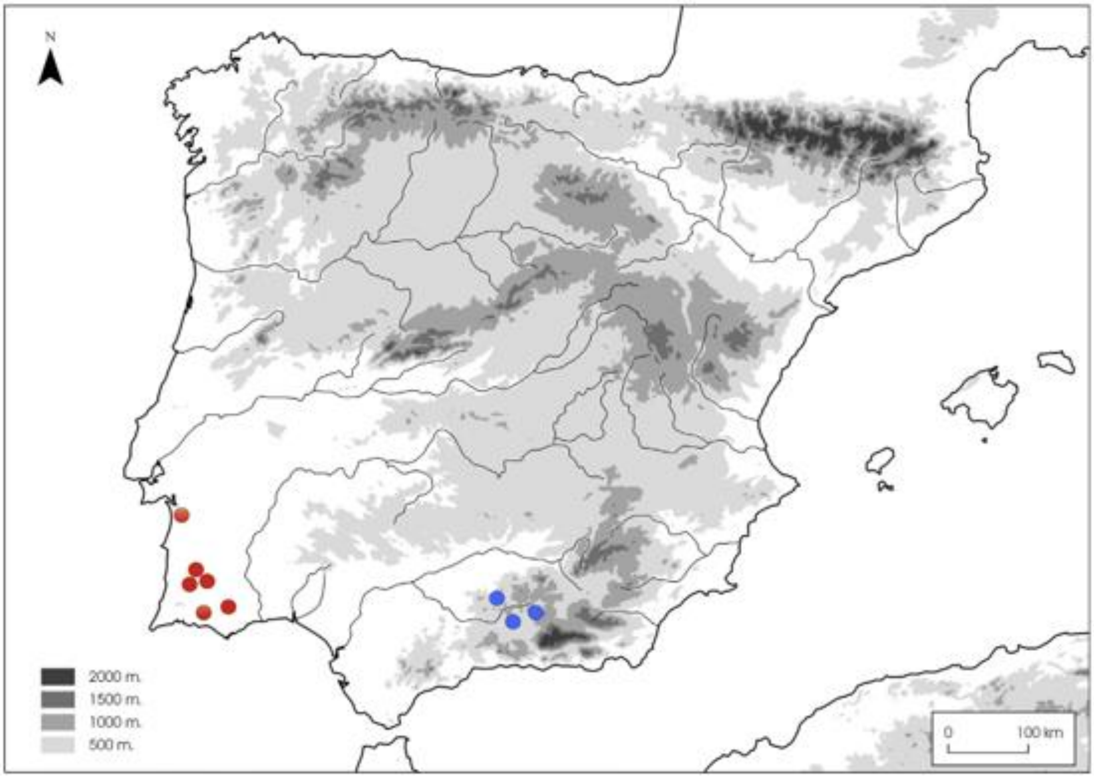


Figure. 1. Locations from which Bonelli's eagle nests samples were collected. In red: Portuguese samples. In blue: Spanish samples.

Figure 2 - Examples of pellets and non-ingested materials recovered from Bonelli's Eagle nesting areas.

2.1 Anatomical representation

Relative abundance was calculated using the formula advocated by Dodson and Wexlar (1979):

RA_i ¼ MNE_i=MNI × E_i

(RA_i = the relative abundance of element *i*; MNE_i = the minimum number of skeleton element *i*; MNI = the minimum number of individuals based on the highest number of any single element in the assemblage; E_i = the number of element *i* in the prey skeleton).

In addition, proportions of skeletal elements in mammalian prey were evaluated using the following ratios (Andrews 1990):

(a) PCRT/CR - the total number of postcranial elements (limb elements, vertebrae and ribs) compared with the total number of cranial elements (mandibles, maxillae and teeth).

(b) PCRAP/CR - the total number of limb elements (long bones, scapulae, innominates, patellae, metapodials, carpals, tarsals and phalanges) compared with the total number of cranial elements (mandibles, maxillae and teeth).

(c) PCRLB/CR - the total number of postcranial long bones (humeri, radii, ulnae, femora and tibiae) compared with the total number of cranial elements (mandibles and maxillae).

Loss of distal limb elements was shown by two indices (Lloveras et al. 2008a):

(d) AUT/ZE - autopodia (metapodials, carpals, tarsals and phalanges) compared with zygopodia and stylopodia (tibiae, radii, ulnae, humeri, femora and patellae);

(e) Z/E - zygopodia (tibiae, radii and ulnae) compared with stylopodia (femora and humeri).

A further index compared anterior to posterior limb elements:

(f) AN/PO - scapulae, humeri, radii, ulnae and metacarpals compared with innominates, femora, tibiae and metatarsals.

The following ratios were calculated for birds:

a) To assess the differential representation of wings and legs (following Ericson, 1987), the number of wing elements (humeri, ulnae, carpometacarpi) was divided by the sum of wing and leg elements (femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.

b) To evaluate the presence of proximal and distal elements (Bochenski & Nekrasov 2001), the number of proximal elements (scapulae, coracoids, humeri, femora, tibiotarsi) was divided by the sum of proximal and distal fragments (ulnae, radii, carpometacarpi, tarsometatarsi), and expressed as a percentage.

c) To appraise the proportions of core and limb elements (Bochenski 2005), the number of core elements (sterna, pelves, scapulae, coracoids) was divided by the sum of core and limb elements (humeri, ulnae, radii, carpometacarpi, femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.

All the ratios were calculated using the MNE.

Chi-square test and Z-test were used to evaluate the significance of differences in survivorship of particular skeletal elements or their fragments.

2.2 Breakage

The breakage pattern was described by the maximum length of all identified skeletal elements. Percentages of complete elements, isolated teeth (for mammals) and articulated elements were also calculated (Andrews 1990). Fragmentation of bones was analysed using separate categories for mammals and birds. For all mammals, bone fragments were categorised depending on bone type:

- Patellae, carpals, tarsals and ribs were classified as complete (C) or fragmented (F).
- Phalanges were recorded as complete (C), proximal (P) or distal (D) fragments. When the distinction between proximal or distal was not possible, they were recorded as fragment (F).
- Vertebrae were registered as complete (C), vertebral body (VB), vertebral epiphysis (VE) or spinous process (SP).
- Breakage of teeth was calculated separately for isolated and in situ elements (Fernández-Jalvo & Andrews 1992) and they were classified as complete (C) or fragmented (F).
- Breakage categories for long bones, metapodials, mandibles, crania, scapulae and innominates follow those proposed by Lloveras et al. (2008a) and applied in subsequent studies (Lloveras et al. 2008b, 2009, 2012a, 2014a).

Breakage of bird bones was analysed using the methodology proposed by Bochenski et al. (1993). The ratio of proximal and distal portions of long bones (Bochenski 2005) was calculated to observe the differences between whole bones and proximal and distal parts.

2.3 Digestion

Damage to the bone surface was observed under light microscope (x10 - x40 magnification). Different categories of digestion damage were applied to bones and teeth (Fernández-Jalvo & Andrews 1992; Lloveras et al. 2008a, 2008b, 2014b). Five categories of digestion were distinguished: null (0); light (1); moderate (2); heavy (3); and extreme (4).

2.4 Beak/talon marks

Damage to bone surfaces caused by beaks were noted and counted. Following the methodology used in previous studies (Lloveras et al. 2008a, 2008b, 2009, 2012a, 2014a) beak marks were classified as scoring, notches, tooth punctures/tooth pits and crenulated/fractured edges (Andrews 1990; Binford 1981; Brain 1981). Punctures and pits were also classified by their number (isolated or multiple) and distribution (unilateral - *i.e.* located on one surface - or bilateral) (Sanchis Serra et al. 2013).

3. RESULTS

A total of 826 skeletal fragments was analysed, 321 from south Portugal and 505 from south Spain. For analytical purposes the data from all nest sites have been combined and analysed as a single assemblage. Since the accumulating agent is the same for each sample it was assumed that the taphonomic pattern would be identical.

3.1 Taxonomic representation

The taxa recovered from the samples are presented in Table 1. The leporid sample was exclusively European wild rabbit (*Oryctolagus cuniculus*). Two unidentified small mammal bone fragments were also present. The birds included red-legged partridge (*Alectoris rufa*), pigeon (Columba spp.), dove (*Streptopelia* spp.), Eurasian jay (*Garrulus glandarius*), yellow-legged gull (*Larus michahellis*) and unidentified corvids, Ciconiiformes and passerine remains. Fish were represented by a single specimen attributed to Cyprinidae (carps, true minnows, and their relatives).

The most abundant taxon was European rabbit, which made up 53% of the total sample, followed by birds (46.6% e red-legged partridge (21.5%), pigeon (16.3%) and dove (3.4%)), small mammals (0.2%) and fish (0.1%) (Table 1, Fig. 3). The most abundant taxa when quantified by MNI were European rabbit (9), red-legged partridge (8) and pigeon (7).

Table 1 separates the taxonomic abundance for the Portuguese and Spanish samples. In both regions rabbits, red-legged partridges and pigeons were clearly the most numerous species. However, rabbits and pigeons were better represented in the Spanish sample. Partridges were more common in the Portuguese sample, which also included a greater diversity of taxa.

Table 1 – NISP (Number of Identified Specimens), MNE (Minimum Number of Elements) and MNIs (Minimum Number of Individuals) by taxon recovered in Portuguese and Spanish samples.

	Portuguese sample		**Spanish sample**		**Whole sample**			
TAXA	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**MNE**	**MNIs**
Leporids								
Oryctilgus cuniculus	140	43.6	298	59	438	53	385	9
Small mammals								
Unindentified Birds	-	-	2	0.4	2	0.2	2	1
Alectoris rufa	116	36.1	62	12.3	178	21.5	147	8
Columba spp.	31	9.7	104	20.6	135	16.3	125	7
Streptopelia spp.	-	-	28	5.5	28	3.4	28	2
Garrulus glandarius	7	2.2	-	-	7	0.8	7	1
Corvidae	1	0.3	-	-	1	0.1	1	1
Ciconiiformes	12	3.7	-	-	12	0.8	12	1
Larus michahellis	5	1.6	-	-	5	1.5	5	1
Passeriformes	7	2.2	-	-	7		7	1
Unidentified Fish	1	0.3	11	2.2	12		12	1
Cyprinidae	1	0.3			1	0.1	1	1
Total	321		505		826		732	

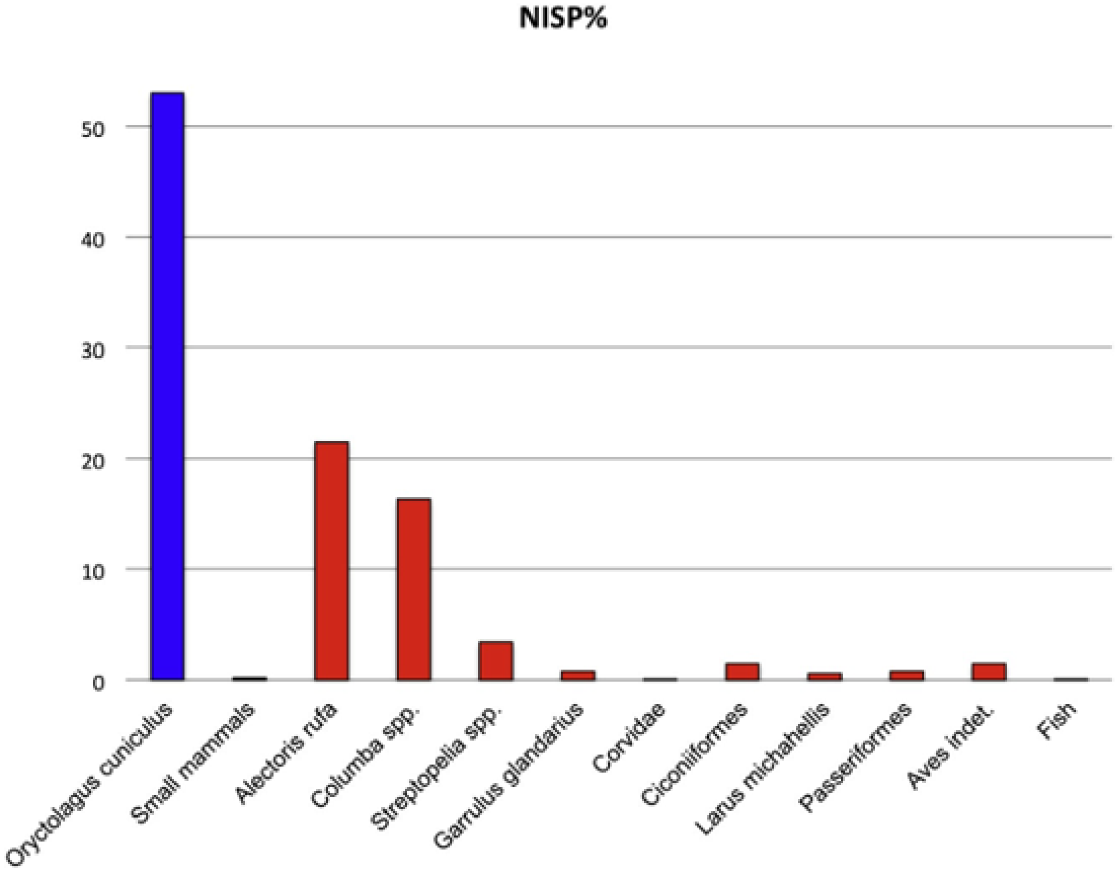


Figure 3 - Relative abundance of prey taxa (%NISP).

3.2 Age at death

Age at death was only estimated for rabbits and revealed a preponderance of immature individuals (N = 34, 58.6%).

3.3 Taphonomic analysis

All body parts were represented in the samples, though their presence and frequency varied by taxonomic group. Observation of breakage patterns reveals that prey remains were moderately fragmented with an average percentage of complete bones of 62.6%. Additionally, a total of 43.4% of the remains measured less than 10 mm in length, 38.7% of bones were articulated and 62.7% of teeth remained in situ. Damage from digestion affected 44.7% of the re- mains and most (49.2%) showed a heavy degree of corrosion. Beak or talon marks occurred on 34 remains (4.1%), crenulated edges (41.9%) and beak punctures (27.9%) were the most common form.

Henceforth, the taphonomic analysis for leporids and birds is treated separately given the potential for different groups of taxa to exhibit different taphonomic signatures.

3.3.1 Leporids

The total number of recovered leporid remains was 438, 245 were non-ingested remains and 193 were extracted from pellets.

3.3.1.1 Anatomical representation

The anatomical composition of the identified remains in the leporid sample is presented in Table 2. The entire skeleton was represented e upper molars (22.4%), vertebrae (18%), phalanges (15.1%) and cranial remains (8.9%) were the most numerous elements (N%). The relative abundance of skeletal elements (RA%) is also shown in Table 2 and Fig. 4. The mean value (28.5%) was very low indicating an important loss of bones in the assemblage. The best-represented elements were the cranium (100%), upper molars (90.7%) and the innominate (88.9%), whilst metacarpals and ribs were rare (4.4% and 4.6% respectively). Relative proportions of skeletal elements are shown in Table 3.

Table 2 - Leporid skeletal elements recovered from Bonelli's Eagle nest accumulations. Key: *N* - number of skeletal elements; *N%* - percentage of skeletal elements; MNE - minimum number of elements; RA% - relative abundance. Abbreviations: cra - cranium; man - mandible; inc - incisors; u mol - upper molar; l mol - lower molar; sc - scapula; hum - humerus; rad - radius; uln - ulna; mtc - metacarpal; inn - innominate; fem - femur; pat - patella; tib - tibia; mts - metatarsal; cal - calcaneum; ast - astragalus; c/t - carpal/tarsal; phal - phalanges; ver - vertebrae; rib – rib.

LEPORIDS	Whole sample (MNI ¼ 9)					Non-ingested (MNI ¼ 8)				Pellets (MNI ¼ 4)			
	N	*N%*	MNE	RA%	MNI	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%
cra	39	8.9	9	100	9	15	6.1	7	87.5	24	12.4	2	50
man	4	0.9	4	22.2	2	0	0	0	0	4	2.1	4	50
inc	24	5.5	24	44.4	5	19	7.8	19	39.6	5	2.6	5	20.8
u mol	98	22.4	98	90.7	9	61	24.9	61	63.5	37	19.2	37	77.1
l mol	10	2.3	10	11.1	1	0	0	0	0	10	5.2	10	25
sc	6	1.4	4	22.2	2	3	1.2	2	12.5	3	1.6	2	25
hum	4	0.9	3	16.7	2	2	0.8	2	12.5	2	1	1	12.5
rad	6	1.4	5	27.8	3	2	0.8	2	12.5	4	2.1	3	37.5
uln	4	0.9	3	16.7	2	2	0.8	2	12.5	2	1	1	12.5
mtc	4	0.9	4	4.4	1	0	0	0	0	4	2.1	4	10
inn	18	4.1	16	88.9	8	14	5.7	13	81.3	4	2.1	3	37.5
fem	8	1.8	7	38.9	4	6	2.4	5	31.3	2	1	2	25
pat	2	0.5	2	11.1	1	2	0.8	2	12.5	0	0	0	0
tib	7	1.6	4	22.2	3	4	1.6	3	18.8	3	1.6	1	12.5
mts	19	4.3	15	20.8	2	8	3.3	8	16.7	11	5.7	7	21.9
cal	3	0.7	3	16.7	2	2	0.8	2	12.5	1	0.5	1	12.5
ast	2	0.5	2	11.1	1	2	0.8	2	12.5	0	0	0	0
c/t	23	5.3	23	10.6	2	10	4.1	10	5.2	13	6.7	13	13.5
phal1/2	42	9.6	42	13.7	2	16	6.5	16	5.9	26	13.5	26	19.1
phal3	24	5.5	24	14.8	2	8	3.3	8	5.6	16	8.3	16	22.2
ver	79	18	73	17.6	2	62	25.3	62	16.8	17	8.8	11	6
rib	12	2.7	10	4.6	1	7	2.9	6	3.1	5	2.6	4	4.2
Total	438		385			245		232		193		153	

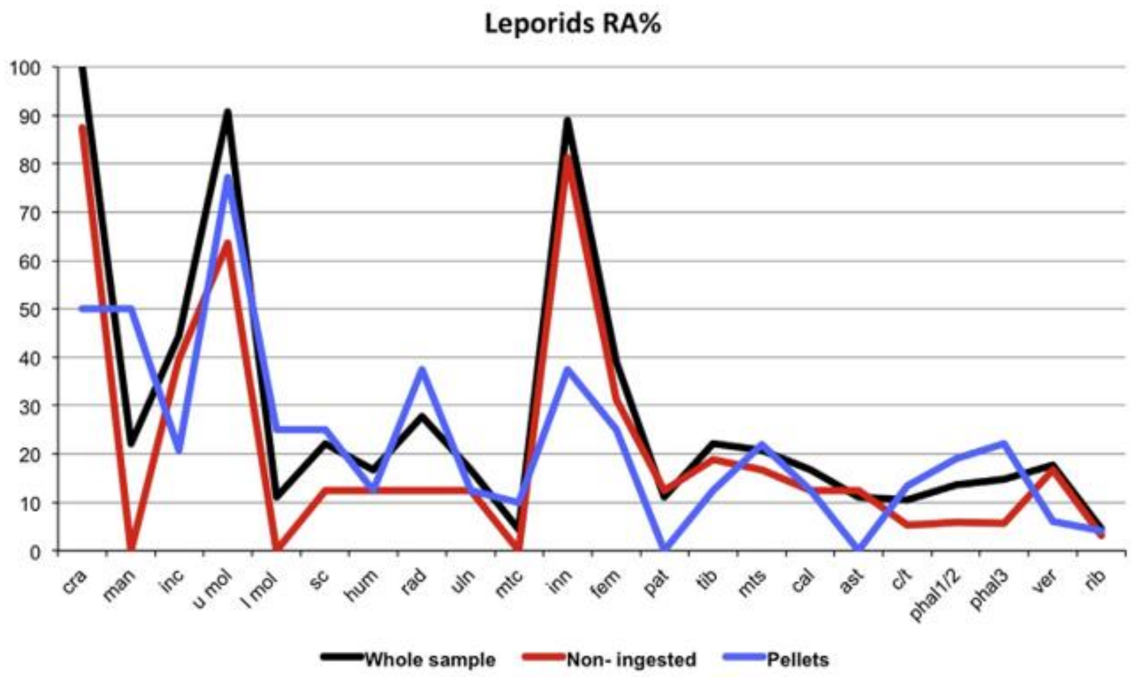


Figure 4 - Relative abundance of different parts of the skeleton for leporid remains. For abbreviations see the caption for Table 2.

Results indicate that there was a deficiency in the numbers of:

- postcranial compared to cranial remains;
- lower compared to upper limb elements, indicating an important loss of distal elements (specially the smallest ones, i.e., third phalanges and carpal/tarsal bones) and;
- anterior compared to posterior limb elements.

Analysis of the leporids by the origin of remains (non-ingested and pellets), reveals that the absolute numbers of cranial remains, metapodials and phalanges were higher in pellets, whereas vertebrae and innominates were better-represented in non-ingested remains (Table 2). Relative abundance profiles were similar in both samples (Table 2, Fig. 4), but long bones, mandibles and phalanges were more abundant in pellets, and crania and innominates predominated in non-ingested remains. This difference is statistically significant ($\chi2 = 187.9$, $P < 0.01$, df = 21).

3.3.1.2. Breakage

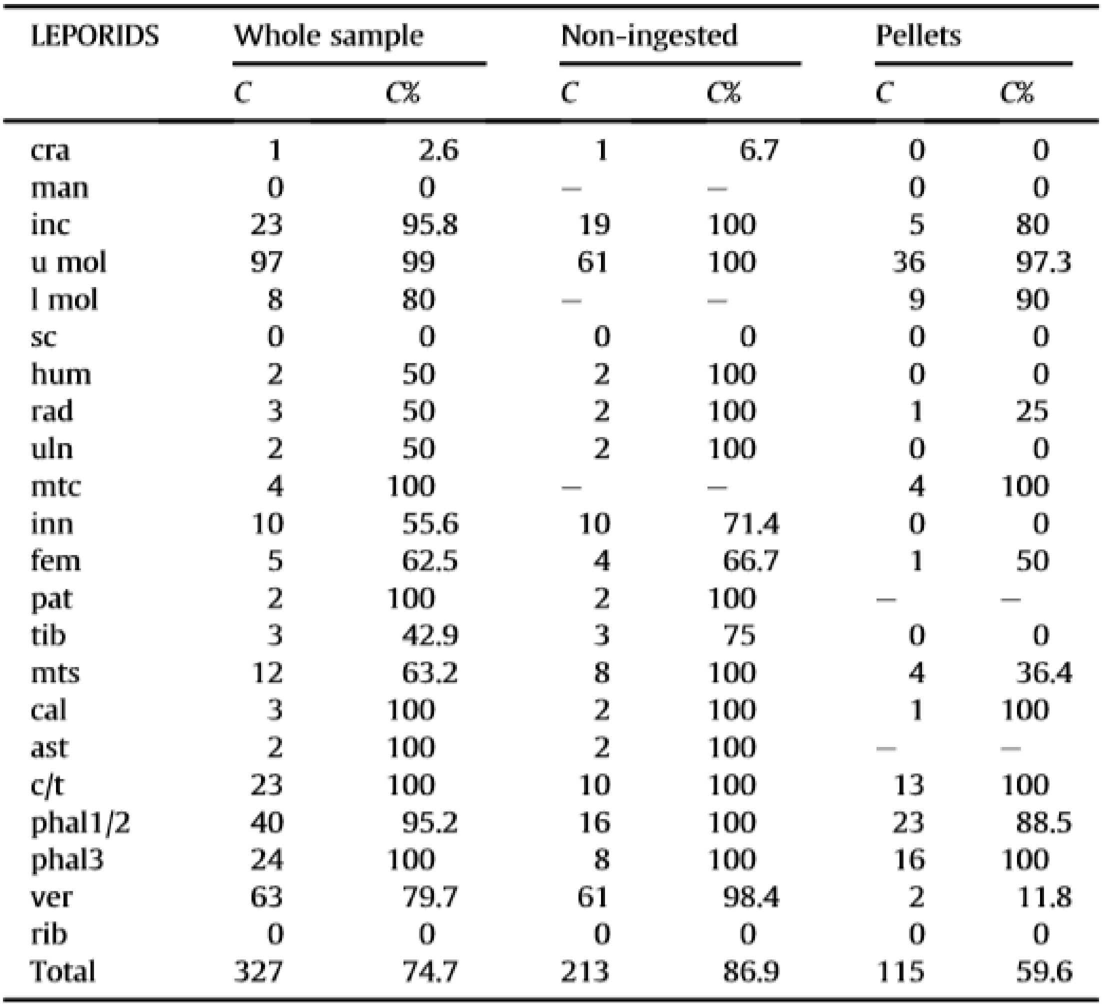
The size of leporid bone fragments ranges between 1.7 and 89.6mm; the average maximum length was 19,7mm and 54.9% of the rabbit remains had length values under 10 mm. The percentage of complete elements was 74.7%. Values vary ac- cording to bone size, with the highest percentages obtained for the smallest bones: carpals/tarsals; patellae; calcanei; astragali; phalanges; and teeth (Table 4). Long bones were complete in 51.7% of cases.

A total of 172 (39.3%) remains within the entire leporid sample were articulated and 63.6% of teeth were recovered in situ.

Table 3 – Proportions of different parts of skeleton for leporids.

INDICES %	LEPORIDS SAMPLE
PCRT/CR	32.1
PCRAP/CR	30.4
PCRLB/CR	48.6
AUT/ZE	57.7
Z/E	80
AN/PO	35.2

Table 4 - Numbers (C) and percentages (C%) of complete skeletal remains of leporids. For abbreviations see the caption for Table 2.



LEPORIDS	Whole sample		Non-ingested		Pellets	
	C	*C%*	*C*	*C%*	*C*	*C%*
cra	1	2.6	1	6.7	0	0
man	0	0	–	–	0	0
inc	23	95.8	19	100	5	80
u mol	97	99	61	100	36	97.3
l mol	8	80	–	–	9	90
sc	0	0	0	0	0	0
hum	2	50	2	100	0	0
rad	3	50	2	100	1	25
uln	2	50	2	100	0	0
mtc	4	100	–	–	4	100
inn	10	55.6	10	71.4	0	0
fem	5	62.5	4	66.7	1	50
pat	2	100	2	100	–	–
tib	3	42.9	3	75	0	0
mts	12	63.2	8	100	4	36.4
cal	3	100	2	100	1	100
ast	2	100	2	100	–	–
c/t	23	100	10	100	13	100
phal1/2	40	95.2	16	100	23	88.5
phal3	24	100	8	100	16	100
ver	63	79.7	61	98.4	2	11.8
rib	0	0	0	0	0	0
Total	327	74.7	213	86.9	115	59.6

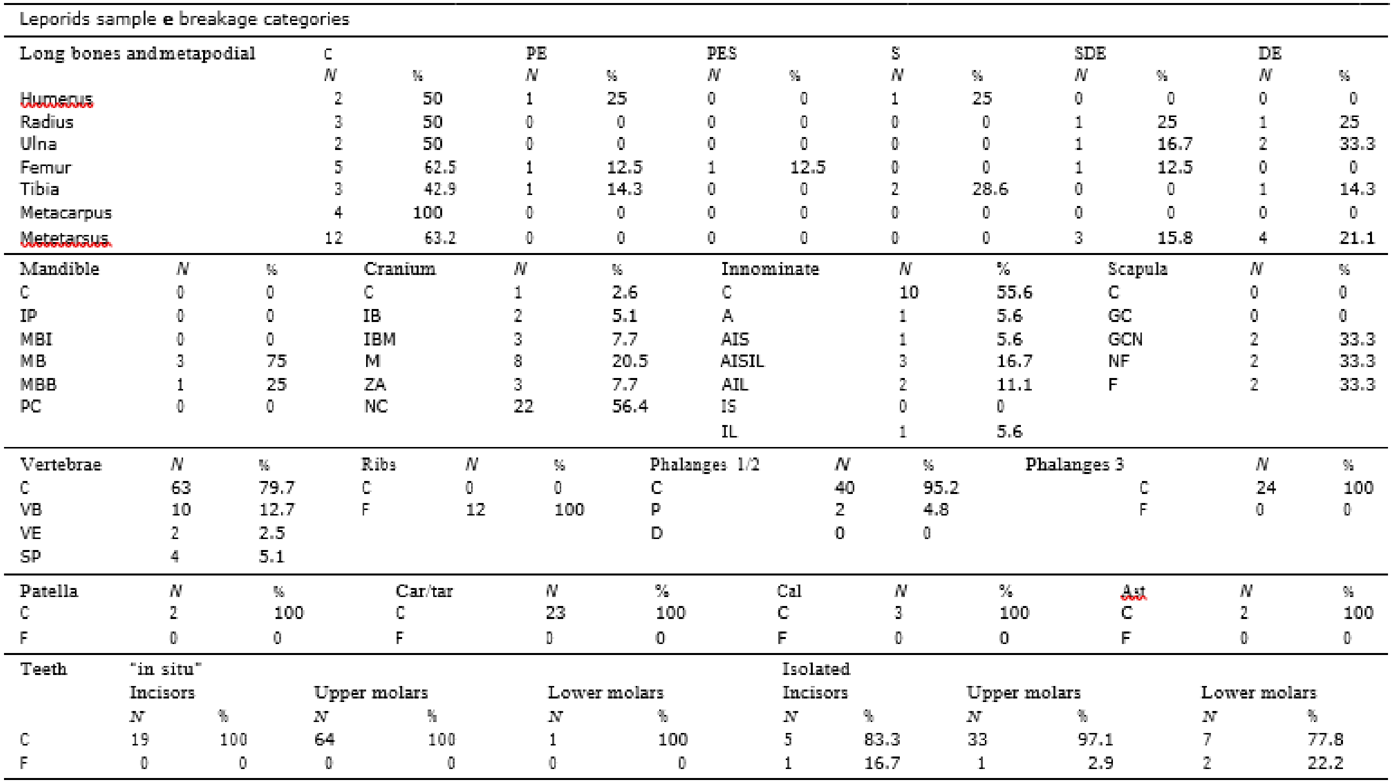
Breakage categories (Table 5) show that:

- crania were complete in only 2.6% of cases and their fragments were mostly identified by parts of the neurocranium (NC) and maxilla (M);
- mandibles were never complete, their fragments were represented by body portions (including MB and MBB);
- teeth located in situ were always complete and isolated teeth were complete in 91.8% of cases;

- vertebrates were complete in 79.7% of cases, their fragments were mainly represented by the vertebral body (VB); there were a few instances of vertebral epiphyses (VE) and spinous processes (SP);
- innominates were complete in 55.6% of cases, fragments were represented by portions containing the acetabulum (AISIL, AIL, AIS);
- scapulae were never complete and most fragments comprised the glenoid cavity (GC, GCN);
- all breakage categories were found on the limb bones, which were mostly complete; the majority of radius and ulna fragments included the distal epiphysis;
- metapodials were well preserved; metacarpals and metatarsals were complete in 100% and 63.2% of cases respectively.

Non-ingested remains were clearly less affected by breakage than bones from pellets. The size of the leporid remains differs noticeably; in the non-ingested remains sample the average maximum length was 43.1 mm and only 6.8% of the rabbit remains had length values under 10 mm, whereas those in the pellets had an average maximum length of 8.3 mm and 78.1% of remains had length values under 10 mm. The percentage of complete elements was also distinct: 86.9% in non-ingested remains compared with 59.6% in pellets. Differences were mostly concentrated in large skeletal elements (Table 4) such as: long bones (88.3% vs 15%); in- nominates (55.6% vs 0%); and metatarsi (100% vs 36.4%).

Table 5 - Numbers and percentages of parts of the skeleton included in each breakage category for leporids. Long bones, metacarpal and metatarsal bones were classified as: complete (C); proximal epiphysis (PE); proximal epiphysis þ shaft (PES); shaft (S); shaft þ distal epiphysis (SDE); and distal epiphysis (DE). Mandible as: complete (C); incisive part (IP); mandible body þ incisive part (MBI); mandible body (MB); mandible body þ branch (MBB); and condylar process (CP). Cranium as: complete (C); incisive bone (IB); incisive bone þ maxilla (IBM); maxilla (M); zygomatic arch (ZA); and neurocranium (NC). Innominate as: complete (C); acetabulum (A); acetabulum þ ischium (AIS); acetabulum þ ischium þ ilium (AISIL); acetabulum þ ilium (AIL); ischium (IS); and illium (IL). Scapula as: complete (C); glenoid cavity (GC); glenoid cavity þ neck (GCN); neck þ fossa (NF); and fossa (F). Vertebrae as: complete (C); vertebral body (VB); vertebral epiphysis (VE); and spinous process (SP). Phalanges as: complete (C); proximal fragment (P); distal fragment (D); and fragment (F). Patella, carpal/tarsal, calcaneum, astragalus, ribs and teeth as: complete (C); and fragment (F).



Leporids sample e breakage categories

Long bones andmetapodial	C		PE		PES		S		SDE		DE	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Humerus	2	50	1	25	0	0	1	25	0	0	0	0
Radius	3	50	0	0	0	0	0	0	1	25	1	25
Ulna	2	50	0	0	0	0	0	0	1	16.7	2	33.3
Femur	5	62.5	1	12.5	1	12.5	0	0	1	12.5	0	0
Tibia	3	42.9	1	14.3	0	0	2	28.6	0	0	1	14.3
Metacarpus	4	100	0	0	0	0	0	0	0	0	0	0
Metetarsus	12	63.2	0	0	0	0	0	0	3	15.8	4	21.1

Mandible	*N*	%	Cranium	*N*	%	Innominate	*N*	%	Scapula	*N*	%
C	0	0	C	1	2.6	C	10	55.6	C	0	0
IP	0	0	IB	2	5.1	A	1	5.6	GC	0	0
MBI	0	0	IBM	3	7.7	AIS	1	5.6	GCN	2	33.3
MB	3	75	M	8	20.5	AISIL	3	16.7	NF	2	33.3
MBB	1	25	ZA	3	7.7	AIL	2	11.1	F	2	33.3
PC	0	0	NC	22	56.4	IS	0	0			
						IL	1	5.6			

Vertebrae	*N*	%	Ribs	*N*	%	Phalanges 1/2	*N*	%	Phalanges 3	*N*	%
C	63	79.7	C	0	0	C	40	95.2	C	24	100
VB	10	12.7	F	12	100	P	2	4.8	F	0	0
VE	2	2.5				D	0	0			
SP	4	5.1									

Patella	*N*	%	Car/tar	*N*	%	Cal	*N*	%	Ast	*N*	%
C	2	100	C	23	100	C	3	100	C	2	100
F	0	0	F	0	0	F	0	0	F	0	0

Teeth	"in situ"						Isolated					
	Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	19	100	64	100	1	100	5	83.3	33	97.1	7	77.8
F	0	0	0	0	0	0	1	16.7	1	2.9	2	22.2

3.3.1.3. Digestion and beak/talon marks

Digestion damage was present in 31.2% of the overall leporid sample (Fig. 5). Different degrees of digestion damage were observed on the surface of rabbit remains; specifically, 2.3% of the skeletal elements were altered by a light degree, 7.9% by a moderate degree, 14.4% by a heavy degree and 6.5% by an extreme degree of corrosion.

No digested remains were recovered in the non-ingested sample. Considering the pellet sample, the percentage of remains affected by digestion was considerably higher (72%). In this sample, the percentage of elements included in each degree of digestion damage was: 5.4% light, 18.3% moderate, 33.3% heavy and 15.1% extreme (Fig. 6 and Table 6). Different skeletal elements were altered in different proportions: vertebrae, scapulae, skull remains, humerus and tibia were more corroded than the remains of auto- podia (carpals/tarsals, metapodials and phalanges) (Table 6). Whole surfaces of bones were often affected by digestive corrosion, the most altered areas were fractured or articular surfaces. A high proportion of teeth (92%) were corroded (Table 6).

Beak marks were observed on ten specimens (2.3% of the sample); all occurred on non-ingested remains (4.1% of the sample) and were mostly situated on the innominates (5) and scapulae (2), although crania (1), vertebrae (1) and femora (1) were also affected. The most common form of damage was crenulated edges (36.4%), followed by notches (27.3%), punctures (18.2%), pits (9.1%) and fractured edges (9.1%) (Fig. 5). Pits and punctures were always isolated and limited to a single surface (i.e. not opposed). Some of the recorded marks may have been inflicted by talons, however, there are no reliable criteria by which these might be separated.

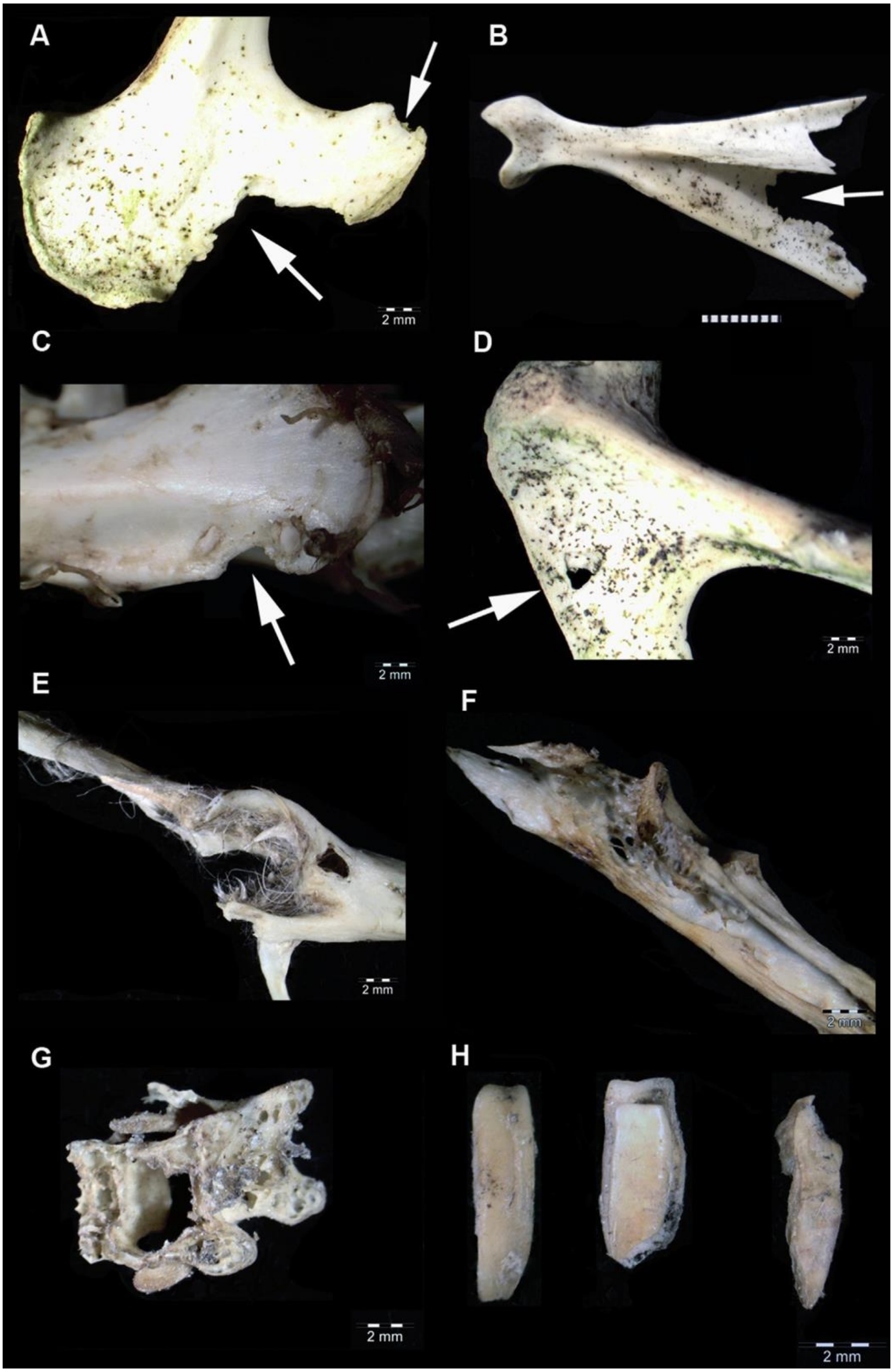


Figure 5 - Examples of leporid bones and teeth displaying beak marks (A - D) and digestion damage with extensive corrosion (E ¼ 4, F ¼ 3, G ¼ 4 and H ¼ 3) caused by Bonelli's eagles.

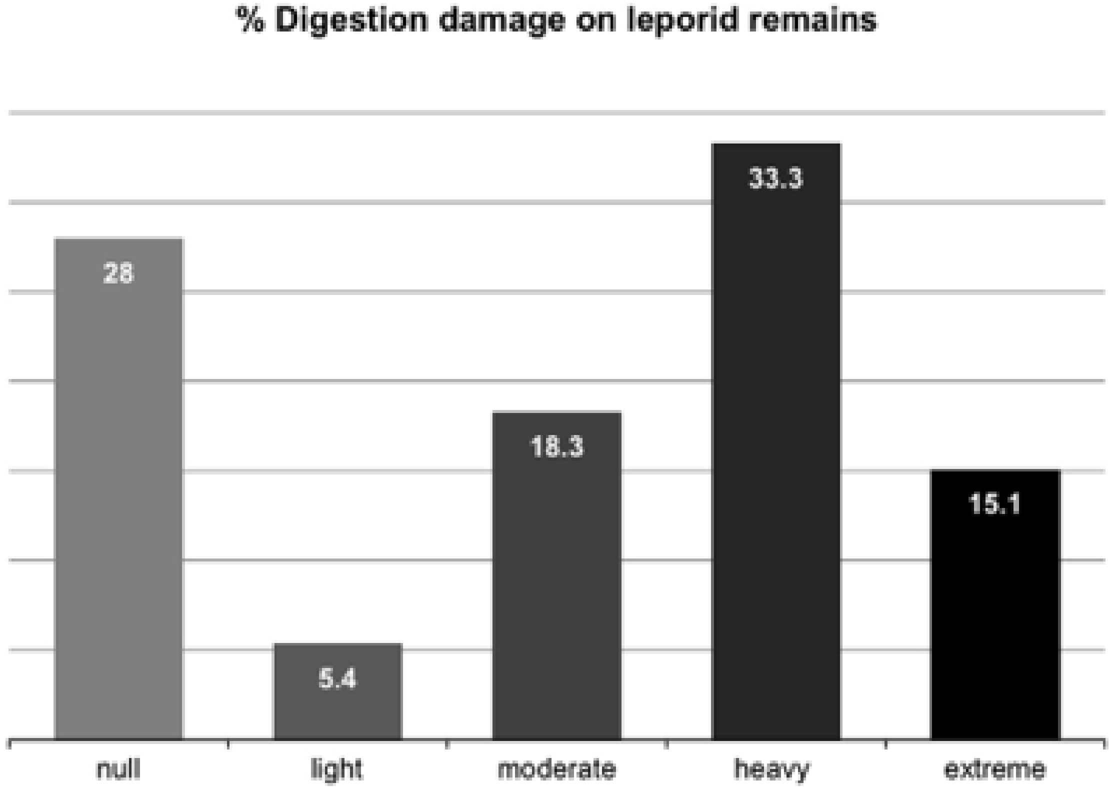
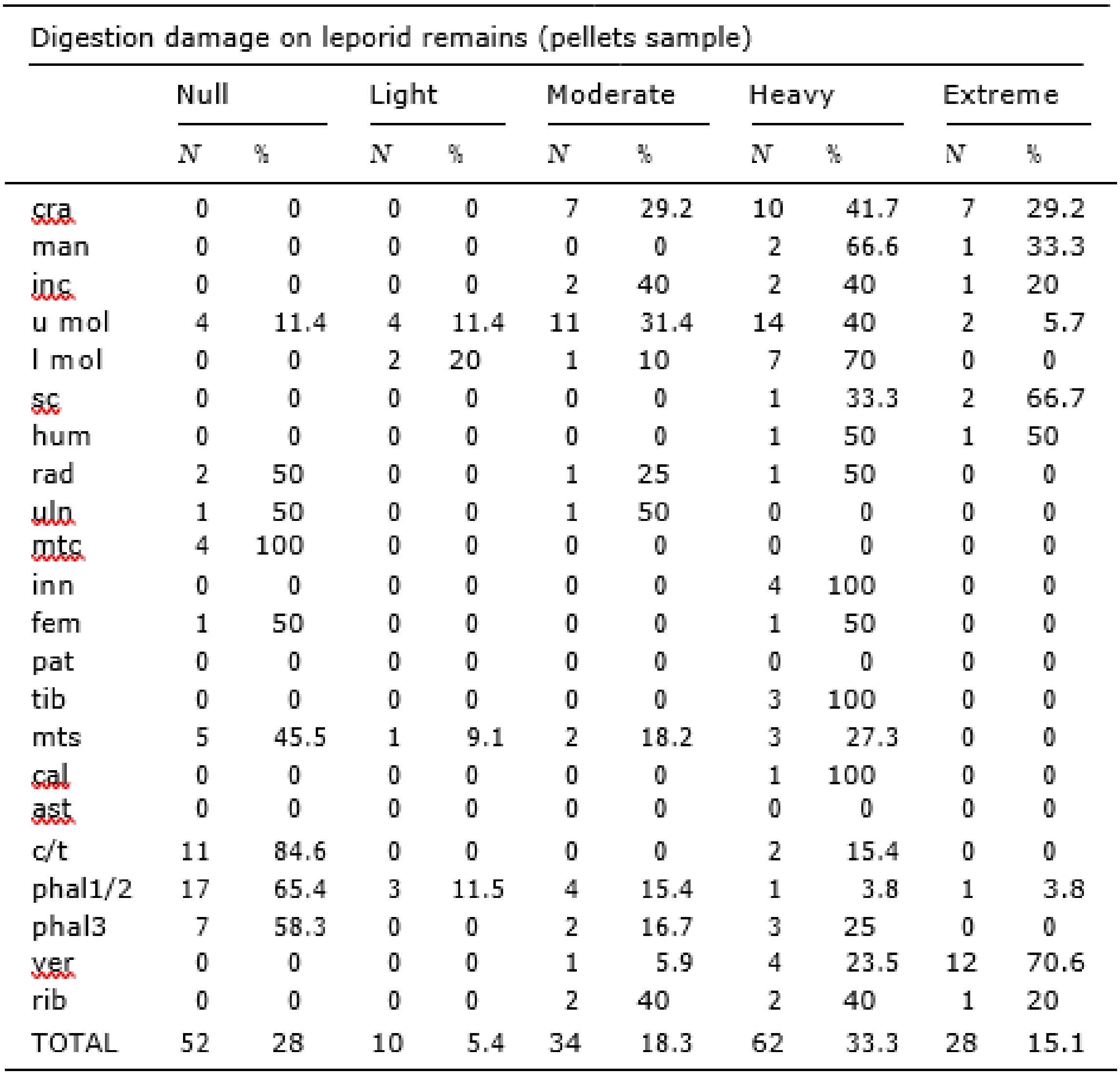


Figure 6 - Percentage of leporid remains from the pellets sample included in each digestion category.

Table 6 - Numbers and percentage of leporid bones and teeth included in each digestion category. For abbreviations see the caption for Table 2. The number of bones considered was 186, a total of 7 bones from pellets were not used because surface damage could not be observed, therefore no digestion corrosion category could be attributed.



Digestion damage on leporid remains (pellets sample)

	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
cra	0	0	0	0	7	29.2	10	41.7	7	29.2
man	0	0	0	0	0	0	2	66.6	1	33.3
inc	0	0	0	0	2	40	2	40	1	20
u mol	4	11.4	4	11.4	11	31.4	14	40	2	5.7
l mol	0	0	2	20	1	10	7	70	0	0
sc	0	0	0	0	0	0	1	33.3	2	66.7
hum	0	0	0	0	0	0	1	50	1	50
rad	2	50	0	0	1	25	1	50	0	0
uln	1	50	0	0	1	50	0	0	0	0
mtc	4	100	0	0	0	0	0	0	0	0
inn	0	0	0	0	0	0	4	100	0	0
fem	1	50	0	0	0	0	1	50	0	0
pat	0	0	0	0	0	0	0	0	0	0
tib	0	0	0	0	0	0	3	100	0	0
mts	5	45.5	1	9.1	2	18.2	3	27.3	0	0
cal	0	0	0	0	0	0	1	100	0	0
ast	0	0	0	0	0	0	0	0	0	0
c/t	11	84.6	0	0	0	0	2	15.4	0	0
phal1/2	17	65.4	3	11.5	4	15.4	1	3.8	1	3.8
phal3	7	58.3	0	0	2	16.7	3	25	0	0
ver	0	0	0	0	1	5.9	4	23.5	12	70.6
rib	0	0	0	0	2	40	2	40	1	20
TOTAL	52	28	10	5.4	34	18.3	62	33.3	28	15.1

3.3.2 Birds

The total number of recovered bird remains was 385, of which 57 came from non-ingested remains and 328 were from pellets.

3.3.1.1. Anatomical representation

All parts of the avian skeleton were recovered (Table 7). Phalanges (36.9%) showed the highest values. Vertebrae (7%), crania (6.2%), tarsometatarsi (4.9%), tibiotarsi (4.4%) and scapulae (4.2%) were also common. Relative abundance varied by skeletal element (Table 7, Fig. 7): fragments of the trunk (sternum and pelvis) were the best represented (100% and 91.7% respectively) followed by cranial remains (75%). Pectoral arch (scapula, coracoid and clavicle), wing and leg bones were also well represented: most displayed values over 50% (Table 7, Fig. 7). Vertebrae and ribs showed the lowest percentages (6.9% and 3.1% respectively).

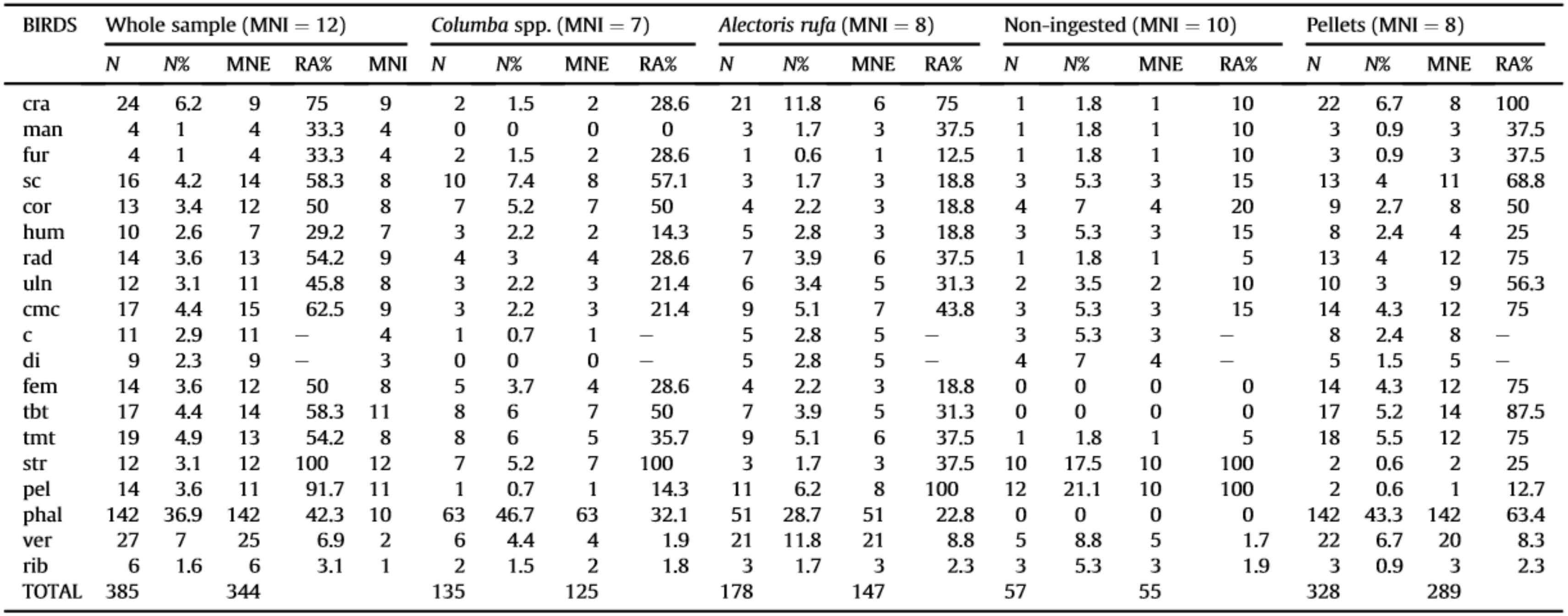
Relative abundance was calculated separately for Columba spp. and red-legged partridge because these were the best represented taxa. Results show that anatomical representation is similar in both taxa; however, the pelves and crania were the most frequent elements for red-legged partridge whereas sterna and scapulae dominated the Columba spp. assemblage (Table 7, Fig. 7). Differences in the relative abundance of both taxa were statistically significant (χ^2 = 213.4, P < 0.01, df =16).

Wing bones account for 45.8% of the sum of wing and leg bones evidencing a slightly higher representation of leg bones. The deviation from the expected 50% (1:1 proportion) is not statistically significant (Z = 0.53, p > 0.05). The ratio of proximal to distal portions was almost equal (53.2%). Deviation from the expected percentage (50%) is not statistically significant (Z - 0.05, p > 0.05). The ratio of the core to limb elements was 36.6%, the predominance of limb elements is highly statistically significant (Z = 2.54, p < 0.01).

Separate analysis of the sample by origin (non-ingested vs pellets) reveals that sterna and pelves were the most common elements in the non-ingested sample, with poor representation or absence of other elements. In contrast, crania, pectoral arch and most wing and leg bones (including phalanges) were abundant in pellets and sterna and pelves were rare, demonstrating that Bonelli's eagles do not normally ingest these skeletal elements. Vertebrae and ribs were very scarce indicating almost total loss of these elements (Table 7, Fig. 7). Differences in anatomical representation in both samples were statistically highly significant (χ^2 = 424.8, P < 0.01, df 12).

The ratio of wing to leg elements varied in both samples (88.9% in non-ingested and 39.7% in pellets) indicating that leg bones were very scarce in non-ingested remains. The ratio of proximal to distal bones did not show great differences (58.8% and 46.4%), but the ratio of the core to limb elements (65.9% and 22.7%) pointed to a major presence of core elements in the non-ingested remains sample. Differences in survivorship of particular skeletal elements in both types of samples are statistically significant (χ^2 = 8.43, P = 0.014, df = 2).

Table 7 – Bird skeletal elements recovered from Bonelli's Eagle nests. Key: N = number of skeletal elements; N% = percentage of skeletal elements; MNE = minimum number of elements; MNI = minimum number of individuals; RA% = relative abundance. Abbreviations: cra - cranium; man - mandible; fur - furcula; sc - scapula; cor - coracoid; hum - humerus; rad - radius; uln - ulna; cmc - carpometacarpus; c - carpal (carpi radial, carpi ulnare); di - wing digit; fem - femur; tbt - tibiotarsus; tmt - tarsometatarsus; str - sternum; pel - pelvis; phal - leg phalanges; ver - vertebrae; rib - rib.



BIRDS	Whole sample (MNI = 12)					*Columba* spp. (MNI = 7)				*Alectoris rufa* (MNI = 8)				Non-ingested (MNI = 10)				Pellets (MNI = 8)			
	N	*N%*	MNE	RA%	MNI	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%	*N*	*N%*	MNE	RA%
cra	24	6.2	9	75	9	2	1.5	2	28.6	21	11.8	6	75	1	1.8	1	10	22	6.7	8	100
man	4	1	4	33.3	4	0	0	0	0	3	1.7	3	37.5	1	1.8	1	10	3	0.9	3	37.5
fur	4	1	4	33.3	4	2	1.5	2	28.6	1	0.6	1	12.5	1	1.8	1	10	3	0.9	3	37.5
sc	16	4.2	14	58.3	8	10	7.4	8	57.1	3	1.7	3	18.8	3	5.3	3	15	13	4	11	68.8
cor	13	3.4	12	50	8	7	5.2	7	50	4	2.2	3	18.8	4	7	4	20	9	2.7	8	50
hum	10	2.6	7	29.2	7	3	2.2	2	14.3	5	2.8	3	18.8	3	5.3	3	15	8	2.4	4	25
rad	14	3.6	13	54.2	9	4	3	4	28.6	7	3.9	6	37.5	1	1.8	1	5	13	4	12	75
uln	12	3.1	11	45.8	8	3	2.2	3	21.4	6	3.4	5	31.3	2	3.5	2	10	10	3	9	56.3
cmc	17	4.4	15	62.5	9	3	2.2	3	21.4	9	5.1	7	43.8	3	5.3	3	15	14	4.3	12	75
c	11	2.9	11	–	4	1	0.7	1	–	5	2.8	5	–	3	5.3	3	–	8	2.4	8	–
di	9	2.3	9	–	3	0	0	0	–	5	2.8	5	–	4	7	4	–	5	1.5	5	–
fem	14	3.6	12	50	8	5	3.7	4	28.6	4	2.2	3	18.8	0	0	0	0	14	4.3	12	75
tbt	17	4.4	14	58.3	11	8	6	7	50	7	3.9	5	31.3	0	0	0	0	17	5.2	14	87.5
tmt	19	4.9	13	54.2	8	8	6	5	35.7	9	5.1	6	37.5	1	1.8	1	5	18	5.5	12	75
str	12	3.1	12	100	12	7	5.2	7	100	3	1.7	3	37.5	10	17.5	10	100	2	0.6	2	25
pel	14	3.6	11	91.7	11	1	0.7	1	14.3	11	6.2	8	100	12	21.1	10	100	2	0.6	1	12.7
phal	142	36.9	142	42.3	10	63	46.7	63	32.1	51	28.7	51	22.8	0	0	0	0	142	43.3	142	63.4
ver	27	7	25	6.9	2	6	4.4	4	1.9	21	11.8	21	8.8	5	8.8	5	1.7	22	6.7	20	8.3
rib	6	1.6	6	3.1	1	2	1.5	2	1.8	3	1.7	3	2.3	3	5.3	3	1.9	3	0.9	3	2.3
TOTAL	385		344			135		125		178		147		57		55		328		289	

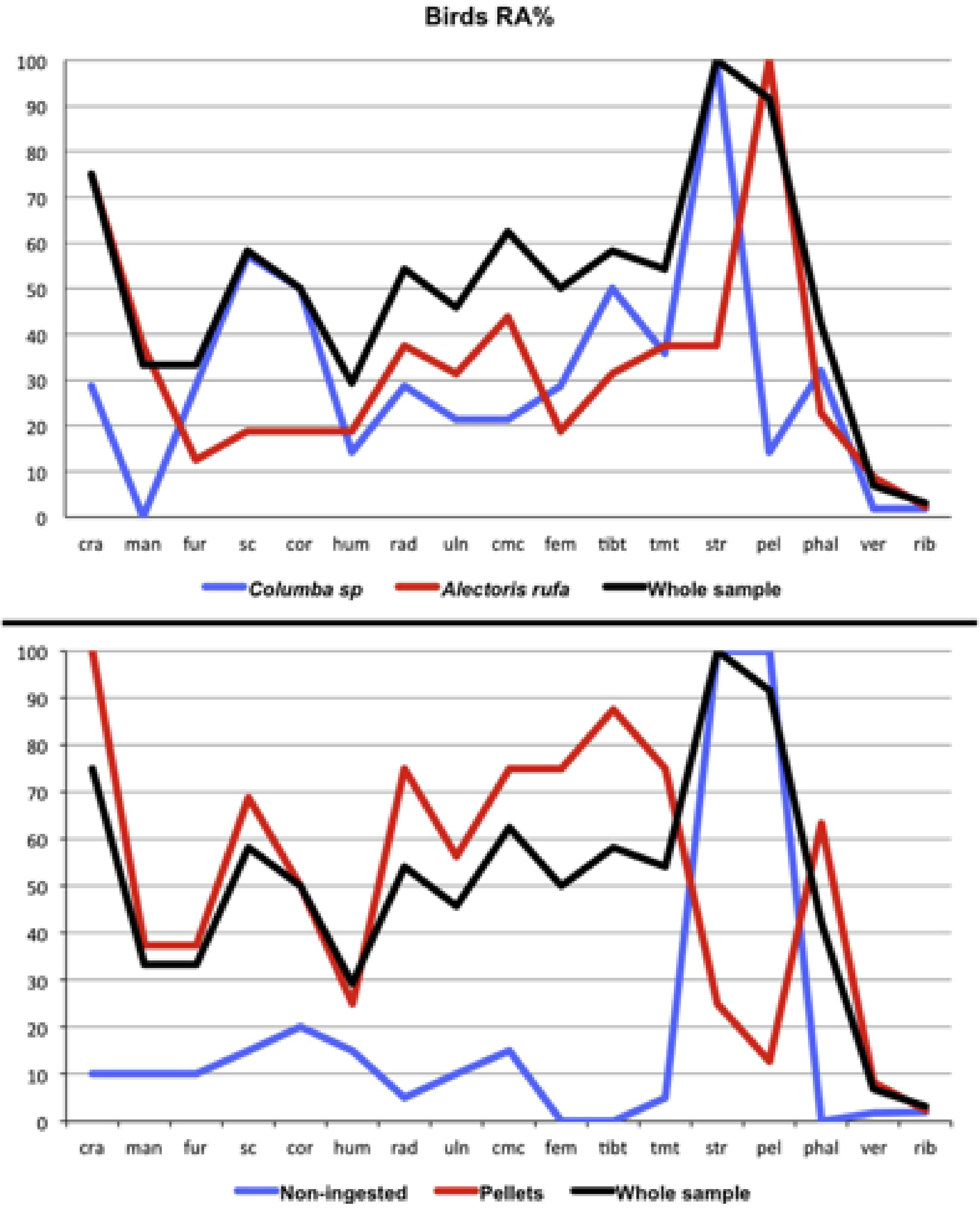


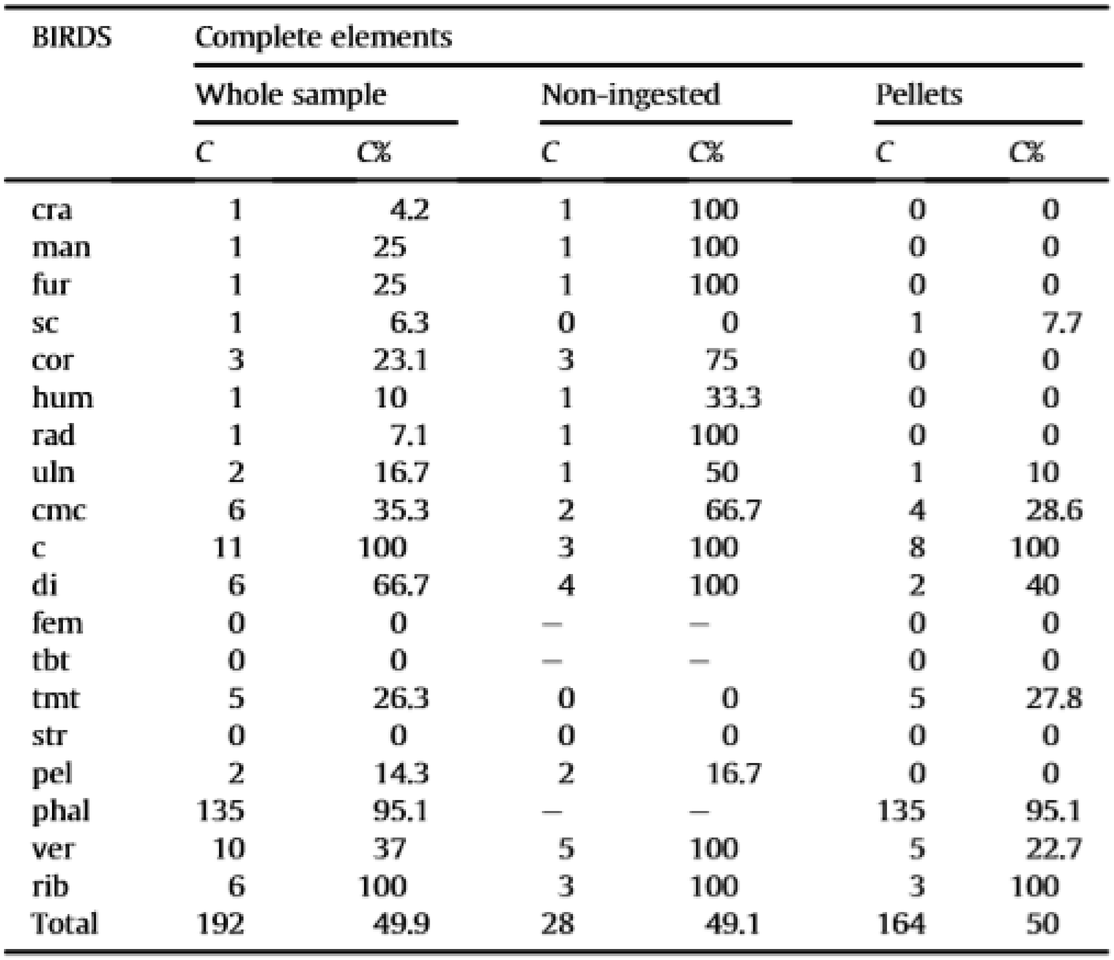
Figure 7 - Relative abundance of different parts of the skeleton in the bird remains samples. For abbreviations see the caption for Table 7.

3.3.2.2. Breakage

The size of the recovered avian remains ranged between 2.3 mm and 90.4 mm (average maximum length 17.6 mm) and 35.4% of bones had length values under 10 mm.

The degree of fragmentation was moderate; on average 49.9% of the elements were complete, with the small bones such as carpals, ribs and phalanges being the least fragmented (Table 8). The tarsometatarsi and coracoids were the best preserved (26.3% and 23.1% respectively) limb/core bones, whereas the femur and tibiotarsus were never complete.

Table 8 - Numbers (C) and percentages (C%) of complete skeletal remains of birds. For abbreviations see the caption for Table 7.



BIRDS	Complete elements					
	Whole sample		Non-ingested		Pellets	
	C	C%	C	C%	C	C%
cra	1	4.2	1	100	0	0
man	1	25	1	100	0	0
fur	1	25	1	100	0	0
sc	1	6.3	0	0	1	7.7
cor	3	23.1	3	75	0	0
hum	1	10	1	33.3	0	0
rad	1	7.1	1	100	0	0
uln	2	16.7	1	50	1	10
cmc	6	35.3	2	66.7	4	28.6
c	11	100	3	100	8	100
di	6	66.7	4	100	2	40
fem	0	0	–	–	0	0
tbt	0	0	–	–	0	0
tmt	5	26.3	0	0	5	27.8
str	0	0	0	0	0	0
pel	2	14.3	2	16.7	0	0
phal	135	95.1	–	–	135	95.1
ver	10	37	5	100	5	22.7
rib	6	100	3	100	3	100
Total	192	49.9	28	49.1	164	50

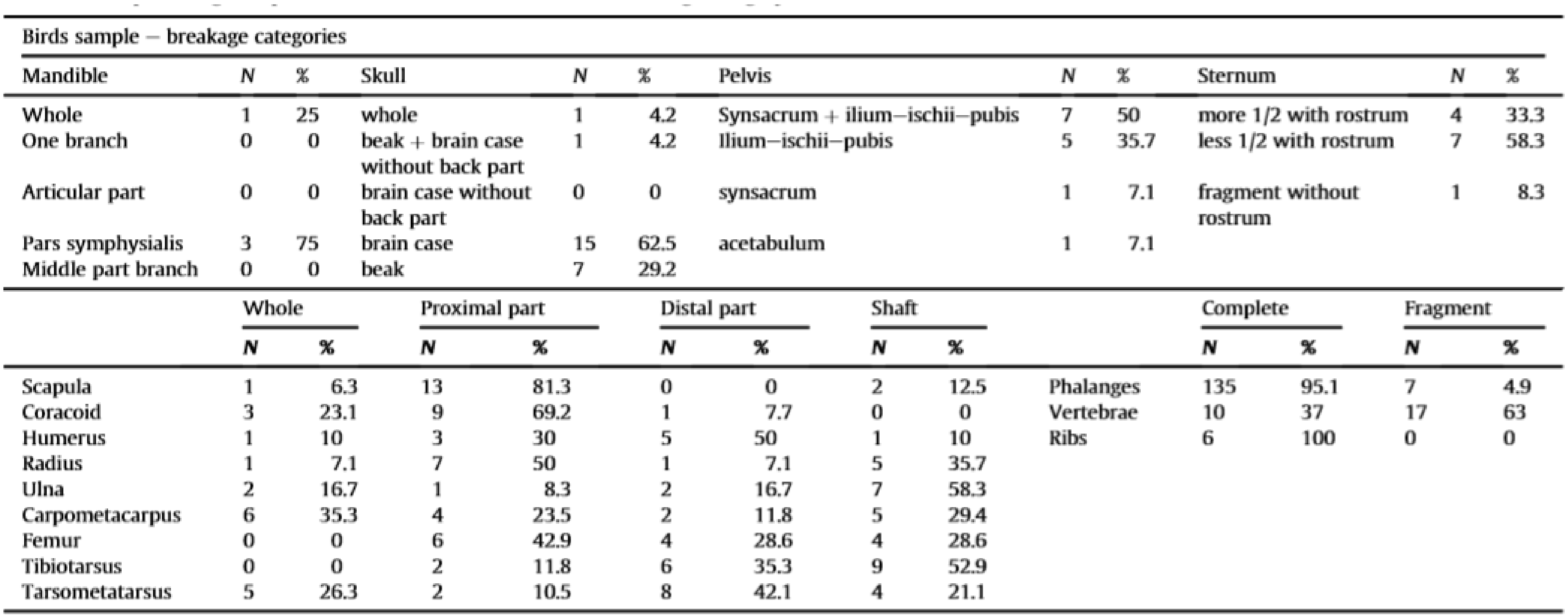
A notable number of skeletal remains was articulated (N = 148, 38.4%); most being leg bones (tarsometatarsi and phalanges, 55.4%).

Breakage categories (Table 9) show that:

- all breakage categories occurred on long bones, scapulae and coracoids; few bones were complete (14.4%), but proximal and distal ends and shaft (with missing articular ends) were well represented (35.6%, 22% and 28% respectively);
- most scapula, coracoid, radius and femur fragments were proximal ends; the best represented fragments of humeri and tarsometatarsi were distal ends; the tibiotarsi and ulnae were mostly shaft fragments and most carpometacarpi were complete;
- skulls were generally represented by brain case and beak fragments;
- most mandibles were represented by fragments of pars symphysialis;
- most pelves fragments included the synsacrum and iliumeischiumepubis bones (50%), fragments of ilium-ischium- pubis bones were also abundant (35.7%);
- a high percentage of sternae fragments included the rostrum (91.6%), but most were less than half complete (58.3%).

Non-ingested remains were less affected by breakage than those from pellets. The average maximum length of uneaten remains was 43.9 mm and all bones were over 10 mm in length; the average maximum length in the pellets sample was 14.9 mm and 40.1% of remains had length values under 10 mm. The percentage of complete elements was very similar in both samples (around 50%, Table 8) because of the presence of high numbers of small elements (phalanges, carpals) in the pellets sample, which were normally complete. When long bones are considered in isolation, the per- centage of complete elements decreases to 47.1% (in non-ingested remains) and 9.5% (in pellets).

Table 9 - Numbers and percentages of parts of the skeleton included in each breakage category for birds.



Birds sample – breakage categories

Mandible	*N*	%	Skull	*N*	%	Pelvis	*N*	%	Sternum	*N*	%
Whole	1	25	whole	1	4.2	Synsacrum + ilium–ischii–pubis	7	50	more 1/2 with rostrum	4	33.3
One branch	0	0	beak + brain case without back part	1	4.2	Ilium–ischii–pubis	5	35.7	less 1/2 with rostrum	7	58.3
Articular part	0	0	brain case without back part	0	0	synsacrum	1	7.1	fragment without rostrum	1	8.3
Pars symphysialis	3	75	brain case	15	62.5	acetabulum	1	7.1			
Middle part branch	0	0	beak	7	29.2						

	Whole		Proximal part		Distal part		Shaft			Complete		Fragment	
	N	%	*N*	%	*N*	%	*N*	%		*N*	%	*N*	%
Scapula	1	6.3	13	81.3	0	0	2	12.5	Phalanges	135	95.1	7	4.9
Coracoid	3	23.1	9	69.2	1	7.7	0	0	Vertebrae	10	37	17	63
Humerus	1	10	3	30	5	50	1	10	Ribs	6	100	0	0
Radius	1	7.1	7	50	1	7.1	5	35.7					
Ulna	2	16.7	1	8.3	2	16.7	7	58.3					
Carpometacarpus	6	35.3	4	23.5	2	11.8	5	29.4					
Femur	0	0	6	42.9	4	28.6	4	28.6					
Tibiotarsus	0	0	2	11.8	6	35.3	9	52.9					
Tarsometatarsus	5	26.3	2	10.5	8	42.1	4	21.1					

3.3.2.3 Digestion and beak/talon marks

Digestion corrosion was evident in 60.4% of the whole bird sample (Fig. 8). Most bones showed heavy corrosion (30.8%) whereas it was light on only 3.3% of the elements. The percentage of elements recorded as being affected by a moderate and extreme degree was 14.8% and 11.5% respectively.

Figure 8 - Examples of bird bones displaying beak marks (A = F) and digestion damage with extensive corrosion (G = 3, H = 3, I = 4, J = 4, K = 4, L = 3) produced by the Bonelli's eagle.

No bones exhibiting digestion damaged were recorded in the non-ingested sample. Considering only the pellets sample, the percentage of digested remains was 71.4%. Heavy corrosion (36.4%) predominated, followed by moderate (17.5%) and extreme (13.6%) (Fig. 9 and Table 10).; light digestion was very low (3.9%).

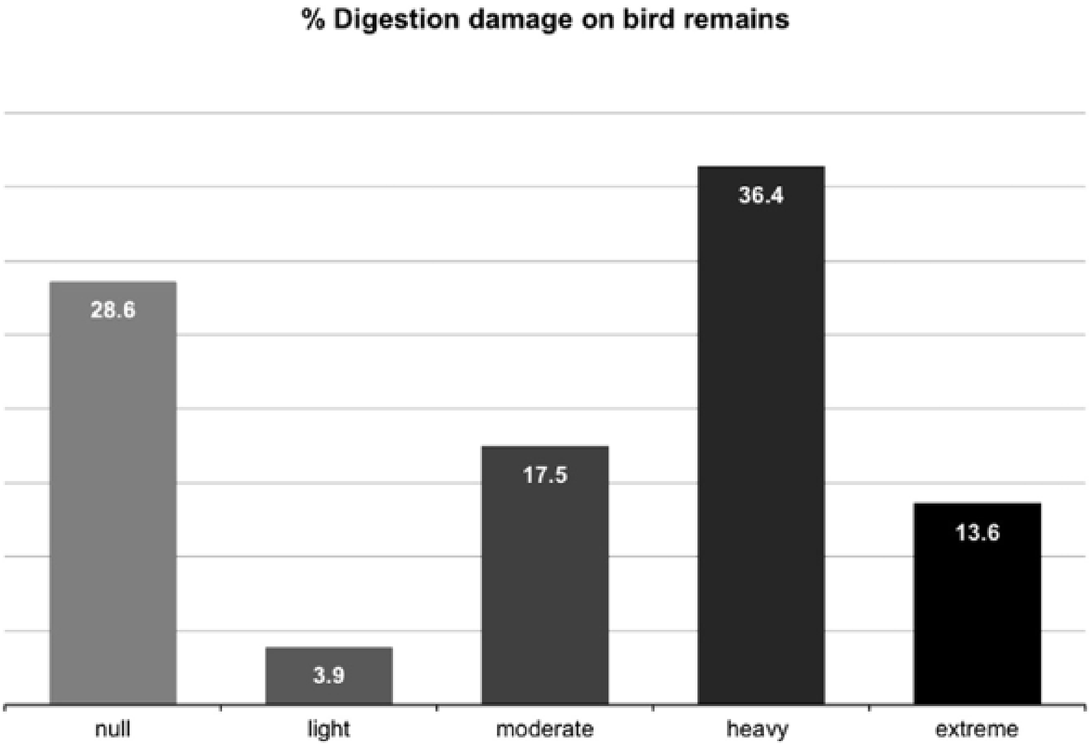
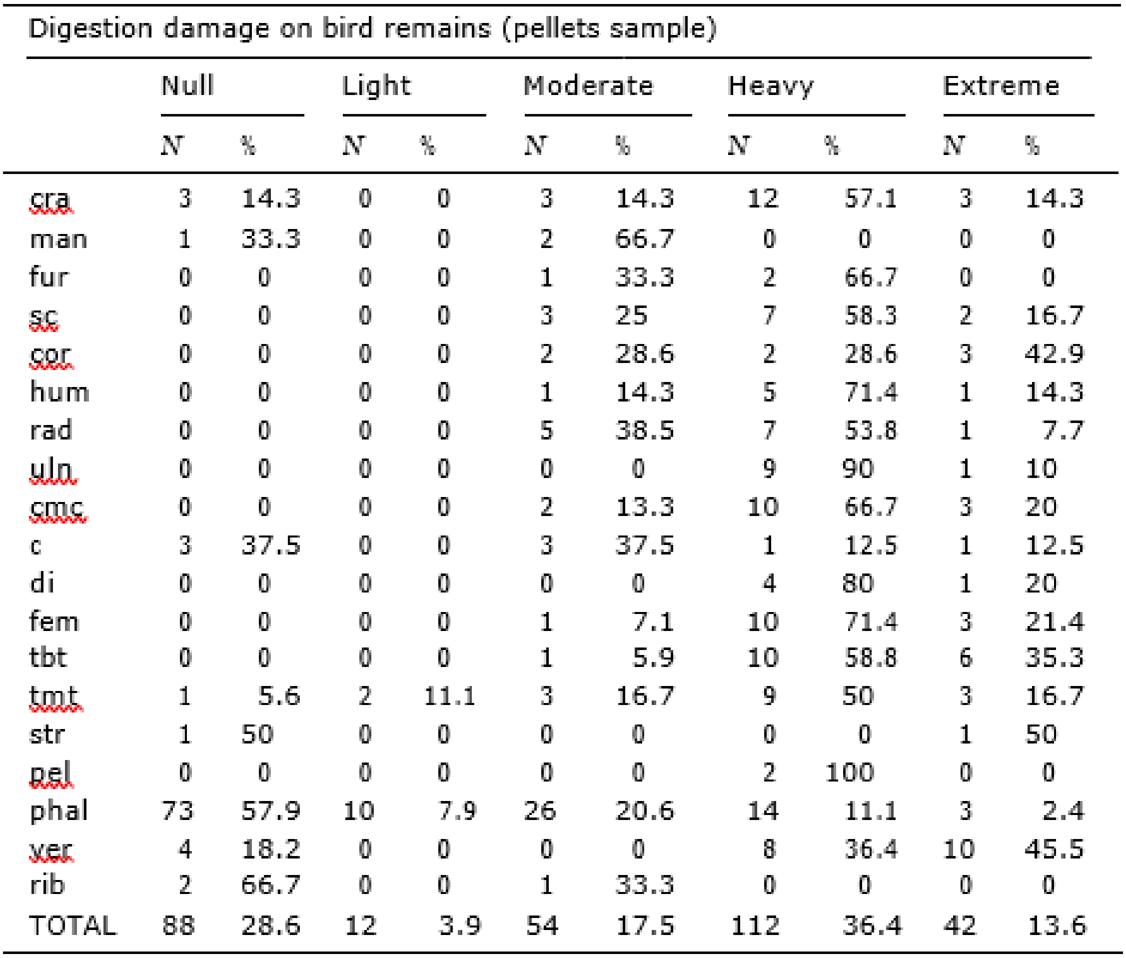


Figure 9 - Percentage of bird remains from the pellets sample included in each digestion category.

Table 10 - Numbers and percentage of bird bones included in each digestion category. For abbreviations see the caption for Table 7. The number of bones considered was 308, a total of 20 bones from pellets were not used because surface damage could not be observed, therefore no digestion corrosion category could be attributed.



Digestion damage on bird remains (pellets sample)

	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
cra	3	14.3	0	0	3	14.3	12	57.1	3	14.3
man	1	33.3	0	0	2	66.7	0	0	0	0
fur	0	0	0	0	1	33.3	2	66.7	0	0
sc	0	0	0	0	3	25	7	58.3	2	16.7
cor	0	0	0	0	2	28.6	2	28.6	3	42.9
hum	0	0	0	0	1	14.3	5	71.4	1	14.3
rad	0	0	0	0	5	38.5	7	53.8	1	7.7
uln	0	0	0	0	0	0	9	90	1	10
cmc	0	0	0	0	2	13.3	10	66.7	3	20
c	3	37.5	0	0	3	37.5	1	12.5	1	12.5
di	0	0	0	0	0	0	4	80	1	20
fem	0	0	0	0	1	7.1	10	71.4	3	21.4
tbt	0	0	0	0	1	5.9	10	58.8	6	35.3
tmt	1	5.6	2	11.1	3	16.7	9	50	3	16.7
str	1	50	0	0	0	0	0	0	1	50
pel	0	0	0	0	0	0	2	100	0	0
phal	73	57.9	10	7.9	26	20.6	14	11.1	3	2.4
ver	4	18.2	0	0	0	0	8	36.4	10	45.5
rib	2	66.7	0	0	1	33.3	0	0	0	0
TOTAL	88	28.6	12	3.9	54	17.5	112	36.4	42	13.6

Most skeletal remains exhibited substantial damage with long bones, specifically humeri, ulnae, femora and tibiotarsi, exhibiting the highest degree of alteration (Table 10). Phalanges appeared to be less damaged, probably because they were ingested in anatomical connection and protected by the skin of the feet. Sterna and pelves were the least affected by digestion because these skeletal elements do not seem to be ingested regularly by Bonelli's eagles.

Traces left by beaks were observed on 24 bones, 6.2% of the sample (Fig. 8). Most of them occurred on the pelves (10) and sterna (9). The rest were located on crania (1), coracoids (1), scapulae (1), humeri (1) and femora (1). Crenulated edges (41.2%) were the most common form of damage, followed by punctures (32.3%), pits (20.6%) and fractured edges (5.9%). One coracoid and two pelves displayed two simultaneous pit/puncture marks; pits and punctures were isolated in all other specimens and they were always unilateral (not opposed).

Most elements affected by beak marks came from the non- ingested sample (N = 20; 35.1%), marks occurred on only four bone fragments from the pellets (1.2%).

4. Discussion

The prey taxa identified in our samples is characteristic of Bonelli's eagles. In most feeding studies, leporids and birds are the most abundant prey, with European rabbit, red-legged partridge and pigeons playing a major dietary role (Caro et al. 2011; Del Amo et al. 2008; Moleón et al. 2009; Ontiveros et al. 2005; Palma et al. 2006; Resano et al. 2011). Our observations support the reported diet of Bonelli's eagle, which appears to be adapted to the most abundant prey available in each region, with rabbits always predominating in regions where they are present (Moleón et al. 2009).

This variation is evident in the slightly different relative composition of prey in each of our study areas. It is apparent, therefore, that prey diversity must be taken into account when analysing archaeological samples.

Body part representation at the Bonelli's eagle nests varied with taxonomic group or species. Real's (1996) study of prey consumption behaviour at nests of these raptors showed that the lowest weight class prey (red squirrel (*Sciurus vulgaris*), ocellated lizard (*Timon lepidus*), or corvids), were consumed whole in most cases and no remains were left in the nest. In the case of rabbits and pigeons, more than half of the individuals were not completely eaten. However, while rabbit remains were frequently removed from the nest by the eagles, one third of the pigeons were left. This behaviour undoubtedly affects the relative frequencies and anatomical representation of different prey types.

Our study shows that Bonelli's eagles often fragment the bones of their prey, although the degree of fragmentation varies markedly among prey species. The percentage of complete elements and complete long bones was clearly higher for rabbits (74.7% and 51.7%) than for birds (49.9% and 14.4%). Differences between taxa were also found in bone surface alterations. For example, birds were more affected by digestion corrosion than rabbits (60.4% vs 31.2%), which is related to the fact that fewer parts of the rabbit carcass were ingested by Bonelli's eagles. Beak marks were also more common on bird remains (6.2% vs 2.3%). It is manifest that the taphonomic pattern obtained is strongly related to the prey/predator size, to the type of prey and to the feeding behaviour of the predator.

4.1 The taphonomic signature of Bonelli's eagle on leporid remains

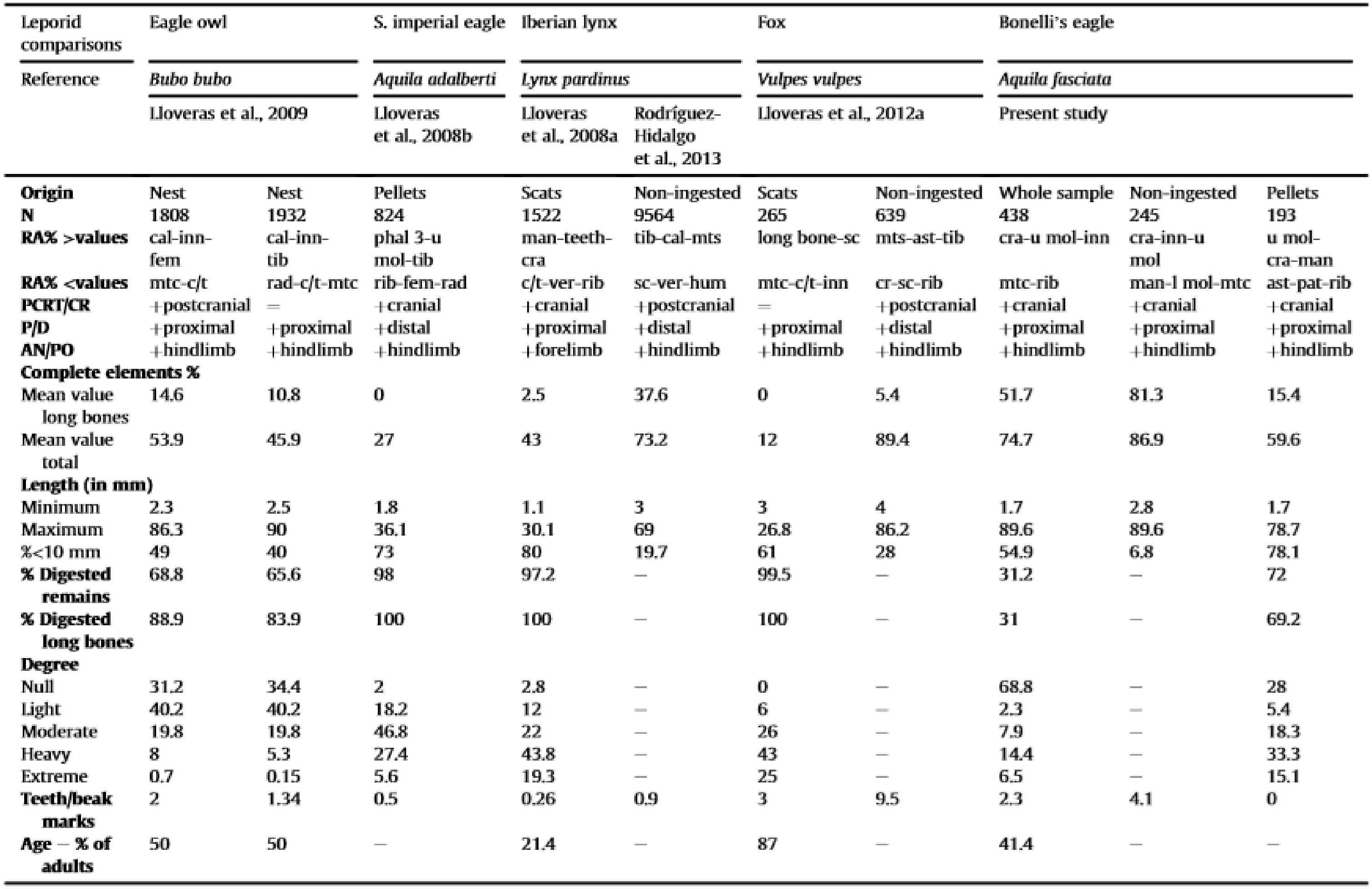
To facilitate comparisons, we present a summary of results obtained from different leporid predators, where the data have been collected using the same methods (Table 11). In relation to the age at death, we found that the majority of rabbits (58.6%) were immature. Palma et al. (2006) in their study of the feeding habits of Bonelli's eagle found that 86.2% of rabbits were adult. This suggests that the percentage of adult individuals can be variable. Lloveras et al. (2012b), observed a similar phenomena in their study of eagle owl prey at nests. The implication is that leporid age may be an insufficiently distinctive character to separate accumulations generated by Bonelli's eagle and potentially other predators as well. The main taphonomic features observed in the leporid sample point to anatomical representation characterized by an abundance of cranial remains and innominates, a low frequency of axial elements and autopodia and a greater presence of hindlimbs relative to forelimbs. While some differences were observed between non- ingested remains and pellets, these traits prevailed in both samples. Comparisons with other diurnal raptors reveal that the taphonomic signature of Bonelli's eagle leporid accumulations is distinctive. Hockett (1995, 1996) and Schmit

(1995) reported that the most common skeletal elements in leporid assemblages accumulated by golden eagles (*Aquila chrysaetos*) were hindlimb bones, specifically tibiae and associated elements (calcanei and astragali) followed by femora. Cranial remains and innominates were also represented in their samples but in lower frequencies. In contrast, femora outnumbered tibiae in the Bonelli's eagle whole sample, whilst calcanei and astragali were rare. Comparison with the taphonomic signature of Spanish imperial eagle (*Aquila adalberti*) pellet samples also shows clear differences. This eagle tends to accumulate large numbers of tibiae, calcanei and phalanges (Lloveras et al. 2008b); all of which were scarce in our Bonelli's eagle pellet sample. Greater differences are found with nocturnal raptors, such as the European eagle owl (*Bubo bubo*), in which the anatomical profile is characterized by high percentages of postcranial remains, specifically long bones, innominates and autopodia (Cochard 2004b; Lloveras et al. 2009; Sanchis 2000). With regards to terrestrial carnivores, both Iberian lynx (*Lynx pardinus*) and red fox (*Vulpes vulpes*) leporid assemblages of non-ingested remains are characterised by low frequencies of cranial remains, with long bones and autopodia much more abundant than in our study (Lloveras et al. 2008a, 2012a; Rodríguez-Hidalgo et al. 2013). The scat accumulations of both carnivores display high percentages of cranial remains; nevertheless long bones are far more abundant than in the Bonelli's eagles samples, especially those of the forelimbs (Lloveras et al. 2008a, 2012a).

As far as breakage patterns are concerned, the percentage of complete elements was surprisingly high in our study. Diurnal raptors have been defined as important bone destroyers compared to owls (Andrews 1990). However, the 74.7% of complete bones recorded in the Bonelli's eagle whole sample is clearly higher than the 38 - 32.3% obtained with golden eagle accumulations (Schmit 1995) and the 53.9 - 45.9% found in European eagle owl nest assemblages (Lloveras et al. 2009). In the pellets sample, the per- centage of complete bones and complete long bones was 59.6% and 15.4%, again higher than the values recorded for Spanish imperial eagles (27% and 0%) or for terrestrial carnivore scat accumulations (Table 11). These results indicate that leporid bones accumulated by Bonelli's eagles are less-fragmented than those generated by other predators. This could be related to the size of the raptor, and more specifically to its beak size. Bonelli's eagle beaks are smaller than those of Spanish imperial eagles, golden eagles and European eagle owls (Cramp & Simmons 1980), and are thus less capable of breaking the bones of large prey, such as rabbits and hares.

The percentage of digested remains in our Bonelli's eagle samples is lower than those recorded for other predators. Values obtained for the pellets sample (72%) are lower than those recorded for Spanish imperial eagle pellets (98%) and for Iberian lynx and fox scat accumulations (97.2% and 99.5%). Even in eagle owl nest ac- cumulations, the percentage of digested remains is higher (Table 11). However, digested remains in our samples were damaged to a very high degree. This clearly distinguishes Bonelli's eagles from European eagle owls, which are characterised by high percentages of light corrosion. Digesting damage was also more pronounced than in Spanish imperial eagle pellets, where high percentages of moderate corrosion were recorded. The values for Bonelli's eagles are similar to those of terrestrial carnivores (Fig. 10). The percentage of bones with beak marks is similar to those recorded in European eagle owl nest accumulations but clearly lower than those obtained for other raptors such as the Egyptian vulture (*Neophron percnopterus*), which reached values of 7.5%e 10.4% (Lloveras et al. 2014a; Sanchis Serra et al. 2013). Beak marks were not found in pellet remains, but this type of damage was also rare in other raptors such as Spanish imperial eagles (0.5%, Table 10). Iberian lynx produces much less damage in non-ingested remains (0.9%), while the percentage of tooth damage in red fox leporid accumulations was much higher (9.5%). Nevertheless, the lack of gnawing and location of the puncture marks is not typical of the action of carnivores but of birds of prey (Sanchis Serra et al. 2013).

Table 11 – Anatomical representation, breakage, digestion and teeth/beak marks for leporid remains accumulated by different types of predators compared with the results obtained for Bonelli's eagles in the present study.



Leporid comparisons	Eagle owl		S. imperial eagle	Iberian lynx		Fox		Bonelli's eagle		
Reference	*Bubo bubo*		*Aquila adalberti*	*Lynx pardinus*		*Vulpes vulpes*		*Aquila fasciata*		
	Lloveras et al., 2009		Lloveras et al., 2008b	Lloveras et al., 2008a	Rodríguez-Hidalgo et al., 2013	Lloveras et al., 2012a		Present study		
Origin	Nest	Nest	Pellets	Scats	Non-ingested	Scats	Non-ingested	Whole sample	Non-ingested	Pellets
N	1808	1932	824	1522	9564	265	639	438	245	193
RA% >values	cal-inn-fem	cal-inn-tib	phal 3-u mol-tib	man-teeth-cra	tib-cal-mts	long bone-sc	mts-ast-tib	cra-u mol-inn	cra-inn-u mol	u mol-cra-man
RA% <values	mtc-c/t	rad-c/t-mtc	rib-fem-rad	c/t-ver-rib	sc-ver-hum	mtc-c/t-inn	cr-sc-rib	mtc-rib	man-l mol-mtc	ast-pat-rib
PCRT/CR	+postcranial	=	+cranial	+cranial	+postcranial	=	+postcranial	+cranial	+cranial	+cranial
P/D	+proximal	+proximal	+distal	+proximal	+distal	+proximal	+distal	+proximal	+proximal	+proximal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+forelimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb
Complete elements %										
Mean value long bones	14.6	10.8	0	2.5	37.6	0	5.4	51.7	81.3	15.4
Mean value total	53.9	45.9	27	43	73.2	12	89.4	74.7	86.9	59.6
Length (in mm)										
Minimum	2.3	2.5	1.8	1.1	3	3	4	1.7	2.8	1.7
Maximum	86.3	90	36.1	30.1	69	26.8	86.2	89.6	89.6	78.7
%<10 mm	49	40	73	80	19.7	61	28	54.9	6.8	78.1
% Digested remains	68.8	65.6	98	97.2	–	99.5	–	31.2	–	72
% Digested long bones	88.9	83.9	100	100	–	100	–	31	–	69.2
Degree										
Null	31.2	34.4	2	2.8	–	0	–	68.8	–	28
Light	40.2	40.2	18.2	12	–	6	–	2.3	–	5.4
Moderate	19.8	19.8	46.8	22	–	26	–	7.9	–	18.3
Heavy	8	5.3	27.4	43.8	–	43	–	14.4	–	33.3
Extreme	0.7	0.15	5.6	19.3	–	25	–	6.5	–	15.1
Teeth/beak marks	2	1.34	0.5	0.26	0.9	3	9.5	2.3	4.1	0
Age – % of adults	50	50	–	21.4	–	87	–	41.4	–	–

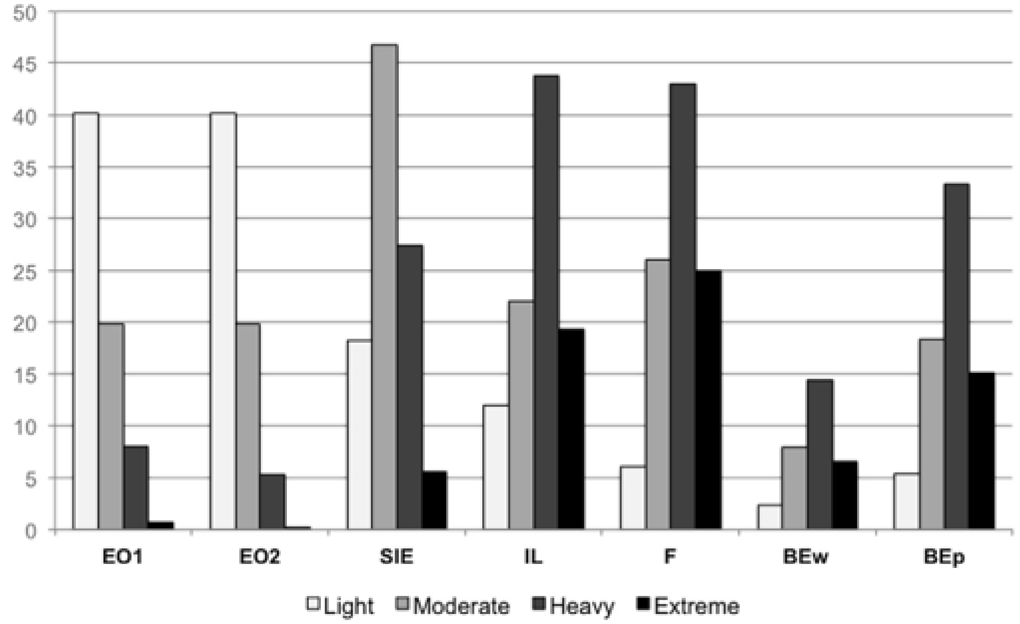


Figure 10. Comparison of percentage of leporid remains included in each digestion category in accumulations produced by eagle owls (EO1 and EO2, Lloveras et al. 2009), Spanish imperial eagle (SIE; Lloveras et al. 2008b), Iberian lynx (IL; Lloveras et al. 2008a), red fox (F; Lloveras et al. 2012a) and Bonelli's eagle whole and pellets sample (BEw, BEp; present study).

In summary, leporid assemblages accumulated by the Bonelli's eagles are characterised by:

- a body part representation with an abundance of cranial remains, upper molars and innominates, very few axial and autopodium elements and a greater abundance of hindlimbs relative to forelimbs;
- a moderate degree of breakage, with high percentages of complete bones;
- a moderate percentage of digested remains but mostly heavy and extreme corrosion;
- a large number of beak/talon marked bones;

Taken separately these features can be shared with other leporid predators, but together they form a distinctive taphonomic signature for Bonelli's eagle.

4.2 The taphonomic signature of Bonelli's eagle on bird remains

Among the bird remains recovered, sterna and pelves were the most abundant elements in the non-ingested sample. The sternum was also the best represented element in non-ingested assemblages from diurnal raptors such as Spanish imperial eagle, golden eagle, gyrfalcon (*Falco rusticolus*), crested caracara (*Caracara plancus*) and Egyptian vulture (Bochenski 2005; Bochenski et al. 1998, 1999, 2009; Lloveras et al. 2014a; Montalvo et al. 2011; Sanchis Serra et al. 2013). In these studies, pelves were also abundant but they do not reach the values we found. Coracoids, scapulae, humeri and carpometacarpi were the best-represented long bones. Coracoids and humeri are the most frequent elements in non-ingested remains of diurnal raptors (Bochenski 2005). In contrast, the tarsometatarsi or crania (or both) are the best-represented bones in pellet assemblages of diurnal and nocturnal raptors (Bochenski 2005; Laroulandie 2002). A similar pattern has been recorded for Bonelli's eagles; however, femora and radii were also abundant in our study whereas in other raptor assemblages they were consistently rare (Bochenski 2005).

Results from the wing/leg ratio indicated a higher abundance of wing elements in non-ingested remains. When comparing these data with other studies (Bochenski 2005; Bochenski et al. 1997, 1999; Laroulandie 2002; Montalvo et al. 2011), it is clear that this is a feature shared with assemblages accumulated by other diurnal raptors. The preponderance of leg bones in the pellet sample has only been recorded for Spanish imperial eagles (Bochenski et al. 1997). The ratio of proximal to distal elements permits the distinction of three groups of avian predators, namely:

(I) pellets of diurnal birds of prey; (II) pellets of owl species and non-ingested remains of some diurnal raptors; and (III) non- ingested remains of golden eagles (Bochenski 2005; Bochenski & Nekrasov 2001). The present material falls into group II, in which proximal elements make up about 60% of the remains (Bochenski et al. 2009). The predominance of limb elements (versus core) observed in pellets has also been recorded for various owls and diurnal birds of prey. The abundance of core elements detected in non-ingested food remains is only shared with golden eagles (Bochenski 2005; Bochenski et al. 1999).

Bonelli's eagles fragment bird bones to a similar extent to other diurnal birds of prey. However, the percentage of complete long bones was 47.1% for uneaten remains, which is comparable with values above 60% reported by Bochenski (2005) for diurnal raptors. This indicates that Bonelli's eagles break their victims' bones somewhat more frequently. In pellets, only 9.5% of long bones were complete. This percentage is consistent with the pattern exhibited in the pellets of diurnal raptors in which less than 30% of complete bones were registered (Bochenski 2005). Particular skeletal ele- ments differ in the degree of fragmentation: scapulae and tibiotarsi are the most affected and carpometacarpi, tarsometatarsi and coracoids are the best preserved. This is a feature related to the physical properties of these skeletal elements and it is common to all predators (Bochenski 2005).

Few data exist on the digestion of bird remains (Bochenski 1997; Bochenski et al. 1998; Laroulandie 2002; Lloveras et al. 2014a; Montalvo et al. 2011). In Bonelli's eagle pellets more than 70% of total remains and practically 100% of long bones were digested. These values are clearly higher than those recorded for the European eagle owl (Laroulandie 2002), Snowy owl (*Bubo scandiacus*) (Bochenski et al. 1997), crested caracara (Montalvo et al. 2011), Egyptian vulture (Lloveras et al. 2014a) and gyrfalcon (Bochenski et al. 1998). Moreover, most remains were digested with a heavy degree of damage (category 3 of damage defined by Bochenski (2005)).

The percentage of remains affected by beak marks was lower for Bonelli's eagle (6.2%) than for Egyptian vulture (28.3%, Lloveras et al. 2014a). The location of most beak marks on pelves (71.4%) and sterna (75%) is replicated on non-ingested assemblages left by other diurnal birds of prey. Bochenski et al. (2009) found punctures on 70% of sterna and 38% of pelves in white-tailed eagle (*Haliaaetus albicilla*) assemblages and punctures were observed on 39% of sterna, 51% of pelves in golden eagles. Our results show that Bonelli's eagles are closer to white-tailed eagles than golden eagles (Bochenski et al.

2009). Coracoids, scapulae, humeri and femora were the most affected long bones in our study. Similar results have also been recorded for other raptors (Bochenski et al. 2009).

In summary, the taphonomic signature observed on bird remains accumulated by Bonelli's eagles is characterised by:

- an abundance of sterna and pelves in non-ingested remains; and crania, pectoral arch and most of the wing and leg bones including phalanges) in pellets;
- a moderate degree of breakage of non-ingested remains, with around 50% complete bones. A high degree of long bone breakage in pellets (less than 10% complete bones);
- a high percentage of digested remains, most of them to a heavy and extreme degree;
- a significant percentage of beak marked bones, most on pelves, sterna and long bones.

Comparisons show clear differences to nocturnal birds of prey. Although many features are shared with other diurnal raptors, especially with Spanish imperial eagles, differences are apparent nevertheless. Some of the differences recorded could relate to different prey species accumulated in the samples analysed. Taphonomic data about avian prey accumulations are still scarce, especially regarding some variables such as digestion damage. Future studies are needed to provide more data that permit a deeper understanding of this variability.

5. Conclusions

This study provides the first detailed taphonomic observations on leporid and bird bones accumulated by Bonelli's eagles. Results from our analysis help to identify and classify the most important characteristics of bones accumulated by this raptor. Where rabbits, partridges and pigeons are abundant, they constitute a very high percentage of their diet. Both, non-ingested elements and bones from pellets are found in nest assemblages.

The observations and results obtained through this study showed that damage caused by Bonelli's eagles on leporids and birds differ sufficiently from other predators. Differences also exist in the character of leporid depending on the origin of the assemblage (i.e. non-ingested remains compared with pellets). The skeletal elements most abundant in non-ingested remains were scarce in the pellets and vice versa. The other taphonomic patterns observed also show divergent results. Non-ingested remains were less fragmented and beak/talons marks were more common, whereas pellet remains were affected by heavy and extreme digestion corrosion.

On archaeological grounds, assemblages of mixed origin are the most likely to be encountered. The criteria presented in this study for mixed samples can reveal the presence of this predator; how- ever, results may vary depending on the relative proportion of re- mains derived from non-ingested accumulations and pellets. The use of the criteria presented in this study together with data on the geographical and biological background (i.e. location of the site and prey species composition of the deposit) can help to assess the potential contribution of Bonelli's eagles in accumulating small prey remains on archaeological sites.

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CHAPTER 3

Habitat selection of the tree-nesting Bonelli's eagle in the South of Portugal

The role of conservative versus innovative nesting behaviour on the 25 - year population expansion of an avian predator

Andreia Dias[1,2], Luís Palma[2], Filipe Carvalho[3,4], Dora Neto[3], Joan Real[1] and Pedro Beja[2,5]

[1] Equip de Biologia de la Conservació, Departament de Biologia Evolutiv, Ecologia i Ciències Ambientals and Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Catalonia, Spain

[2] CIBIO/InBio-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal

[3] CIBIO/InBIO-UE, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade de Évora, Évora, Portugal

[4] Department of Zoology and Entomology, School of Biological and Environmental Sciences, University of Fort Hare, Alice, South Africa

[5] CEABN/InBIO, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal

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ABSTRACT

Species ranges often change in relation to multiple environmental and demographic factors. Innovative behaviours may affect these changes by facilitating the use of novel habitats, although this idea has been little explored. Here, we investigate the importance of behaviour during range change, using a 25-year population expansion of Bonelli's eagle in southern Portugal. This unique population is almost exclusively tree nesting, while all other populations in western Europe are predominantly cliff nesting. During 1991–2014, we surveyed nest sites and estimated the year when each breeding territory was established. We approximated the boundaries of 84 territories using Dirichlet tessellation and mapped topography, land cover, and the density of human infrastructures in buffers (250, 500, and 1,000 m) around nest and random sites. We then compared environmental conditions at matching nest and random sites within territories using conditional logistic regression, and used quantile regression to estimate trends in nesting habitats in relation to the year of territory establishment. Most nests (>85%, *n* = 197) were in eucalypts, maritime pines, and cork oaks. Nest sites were farther from the nests of neighboring territories than random points, and they were in areas with higher terrain roughness, lower cover by agricultural and built--up areas, and lower road and powerline densities. Nesting habitat selection varied little with year of territory establishment, although nesting in eucalypts increased, while cliff nesting and cork oak nesting, and terrain roughness declined. Our results suggest that the observed expansion of Bonelli's eagles was facilitated by the tree nesting behaviour, which allowed the colonization of areas without cliffs. However, all but a very few breeding pairs settled in habitats comparable to those of the initial population nucleus, suggesting that after an initial trigger possibly facilitated by tree nesting, the habitat selection remained largely conservative. Overall, our study supports recent calls to incorporate information on behaviour for understanding and predicting species range shifts.

KEYWORDS

Aquila fasciata, behavioural innovation, conditional logistic regression, conservation, habitat selection, quantile regression, range expansion

1. INTRODUCTION

The geographic range of species is dynamic, often contracting, expanding, or otherwise changing its limits in relation to multiple environmental and demographic drivers (Gaston, 2003). In general, it is expected that a species range will track changes in the geographic distribution of favourable climates and habitats, under the constraints of dispersal limitation (Robillard, Coristine, Soares & Kerr 2015; Schloss, Nuñez & Lawler 2012; Sohl, 2014). This view has been used to fore-cast species range shifts in relation to climate and land use changes (Robillard et al. 2015; Schloss et al. 2012; Sohl 2014) or to predict the ranges of exotic species introduced into new areas (Peterson, Papes & Kluza 2003; Veech, Small & Baccus 2011). Implicit within this idea, however, is that climatic and habitat niches are conserved during range shifts, which may not be warranted due for instance to evolutionary adaptations to changing conditions or the emergence of behaviours that facilitate the use of novel habitats (Broennimann et al. 2007; Van Dyck 2012; Wright, Eberhard, Hobson, Avery & Russello 2010). Understanding these processes is essential to predict species responses to environmental changes (Lavergne, Mouquet, Thuiller & Ronce 2010).

Behavioural innovations, defined as the ability of animals to invent new behaviours or adjust old behaviour to new problems (Overington, Griffin, Sol & Lefebvre, 2011; Sol, Sayol, Ducatez & Lefebvre 2016), may be particularly important during range expansion, when species are bound to face novel environmental conditions (Keith & Bull 2017). For instance, species colonizing landscapes modified by humans often show behavioural adaptations such as changes in the timing of breeding, adjustments of diel activity patterns, and the use of new food sources and foraging strategies (Lowry, Lill & Wong, 2013; Martínez-Abraín & Jiménez 2016). Innovations in breeding habitats include, for instance, avian nesting in human structures such as houses and electric pylons, which permit overcoming scarcity of natural nesting substrates (Martínez-Abraín & Jiménez 2016). Likewise, increasing behavioural tolerance toward humans is normally considered a prerequisite for a species to colonize urban habitats and other heavily disturbed areas (Lowry et al., 2013). Despite these benefits of innovation, however, animal behaviour may often be conservative rather than innovative, thereby restricting or at least delaying range expansion into potentially suitable habitats (Keith & Bull 2017; Sol et al. 2016). For instance, imprinting of young to natal habitat characteristics is judged to strongly constrain breeding habitat selection when individuals reach maturity (Davis & Stamps 2004). Overall, therefore, it is likely that species colonizing new geographic areas should be strongly affected by conservative versus innovative behaviours, although long-term studies examining this topic are lacking.

The Bonelli's eagle (*Aquila fasciata*) in southern Portugal provides a valuable opportunity to examine the role of behaviour during a long-term process of expansion. The Bonelli's eagle is a medium/large bird of prey that is endangered in Europe, where it is largely confined to the Mediterranean region and its numbers have declined since the early 1980s (Hernández-Matías et al. 2013). In Western Europe, the Bonelli's eagle has a metapopulation-like structure with a source-sink dynamics, where the only growing populations are those of south-ern Spain and southern Portugal (Hernández-Matías et al. 2013). The population of southern Portugal is peculiar, because it is almost exclusively made up of tree nesting pairs (Figure 1) and is genetically divergent, whereas Bonelli's eagle populations in northern Portugal and elsewhere in the Iberian Peninsula and France are largely dominated by cliff nesters and well-connected demographically and genetically (Hernández-Matías et al. 2013; Mira, Arnaud-Haond, Palma, Cancela & Beja 2013; Palma, Beja & Sánchez 2013). This population has been closely monitored during the past 25 years, while it grew from about 25 to at least 110 breeding pairs (Beja & Palma 2008; Palma et al. 2013). The original nucleus was largely confined to the uplands of the extreme south of the country, where the landscape is dominated by forests and scrubland, and human population density is low, while the current population occupies a much larger geo-graphic area with a wide range of habitats and human occupation patterns (Palma et al., 2013). Evidence from demographic modeling and genetics suggests that population growth was sustained by the intrinsic demography of the original nucleus, rather than immigration (Hernández-Matías et al. 2013; L. Palma and R. Godinho Unpublished Data). Presumably, tree nesting behaviour had an important role in this expansion, by allowing new pairs to establish in cliffless areas in a wide range of landscape types (Palma et al. 2013). It is uncertain, however, whether this expansion was associated with innovation in terms of new habitats occupied and increasing tolerance toward humans, or rather it was conservative by largely retaining the characteristics of the original population nucleus in terms of nesting substrate and breeding habitats.

Here, we test these ideas by analyzing nesting habitat selection by the Bonelli's eagle, using territories established in southern Portugal from 1990 to 2014 and that were still active at the end of the study period. Specifically, we: (1) assessed the use of nesting substrates by the expanding population; (2) characterized environ-mental conditions within territories and around nests in terms of dominant habitat features and human occupation patterns; (3) quantified factors affecting nesting habitat selection within territories using conditional logistic regression; and used quantile regression to estimated trends in (4) nesting habitat conditions and in (5) the predictive ability of habitat selection models in relation to the year of territory occupation. If habitat selection was conservative, we expected that nesting substrates and the habitats around nesting sites should not change in relation to the year of territory establishment. Also, there should be no trends in the predictive ability of the nesting habitat model in relation to territory age, as it was calibrated considering all the territories occupied during the 25-year study period. In contrast, if behaviour was innovative, we would expect the occurrence of changes in some of these descriptors, including temporal trends in the mean nesting habitat characteristics, or temporal increases in the variability of such habitats at the population level. Results were used to discuss the importance of innovative versus conservative behaviour for the conservation management of Bonelli’s eagles and other species of concern.

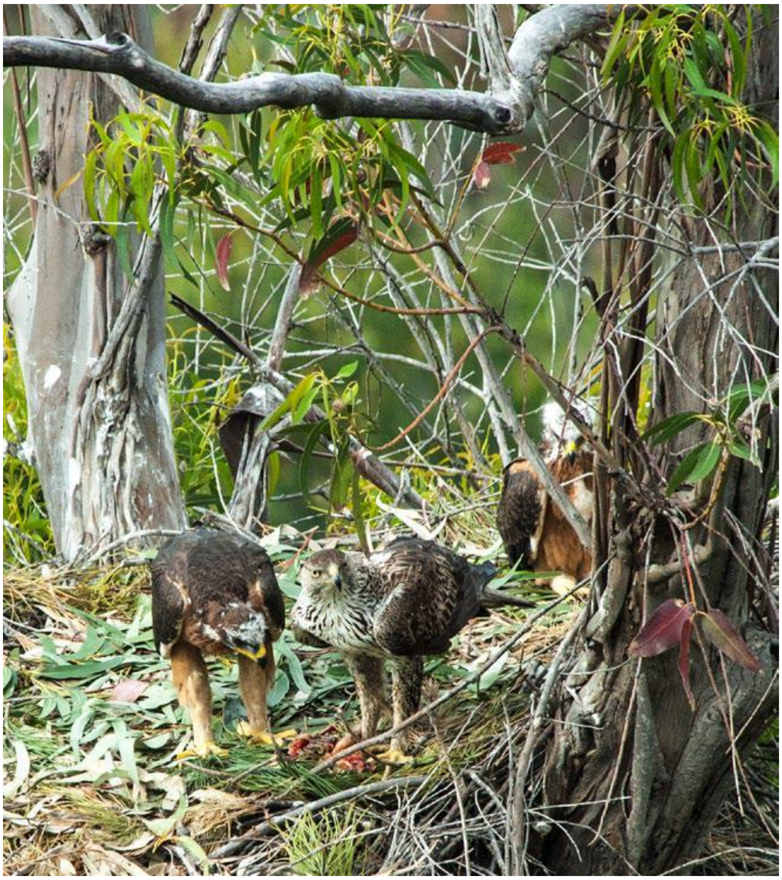

Figure 1 - Bonelli’s eagle (*Aquila fasciata*) nest in a eucalyptus tree, with one adult and two well grown chicks. Photograph by Joaquim Pedro Ferreira.

2. METHODS

2.1 Study area

The study was carried out in southern Portugal, encompassing an area of about 4 × 104 km2. The climate is Mediterranean, with mean annual temperature of ≈17°C, and mean annual precipitation ranging from ≈500 to ≈1,000 mm (IM/AEMet, 2011). The landscape is dominated by an extensive peneplain (200–450 m a.s.l.) punctuated by residual elevations and bordered on its southern and southwestern ends by low altitude (<900 m a.s.l.) uplands. Land cover is varied, but it includes vast areas occupied by irrigated and rainfed annual crops, permanent crops (e.g. vineyards and olive groves), cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*) woodlands and agroforestry systems, Blue gum (*Eucalyptus globulus*) and pine (Pinus spp.) plantations, and scrublands of diverse structure and composition. Human density is low throughout much of the area, with most population concentrated along the coast and in urban centers in the hinterland.

2.2 Study design

Bonelli’s eagles are nonmigratory birds of prey, living in pairs that occupy exclusive territories, where there may be one or several alter-native nests (Hernández-Matías et al. 2013; and references therein). The study was based on a long-term survey (1991–2014) of these breeding pairs and their territories in southern Portugal. For each territory, we estimated the approximate year of first occupation by the breeding pair, and we tried to locate all its nests. In the field, we recorded whether each nest site was built on a cliff or in a tree, and in the latter case, we recorded the nest tree species. Habitats around nests (250-m, 500-m and 1,000-m radius buffers) and random sites (see below) were characterized using variables extracted from GIS layers. We considered three buffers, because factors operating at different spatial scales may affect the selection of nesting habitats. The analysis of habitat selection was based on the comparison of habitat conditions at matching nest and random sites within territories. For each breeding pair, we retained in analysis all nests at >2,000 m from each other, to avoid overlapping buffers. For each group of nests at <2,000 m from each other, we retained the one used most frequently during the study period. Every nest site of each breeding pair was then matched with three points randomly located at >2,000 m from each other and from the nest site, within the corresponding territory boundary (Figure 2). The number of random points was a compromise between the need to avoid overlapping buffers, and to sample adequately the habitat available within each territory (e.g., Carvalho, Carvalho, Mira & Beja 2016). To avoid trivial results, random points falling within urban areas and water reservoirs were randomly relocated. To infer eventual behavioural changes during expansion, we estimated temporal trends in the mean and in the variability of nesting habitat conditions.

2.3 Bonelli’s eagle data

The methods used to collect comprehensive information on the breeding Bonelli’s eagle population in southern Portugal have been detailed elsewhere (e.g., Beja & Palma 2008; Hernández-Matías et al., 2013; Palma, Beja, Pais, & Cancela da Fonseca, 2006; Palma et al., 2013). Briefly, we conducted surveys throughout the region during courtship, nest building and breeding to locate Bonelli’s eagle territories, focusing primarily on areas with potentially suitable habitats. In addition, surveys were directed toward areas with historical information on breeding sites, and areas with observations of individuals reported by other researchers and birdwatchers. Repeated observations of one or two adults or sub-adults within circumscribed areas were used to identify potentially breeding territories, which were then thoroughly surveyed until nests were found. A breeding territory was considered to be pre-sent in a given area when at least one nest was located, and there was at least one breeding attempt (i.e., at least nest building or repair) in at least 1 year. The year of territory establishment was estimated from a combination of information sources, including mainly the history and spatial pattern of Bonelli’s eagle observations in the area, and enquiries to key informers such as shepherds and game managers. Frequently, estimates were made in terms of a likely time interval, for which we used the mid-point in subsequent analysis. Breeding data were collected for the active nests located each year in each territory, based on based on observations carried out using binoculars and telescopes (20–60×) from a distance to minimize disturbance.

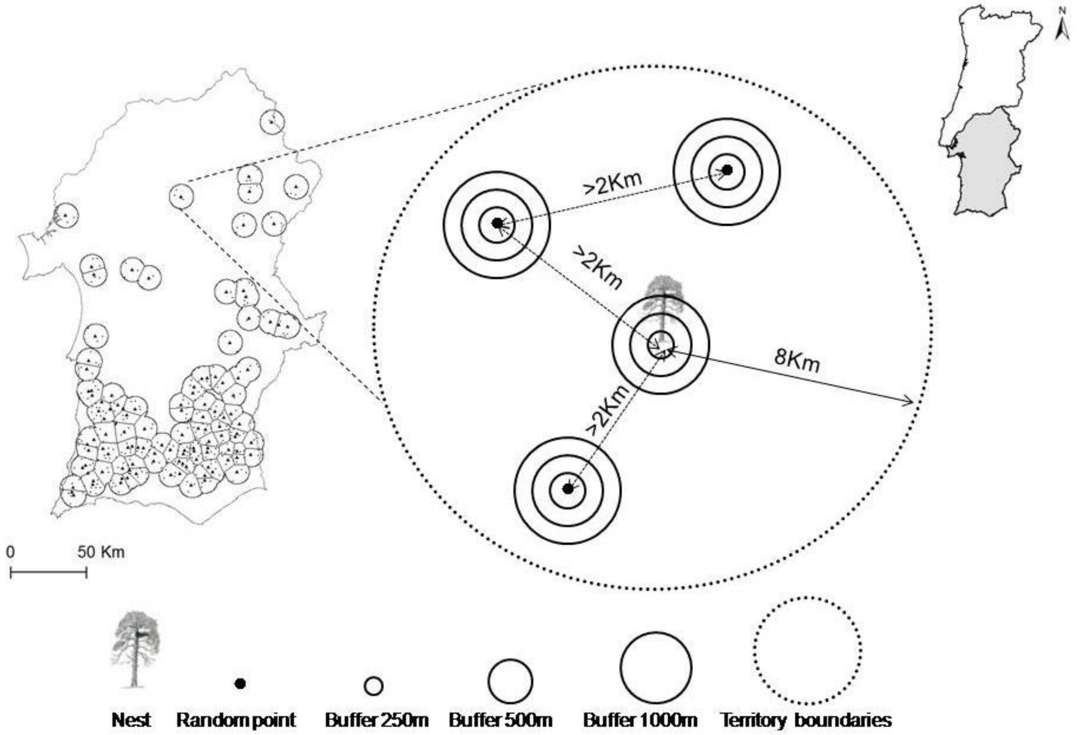

Figure 2 - Location of the study area in southern Portugal showing the Bonelli’s eagle breeding territories and nests considered in this study (1990–2014), and schematic representation of the study design (see text for details).

To match nest sites with random locations within the same territory, we defined the territory boundary of each breeding pair as an 8-km radius buffer around its central point, which was estimated as the geographic centre of all the nests of the breeding pair (Palma et al., 2006). When the centers of neighboring territories were at <16 km from each other, the territory boundaries were defined using Dirichlet tessellation (Schlicht, Valcu & Kempenaers 2014). These assumptions were similar to those taken in a previous study where we found a good matching between diets and food resources across territories (Palma et al. 2006), and they were based on home range data from satellite tracking of ten breeding adults in our study area (L. Palma, unpublished data). Therefore, we believe that these territories provided a reasonable approximation to select random points and thus estimate the habitats available to each breeding pair, although it does not account for eventual variations in territory sizes and shapes (e.g., Bosch, Real, Tintó, Zozaya & Castell 2010; Mure 2003).

2.4 Environmental variables

The buffers around nest sites and random points were characterized from 15 variables reflecting topography, human disturbance, land cover, and potential intraspecific interactions (Table 1, Table S1), which were expected to influence Bonelli's eagles (e.g., Carrascal & Seoane 2008; Di Vittorio, Sarà & López-López 2012; Muñoz & Real 2013; Real, Bosch, Tintó & Hernández-Matías 2016). All variables were extracted on a GIS from digital thematic layers, using ArcMap 10.1. Topographic variables were estimated using a 25-m resolution digital elevation model (http://www.eea.europa.eu/dataand-maps/data/eu-dem). For each buffer, we computed the means and standard deviations of elevation and slope of raster grid cells, and we estimated an index of ruggedness using the Vector Ruggedness Measure Tool (Sappington, Longshore & Thompson 2007). This index measures terrain ruggedness as the variation in three-dimensional orientation of grid cells within a neighborhood, effectively capturing variability in slope and aspect into a single measure (Sappington et al. 2007). The density of paved roads was estimated using the Open Street Map (www. openstreetmap.org/copyright), and it was taken as a broad indicator of potential human disturbance. Distribution power lines were also taken as an indicator of potential disturbance because they are a source of mortality in Bonelli's eagles (Real, Grande, Mañosa & Sánchez-Zapata 2001; Rollan, Real, Bosch, Tintó & Hernández-Matías 2010), and their density was estimated from electric network maps. Land cover was estimated using Portugal's 2007 Land Cover Map with land cover classes aggregated in five main categories judged a priori to be the most relevant for Bonelli's eagles nesting habitat selection (see Table 1 for details). We have used relatively broad habitat land cover classes, because they have changed less over time than more detailed categories (ICNF 2013), thereby reducing errors potentially associated with considering only a land cover map from 2007 to analyze habitat selection from territories established between 1990 and 2014. We also estimated the density of waterlines, because Bonelli's eagles frequently nest along streams and gullies (Palma et al. 2013). Finally, we considered the distance to the nearest nest of a different breeding territory, to account for the possibility of individuals avoiding sites because of their proximity to those occupied by neighboring breeding pairs.

Table 1 - Variables used to analyze the environmental correlates of nesting site selection by the Bonelli's eagle in southern Portugal

Variable (unit)	Code	Description (transformation)
Topography		
Elevation (m)	ELMEN ELSTD	Elevation above sea level (DEM 25m) - mean and standard deviation (log10)
Slope (°)	SLMEN SLSTD	Slope - mean and standard deviation (log10)
Ruggedness Index	VRMEN VRSTD	Terrain ruggedness measured as the variation in three-dimensional orientation of grid cells within a neighbourhood - mean and standard deviation (log10)
Human disturbance		
Paved road network (m/m2)	DEPR	Density of paved roads (Asin [√x])
Power line (m/m2)	DEPL	Density of High/Very High Tension (>60 kv) and Medium Tension (<60Kv) power lines (Asin [√x])
Land cover		
Artificial areas (%)	EXAR	Proportion of artificial areas (urban areas, industrial, commercial and industrial units, mine, dump and construction sites, artificial nonagricultural vegetated areas) (Asin [√x])
Agricultural areas (%)	EXAG	Proportion of heterogeneous agricultural areas, permanent pastures and crops, arable land and rice fields (Asin [√x])
Forests (%)	EXFO	Proportion of forests (broad leaved forests, coniferous forests, mixed forests) (Asin [√x])
Open forests (%)	EXOF	Proportion of open forests, shrubs, herbaceous vegetation, and open spaces with little or no vegetation (Asin [√x])
Water bodies (%)	EXWA	Proportion of water bodies (e.g. reservoirs, lagoons) and wetlands (Asin [√x])
Waterline (m/m2)	DEWL	Density of waterlines (Asin [√x])
Intraspecific relationship		
Distance to nest (m)		Distance to the nearest Bonelli's eagle nest (log10)

2.5 Data analysis

Prior to statistical analysis, skewed variables were transformed to approach normality and to reduce the influence of extreme values using the angular and logarithmic transformations (Table 1). All variables were standardized to zero mean and unit variance, to enhance comparability of effect sizes (e.g., Schielzeth 2010). Principal component analyses (PCA) of ecological variables were used to investigate multicollinearity and to describe dominant environmental gradients (Legendre & Legendre 1998). Varimax normalized rotations were ap-plied to the set of principal components with eigenvalues >1, to obtain simpler and more interpretable gradients (Legendre & Legendre 1998). Varimax rotated axes were then used in subsequent analysis, because they provide a reduced set of synthetic variables, which are orthogonal to each other and thus are not affected by multicollinearity. A separate PCA and varimax rotation was carried out for variables estimated in 250-, 500-, and 1000-m buffers, because we were interested in modeling habitat selection in relation to scale-specific factors. We excluded the distance to the nearest nest from PCAs, because we were interested in estimating its unique effect and because preliminary analysis showed that it was uncorrelated with other variables.

The factors influencing nest site selection were analyzed at each spatial scale by comparing nest site and random locations within territories, using conditional logistic regression (Duchesne, Fortin & Courbin, 2010; Hosmer & Lemeshow 2000). This analysis followed a match-control design framework, using a binomial variable coding the nest (1) vs. three random points (0), thereby creating a group “stratum” (e.g., Hosmer & Lemeshow 2000). Model selection was based on the information theoretical approach of Burnham and Anderson (2002) using the Akaike Information Criterion (AICc) and the corresponding Akaike weights (wi). Candidate models were built based on all possible subsets of the ecological gradients obtained in the vPCA, including the null (i.e., without explanatory variables) and the full (i.e., with all explanatory variables) models. Models were ranked according to their Akaike weights (wi), and the average parameters and their unconditional standard errors (SE) were estimated based on the 95% confidence set of models (Burnham & Anderson 2002). The relative importance of each variable (ecological gradient) was judged based on the sum of Akaike weights of models where the variable was included (w+), and on the magnitude of the average model coefficient. Model fit was assessed with the pseudo R-squared of Tjur (2009), and model discrimination ability was assessed with the area under the remote operating characteristic curve (AUC; Fielding & Bell 1997). These analyses were per-formed using the packages mclogit (Elff 2013), MuMIn (Barton 2013), and modEva (Barbosa, Brown, Jiménez-Valverde & Real 2014) for R 3.3.2 software (R Development Core Team 2016).

The analysis of trends in nesting habitats was based on quantile regression, following the rationale outlined in Cade and Noon (2003). This approach was used because we were interested in assessing changes over time in the mean (median) habitat conditions used by breeding pairs, but also in whether variability in nesting habitats in-creased over time due for instance to a few pairs settling in unusual habitats. In quantile regression, the latter hypothesis may be tested by examining temporal rates of change in quantiles near the maximum (e.g., 95% quantile) or the minimum (e.g., 5%), response. Increases in variability of habitat conditions may be inferred when the absolute value of the slopes estimated for extreme quantiles is significantly larger than that estimated for the median response. The analyses focused on the relations between nesting habitat characteristics described using the PCA axis and the first year of territory occupation. Also, we estimated relations between the prediction errors of the habitat model and the year of territory establishment, assuming that changes in behaviour would lead to temporal changes in the median or in the variability of the prediction errors, or both. Model prediction errors were computed for nest sites as one minus the model predicted probability that a site was a nest site. Analysis was carried out at the level of breeding territories by averaging variables across all nest sites within each territory. Separate analyses were made for the three spatial extents used in this study (i.e., 250, 500, and

1,000 m). We estimated the temporal trend of the response variables using ordinary least squares, and we then estimated trends in the quantiles from 5% to 95% at 5% intervals. For each coefficient of the quantile regression, we computed the 90% confidence intervals based on inverting a quantile rankscore test (Cade & Noon 2003). We also compare the slopes of the regression coefficients of the 5% and 95% quantiles with those of the median, using an ANOVA function for quantile regression fits based on the Wilcoxon score (Koenker et al. 2016). In trend analysis, all territories estimated to be present before the beginning of the study in 1991 were assigned to 1990 as the year of establishment. These analyses were performed using the package quantreg (Koenker et al. 2016), and results were visualized using ggplot2 (Wickham & Chan 2016), for R 3.3.2 software (R Development Core Team 2016).

3. RESULTS

3.1 Bonelli’s eagle nests and nesting population

We estimated the approximate boundaries of 84 Bonelli’s eagle territories from 197 nests (mean number of nests per territory [±SD, range] = 2.3 ± 1.4, 1–8) detected during the study period (Figure 2). The eagle population in southern Portugal before 1991 was estimated at 25 territories (29.8% of the total studied). For the territories established after 1990 (n = 59), the mean (±SD) estimated year of establishment was 2004 ± 5.7 years (1992–2012). From all the nests recorded, only 11 (5.6%) were on cliffs, whereas the others (n = 186) were in *Eucalyptus globulus* (36.5%), *Pinus pinaster* (18.8%), *E. camaldulensis* (15.2%), *Quercus suber* (14.7%), *Pinus radiata* (7.1%), *Pinus pinea* (1.5%), and *Populus nigra* (0.5%). There was a significant tendency (chi-squared = 4.80, p = .030) for the initial territories (<1991) having a higher proportion of nests on cliffs (4.1%) than more recent territories (1.6%). There were also significant differences between periods in the species of nest tree used (chi-squared = 31.4, p < .001), mainly due to a higher use of *E. camaldulensis* (24.6% vs. 2.8%) and a lower use of *Q. suber* (7.0% vs. 29.2%) in the second period.

3.2 Nesting habitat selection

At each spatial scale, the principal component analysis with varimax rotation extracted four dominant environmental gradients that ac-counted for 68%–74% of total variance in the data and that were largely consistent across scales (Table 2). The dominant gradient (PC1; 36%–38% of variance) was largely related to terrain ruggedness, reflecting a joint increase in mean and standard deviation of slope, standard deviation of elevation and index of ruggedness, and a decline in agricultural land cover. The second gradient was related to human infrastructures (PC2; 12%–17%), showing a joint increase in cover by artificial areas, and in paved roads and powerline densities. The third gradient (PC3; 11%) contrasted areas at higher elevation with lowland areas with more waterlines and waterbodies. Finally, the fourth gradient was mostly related to the increase in forest cover (PC4; 8%–9%), showing a contrast between open and closed woodland at the two smaller spatial scales.

The model selection and averaging procedure yielded conditional logistic regression models that were very similar at the three spatial scales considered, consistently showing that within territory boundaries the Bonelli's eagle nests were located in areas with higher terrain ruggedness and lower agricultural cover (PC1), and less human infrastructures (PC2) than random sites (Tables 3 and S2). Also, nests were farther than random points from the nearest nest of a neighbor territory. Support for the negative effect of elevation (PC3) and the positive effect of forest cover (PC4) was moderate at the 1,000-m scale (Akaike weights > 0.8), but it was weak at lower scales. The T-Jur coefficients showed that the models at the three spatial scales had a reasonable fit to the data (0.635–0.655), while the AUCs indicated high model discrimination ability (0.946–0.955).

Table 2 - Scores of habitat variables used to characterize nesting habitats of the Bonelli’s eagle in southern Portugal, on the axis (PC#) extracted through a principal component analysis (PCAs) with varimax rotation. Separate PCAs were performed for variables extracted at three spatial scales. We provide the proportion of variance accounted for by each axis extracted in each PCA

Variables	250 m				500 m				1000 m			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Mean slope	0.95				0.96				0.96			
Standard deviation of slope	0.95				0.96				0.97			
Ruggedness	0.94				0.94				0.95			
Standard deviation of ruggedness	0.90				0.91				0.92			
Standard deviation elevation	0.90				0.91				0.90			
Agricultural areas	−0.75				−0.75				−0,79			
Open forests				−0.81	0.55			−0.77	0.59			
Paved road density		0.81				0.84				0.90		
Artificial areas		0.74				0.74				0.84		
Power line density		0.60				0.78				0.83		
Mean elevation			0.73				0.74				0.71	
Waterline density			−0.54				−0.51				−0.56	
Water bodies			−0.81				−0.83				−0.85	
Forests				0.76				0.77				0.78
% Explained variance	36	12	11	9	37	14	11	9	38	17	11	8

3.3. Temporal trends

Considering the variables most related to nesting site selection (Table 3), there was a very marked tendency for mean and median terrain ruggedness (PC1) to decline in relation to the estimated year of territory occupation at all spatial scales (Table 4). A similar trend was found for most quantiles at all spatial scales, with no significant differences among slopes (ANOVA, $p > .05$), thus suggesting that variability in ruggedness among territories did not change over time (Figures 3 and S1–S5). In contrast, there was no trend in the mean amount of human infrastructures around nests (PC2) in relation to the year of territory establishment, although the median significantly declined at the 250-m scale (Table 4, Figures 3 and S1–S5). There was also some evidence for increasing variability in more recent territories, as underlined by the contrast between the negative slopes estimated for the lower quantiles (5% and 25%) and the positive slope for the upper quantile (95%), particularly at the 1,000-m scale. It should be noted, however, that variation among slopes was not significant (ANOVA, $p > .05$) and that the response for the 95% quantile appeared driven by a few recent territories with an unusually high amount of human infrastructures around nests (Figures 3, S1 and S2). Regarding the distance to the nearest nest of a neighbor territory, there were no significant trends in the mean or in any quantile, although there were a few recent territories where nests were unusually distant from their nearest neighbors (Table 4, Figures 3 and S1–S5). Considering the less influential variables, there was a tendency for the mean and median (except at 250-m scale) elevation (PC3), and the median (only at the 1,000-m scale) of forest cover (PC4), declining in more recent territories, with no significant differences (ANOVA, $p > .05$) among the slopes of different quantiles. There was also no evidence for model prediction error varying in relation to the year of territory establishment (Table 4). It is noteworthy, however, that the highest prediction errors were found in a few recent territories (Figures 3, S1 and S2).

Table 3 - Average models describing the estimated effects of explanatory variables on the nesting area selection of tree nesting Bonelli’s eagle at three spatial scales: 250, 500, and 1,000 m. For each case, multimodel averaging was based on the 95% confidence set of models. For each variable, we show the standardized regression coefficient (β), the unconditional standard errors (SE), the 95% confidence interval of coefficient estimate (CI), and the selection probability (w+). Coefficient estimates whose 95% CI exclude zero are in bold.

Variables	**β**	***SE***	**CI**	**ω+**
Buffer: 250 m				
Terrain ruggedness (PC1)	**2.199**	**0.640**	**0.944, 3.455**	**1.000**
Human infrastructures (PC2)	**−3.845**	**1.555**	**−6.893, −0.797**	**1.000**
Elevation (PC3)	−0.707	0.533	−1.752, 0.337	0.490
Forests (PC4)	0.529	0.533	−0.516, 1.575	0.380
Distance to nest	**4.626**	**1.157**	**2.357, 6.895**	**1.000**
Buffer: 500 m				
Terrain ruggedness (PC1)	**1.782**	**0.599**	**0.606, 2.957**	**1.000**
Human infrastructures (PC2)	**−1,495**	**0.629**	**−2.728, −0.261**	**1.000**
Elevation (PC3)	−0.891	0.458	−1.789, 0.006	0.670
Forests (PC4)	0.607	0.454	−0.283, 1.49	0.490
Distance to nest	**4.336**	**1.088**	**2.203, 6.469**	**1.000**
Buffer: 1000 m				
Terrain ruggedness (PC1)	**2.550**	**0.965**	**0.659, 4.442**	**1.000**
Human infrastructures (PC2)	−1.833	0.956	−3.709, 0.041	1.000

Table 4 - Trends in habitats conditions around Bonelli's eagle nesting sites (250-, 500-, and 1,000-m buffers) in relation to the year of territory establishment. Trends were estimated with both ordinary least squares regression (Mean) and quantile regression (Quantiles), considering the habitat gradients extracted from a principal component analysis (PC#), the distances to the nearest nest from a neighboring territory, and the prediction error of the habitat model. In each case, we provide the slope of the relation, and its 90% confidence interval. Coefficients with confidence interval excluding zero are in bold.

		Quantiles				
Buffer	**Mean**	**5%**	**25%**	**50%**	**75%**	**95%**
Terrain ruggedness (PC1)						
250 m	**−0.044 (−0.062,0.026)**	−0.047 (−0.087, 0.002)	**−0.061 (−0.082, -0,017)**	**−0.056 (−0.065, −0.035)**	**−0.023 (−0.051, 0.021)**	**−0.046 (−0.061, −0.009)**
500 m	**−0.047 (−0.064,0.030)**	−0.053 (−0.073, 0.002)	**−0.064 (−0.081, −0.026)**	**−0.052 (−0.068, −0.035)**	**−0.033 (−0.058, −0.02)**	−0.031 (−0.062, 0.008)
1000 m	**−0.046 (−0.063,0.029)**	**−0.053 (−0.079,−0.006)**	**−0.062 (−0.079, −0.03)**	**−0.052 (−0.066, −0.025)**	**−0.044 (−0.059,−0.024)**	−0.025 (−0.059, 5.4 × 10^{-5})
Human infrastructures (PC2)						
250 m	−0.004 (−0.010, .002)	**−0.009 (−0.013, 0.005)**	**−0.010 (−0.017, −0.005)**	**−0.005 (−0.009, −2.3 × 10^{-4})**	−0.003 (−0.007, 0.002)	0.012 (−0.013, 0.024)
500 m	−0.002 (−0.013,0.009)	**−0.009 (−0.011, 0.005)**	**−0.007 (−0.012, −0.004)**	−0.006 (−0.017, 3.3 × 10^{-5})	−0.001 (−0.021, 0.010)	0.060 (−0.048, 0.087)
1000 m	0.005 (−0.005,0.015)	0.004 (−0.008, 0.005)	−0.003 (−0.011, 0.003)	−0.004 (−0.010, 0.005)	0.002 (−0.006, 0.021)	**0.016 (0.011, 0.084)**
Elevation (PC3)						
250 m	**−0.024 (−0.044,−0.004)**	−0.010 (−0.048, 0.014)	−0.037 (−0.060, 0.001)	−0.034 (−0.047, 0.011)	−0.021 (−0.04, 0.004)	−0.007 (−0.039, 0.035)
500 m	**−0.020 (−0.037,−0.002)**	−0.006 (−0.038, 0.031)	−0.023 (−0.047, 0.010)	**−0.032 (−0.040, −0.009)**	**−0.011 (−0.040, 0.003)**	−0.010 (−0.073, 0.029)
1000 m	**−0.023 (−0.042,−0.005)**	−0.004 (−0.024, 0.047)	**−0.028 (−0.057, 0.004)**	**−0.030 (−0.047, −0.006)**	**−0.018 (−0.032,−0.008)**	−0.039 (−0.066, 0.019)
Forests (PC4)						

		Quantiles				
Buffer	**Mean**	**5%**	**25%**	**50%**	**75%**	**95%**
250 m	−0.010 (−0.012, 0.032)	−0.013 (−0.026, 0.007)	−0.019 (−0.040, 0.004)	−0.023 (−0.056, 0.019)	−0.008 (−0.029, 0.01)	0.023 (−0.095, 0.088)
500 m	−0.019 (−0.042, 0.004)	−0.015 (−0.039, 0.002)	−0.046 (−0.056, 0.003)	−0.012 (−0.059, 0.003)	−0.005 (−0.039, 0.018)	0.016 (−0.107, 0.059)
1000 m	−0.022 (−0.046, 0.002)	−0.020 (−0.046, 0.005)	**−0.040 (−0.067,−0.027)**	−0.04 (−0.056, 0.015)	−0.002 (−0.041, 0.028)	−0.016 (−0.060, 0.052)
Distance to nest						
Distance	47.5 (−120.9, 215.9)	−1.4 (−30.7, 55.9)	20.1 (−75.5, 64.3)	46.1 (−114.7, 89.3)	0.0 (−98.4, 19.8)	588.4 (−986.2, 2110.1)
Model prediction error						
250 m	0.001 (−0.001, 0.003)	0.0 (-1.4×10^{-8}, 1.2×10^{-8})	8.0×10^{-7} (-3.0×10^{-7}, 4.8×10^{-6})	4.8×10^{-6} (-1.0×10^{-4}, 5.4×10^{-5})	4.8×10^{-5} (-9.9×10^{-4}, 1.2×10^{-3})	0.008 (−0.004, 0.030)
500 m	0.002 (−0.001, 0.005)	-7.6×10^{-8} (-1.1×10^{-4}, 9.5×10^{-8})	-7.1×10^{-6} (-1.0×10^{-5}, 1.3×10^{-5})	1.3×10^{-4} (-5.4×10^{-5}, 5.3×10^{-4})	7.2×10^{-4} (−0.003, 0.004)	0.010 (−0.021, 0.042)
1000 m	0.003 (−0.0001,0.007)	0.0 (-2.5×10^{-8}, 6.9×10^{-9})	5.4×10^{-7} (-7.3×10^{-7}, 3.7×10^{-6})	9.1×10^{-5} (-3.0×10^{-5}, 3.1×10^{-4})	1.2×10^{-3} (4.8×10^{-4}, 2.1×10^{-3})	0.030 (−0.026, 0.051)

4. DISCUSSION

Our results suggest that during the 25-year expansion of Bonelli's eagles in southern Portugal, the nesting habitat characteristics and selection patterns remained very similar to those of the initial population nucleus, albeit with some changes over time. In terms of nest substrate, the tree nesting behaviour typical of the initial nucleus was not only retained but even amplified over time, although with some variation in the trees most used. In terms of habitats, nests were consistently located in areas with relatively high terrain ruggedness, low cover by both agricultural land and human infrastructures, and away from conspecific nests in neighboring territories. The main temporal change was a decline in terrain ruggedness around nests in more re-cent territories, although they were still located within the most rugged areas available within each territory. Mean cover by human infrastructures was little affected by territory age, although variability appeared to be somewhat higher in more recent territories, particularly due to the presence of a few territories with unusually high infrastructure cover around nests. Also, a few recent territories appeared to have an unusual pattern of nesting site selection, as suggested by particularly high model prediction errors. Overall, these results suggest that an initial uncommon behaviour, tree nesting, may have triggered the ability of this Bonelli's eagle population to colonize vast areas without suitable cliffs for nesting. However, during the subsequent population expansion, the selection of habitats appeared to be dominantly conservative rather than innovative, although rare unusual behaviours may have started to emerge in recent years.

The interpretation of our results requires due consideration of study design and data analysis approaches, which differed to some extent from other studies on Bonelli's eagle habitat selection. First, our study was conducted at relatively detailed spatial scales, with variables measured at most within 1 km from nests, whereas several other studies considered larger buffers (e.g., Carrete, Sánchez-Zapata Martínez, Sánchez & Calvo, 2002; Di Vittorio, Sara & López-López 2012; Gil Sánchez, Molino Garrido & Valenzuela Serrano 1996) or evaluated species presence/absence using 10 × 10 km squares (e.g. Carrascal & Seoane 2008; Di Vittorio et al. 2012; Muñoz, Márquez, Real 2013; Real et al. 2016). This is important because different aspects of Bonelli's eagle habitat selection may become apparent at different spatial scales (López-López, García-Ripollés, Aguilar, García-López & Verdejo 2006; Muñoz & Real 2013; Real et al. 2016), with studies at smaller scales such as ours probably showing the requirements associated with nest sites, and studies at larger spatial scales probably revealing a combination of nesting and foraging habitat requirements. Second, our analysis was based on conditional logistic regression, matching nesting site conditions with those available within territories, whereas all other studies used unmatched comparisons between sites with and without Bonelli’s eagles. This may affect results, because conditional regression identifies what is selected considering local availability, and so it is able to reveal selection patterns that might be difficult to discern otherwise (e.g., Carvalho et al. 2016; Duchesne et al. 2010). Finally, our study introduced a temporal dimension to habitat selection patterns that had never been considered before. Although we could not incorporate actual temporal changes in habitat composition due to lack of detailed data, we believe that our approach based on comparisons of current conditions in relation to the year of territory establishment provided a first approximation to how nesting habitat characteristics and selection patterns changed over time. We believe this assumption is reasonable, because the main variables used to characterize Bonelli’s eagle habitats have either remained unchanged (e.g., elevation, ruggedness), or they likely varied little over time. In particular, the area occupied by the broad land cover categories used in our study has remained largely stable within Bonelli’s eagle territories, as for instance the growth in urban areas and associated infrastructures has been mostly concentrated in a narrow fringe along the coast (Freire, Santos & Tenedório 2009), while cover by agriculture and forest areas has remained essentially constant in rural areas of southern Portugal (Godinho et al. 2016; ICNF 2013). Estimates of the year of territory establishment were associated with some uncertainties, which may have introduced noise in the data but we believe this is unlikely to have biased trends in selection patterns relative to territory age.

Reasons for the association of Bonelli’s eagle nesting sites to the most rugged areas within territories may be related to the presence of suitable nesting trees and to less human disturbance (Palma et al. 2013; Real et al. 2016). For instance, large eucalypts are among the most used nest trees and they are most often found along waterlines at the bottom of valleys (Palma et al. 2013), which may be one of the factors attracting the eagles to rougher terrain. Also, rugged areas are probably less affected by forest management operations such as understory clearing for fire prevention (Real et al. 2016; Santana, Porto, Reino & Beja 2011) and they may be less often crossed by people. Whatever the reasons for the observed pattern, it is noteworthy that breeding habitat selection of tree nesting Bonelli’s eagles in Cyprus was also affected by local topography and the availability of suitable nesting trees away from disturbance (Kassinis 2010). Cliff nesting Bonelli’s eagles also seem to prefer areas with high terrain ruggedness, which seems to reflect the availability of suitable cliffs for nesting (Di Vittorio et al. 2012; Gil Sánchez et al. 1996; López-López et al. 2006; Real et al. 2016). Overall, therefore, the preference for nesting in rugged areas may be a conservative characteristic of Bonelli’s eagles seemingly maintained across geographical regions and nest site typologies, and that may constrain range expansion into milder terrain.

Bonelli’s eagle nests were also associated with areas with the lowest cover by built-up areas and the lowest densities of roads and powerlines. Comparable patterns have been reported elsewhere (Gil Sánchez et al. 1996; López-López et al. 2006; Real et al. 2016), although other studies did not find significant avoidance of human infra-structures close (<3 km) to occupied nests (Ontiveros 1999; Carrete et al. 2002). Interestingly, Ontiveros (1999) reported that occupied cliffs closer to roads were taller than those farther from roads, suggesting that tolerance to human disturbance may depend on the relative safety of nesting sites (Real et al. 2016; Rollan et al. 2010). Overall, we suggest that our observations regarding human infrastructures, together with the preference for particularly rough terrain, indicates that Bonelli’s eagles avoid human disturbance at small distances (<1 km) from nesting sites. It should be noted, however, that our inferences based on conditional logistic regression imply that Bonelli’s eagles select the least disturbed areas within their territories, although this may correspond to areas that may still have some human disturbance. Therefore, our results do not contradict the general view that Bonelli’s eagles can tolerate a certain degree of human disturbance and that human infrastructures and other indicators of disturbance may be relatively unimportant to explain the species distribution at larger spatial scales (López-López et al. 2006; Carrascal & Seoane 2008; Di Vittorio et al. 2012; Muñoz et al. 2013; but see Bosch et al. 2010; Muñoz & Real 2013 and Real et al. 2016). In addition, it should be noted that a few recent territories had an unusually high cover by human infrastructures around nests, although this patterns was not statistically significant probably due to small sample sizes. The presence of these few pairs apparently more tolerant to human disturbance may imply that in the future the species may be able to expand into more anthropic areas, and this should be the subject of further research.

The trends in nesting habitats in relation to territory age observed in our study suggest that new Bonelli's eagle pairs chose habitats that are structurally comparable to those of the initial population nucleus. This may be a consequence of imprinting of young to natal habitat conditions, which may affect the kind of places the individuals select later in life (Davis & Stamps 2004). Testing this idea, however, would imply detailed information on the natal and breeding habitats of a large number of marked individuals (e.g., Mannan, Mannan, Schmidt, Estes-Zumpf & Boal 2007), which was unavailable in our case. Nevertheless, there is evidence that the new pairs largely originated from the initial population nucleus, based on the assignment of individuals to the unique genetic profile of the population inhabiting southern Portugal (Mira et al. 2013; Palma et al. 2013), and by the tracking of individuals with conventional and genetic tags (L. Palma and R. Godinho, unpublished). Despite this general trend for conservative behaviour, there was still some flexibility in the selection of the nesting area. This was supported to some extent by the decrease in terrain ruggedness in more recent territories, although nests were consistently located in the roughest areas available within territories. Also, there were a few recent territories where nesting site selection was different, as suggested by the higher cover by human infrastructures and the poor predictive ability of the habitat model to differentiate nesting from random sites. Therefore, an even longer time frame would probably be needed to understand whether innovative habitat selection patterns might eventually emerge, although this was not apparent during our 25-year study.

Taken together, our results suggest that Bonelli's eagles expanded in southern Portugal because the individuals produced by the original nucleus could find vacant nesting habitats of basically similar structure in various landscape types across the region (Beja & Palma 2008; Palma et al. 2013), rather than through the occupation of novel habitats. Agricultural land abandonment and the depopulation of the countryside since the 1960s was probably responsible to at least some extent for this process, because it released large areas with low disturbance and that have been progressively occupied by uncultivated woodland and scrublands (Diogo & Koomen 2012; Van Doorn & Bakker 2007), thus becoming available for Bonelli's eagle colonization during the study period. Another main driver was probably the prevalence of tree nesting behaviour, which allowed the colonization of cliffless landscapes that would be unavailable if strict cliff nesting behaviour would be retained, as it is commonest in remaining Iberia (Hernández-Matías et al. 2013; Palma et al. 2013). This idea was supported by genetic studies and demographic modeling, which showed that the genetically isolated tree nesting population of south-ern Portugal was likely the main source of colonists throughout the expansion process (Hernández-Matías et al. 2013; Mira et al. 2013; L. Palma and R. Godinho Unpublished Data). Therefore, the conservation of populations with tree nesting behaviou may be particularly relevant for the conservation of Bonelli's eagles at wider scales, as this behavioual trait may help the species respond better to ongoing climatic and land use changes (Hernández-Matías et al. 2013; Muñoz et al. 2013; Palma et al. 2013).

In general, our study shows the importance of understanding the contribution of habitat selection patterns to population expansion (Butcher et al. 2014; Veech et al. 2011). In particular, we showed that species can expand despite a relatively conservative nest site se-lection behaviou, when changes in land use and human demographics provide new vacant areas open to colonization by the growing population (e.g., Balbontin, Negro, Sarasola, Ferrero & Rivera 2008; Cardador, Carrete & Mañosa 2011). We also found that the fast expansion of this particular eagle population was facilitated by a specific but relatively rare behaviou in the Mediterranean region (tree nesting), which allowed the colonization of habitats that otherwise would be unavailable. The study thus adds to the increasing evidence suggesting that preserving behavioual diversity within populations may be essential for species persistence under anthropogenic environmental change (Caro & Sherman 2012; Sutherland 1998; Van Dyck 2012).

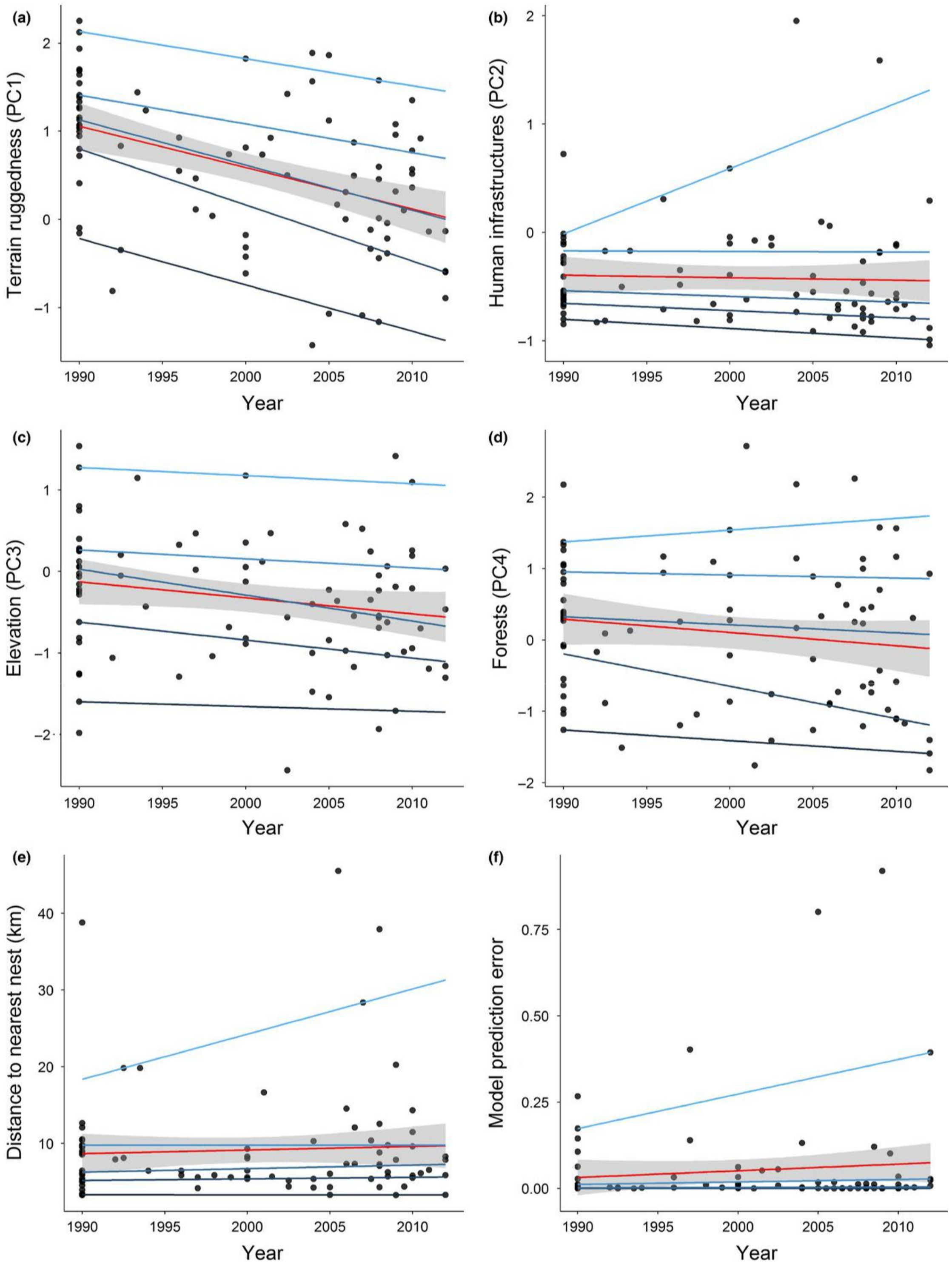

Figure 3 - Scatterplots showing trends in habitat conditions around Bonelli's eagle nests (500-m buffer) in relation to the time of territory establishment. Trends were estimated using ordinary least squares regression (red line, confidence intervals in grey) and quantile regression (light blue to dark blue lines), considering the habitat gradients extracted from a principal component analysis (PC1-4; a-d)), the distances to the nearest nest from a neighboring territory (e), and the prediction error of the habitat model (f). The quantiles represented are 5% (dark blue), 25%, 50%, 75%, and 95% (light blue).

Table S1 - Summary statistics (mean ± SD: Range) of habitat variables used to characterise nesting habitat selection by Bonelli’s eagles in southern Portugal. Each variable was estimated around nesting sites and random points, within 250-, 500-, and 1000-m buffers.

Variables (code)	250 meters		500 meters		1000 meters	
	Nest	Random	Nest	Random	Nest	Random
Mean Elevation (m)	195.9 ± 116.3 (21.5-804.2)	199.5 ± 111.8 (0.0-722.4)	197.8 ± 113.8 (21.6-783.0)	199.6 ± 111.5 (0.0-739.2)	200.2 ± 108.8 (20.9-729.1)	200.0 ± 111.1 (0.0-757.0)
Standard Deviation of Elevation (m)	17.3 ± 8.9 (1.8-49.8)	10.4 ± 8.2 (0.0-48.8)	23.7 ± 11.8 (3.3-69.1)	15.7 ± 11.5 (0.0-81.6)	29.9 ± 14.1 (5.3-76.5)	21.9 ± 14.5 (0.0-86.3)
Mean Slope (°)	10.1 ± 4.3 (1.3-22.7)	6.0 ± 4.1 (0.0-20.8)	9.6 ± 3.9 (1.4-18.8)	6.0 ± 3.8 (0.0-17.4)	8.9 ± 3.6 (1.4-17.6)	6.0 ± 3.5 (0.0-17.1)
Standard deviation of slope (°)	4.7 ± 1.8 (0.7-9.0)	2.9 ± 1.8 (0.0-9.1)	4.9 ± 1.7 (0.7-8.5)	3.3 ± 1.9 (0.0-8.3)	5.0 ± 1.6 (0.9-8.8)	3.5 ± 1.8 (0.0-8.3)
Mean Ruggedness Index (x10^3)	2.6 ± 1.7 (0.1-7.1)	1.2 ± 0.00130 (0.0-7.3)	2.4 ± 1.4 (0.1-6.2)	1.2 ± 01.2 (0.0-5.9)	2.2 ± 1.3 (0.1-5.7)	1.2 ± 1.2 (0.0-5.6)
Standard Deviation Ruggedness Index (x10^3)	1.9 ± 1.2 (0.04-8.0)	0.9 ± 0.9 (0.0-0.5)	2.0 ± 1.1 (0.04-5.4)	1.1 ± 1.0 (0.0-5.7)	2.0 ± 1.1 (0.2-4.5)	1.2 ± 1.0 (0.0-4.5)
Density of waterlines (m/m^2;10^3)	1.8 ± 6.9 (0.0-6.9)	1.1 ± 1.6 (0.0-6.2)	1.6 ± 1.1 (0.0-4.1)	1.1 ± 1.0 (0.0-4.0)	1.3 ± 0.6 (0.2-2.7)	1.0 ± 0.5 (0.0-2.8)
Density of paved roads (m/m^2;10^3)	0.0 (0.0-0.0)	0.4 ± 1.0 (0.0-5.4)	0.1 ± 0.3 (0.0-2.0)	0.5 ± 1.0 (0.0-7.1)	0.1 ± 2.8 (0.0-1.3)	0.6 ± 0.9 (0.0-7.8)
Density of power lines (m/m^2;10^3)	0.1 ± 0.3 (0.0-2.4)	0.1 ± 1.2 (0.0-7.7)	0.1 ± 0.3 (0.0-1.5)	0.6 ± 1.0 (0.0-10.2)	0.2 ± 0.3 (0.0-1.1)	0.6 ± 0.8 (0.0-8.5)
Proportion of artificial areas (%)	0.02 ± 0.3 (0.0-2.8)	0.04 ± 0.2 (0.0-29.4)	0.2 ± 1.4 (0.0-11.9)	0.8 ± 3.2 (0.0-37.2)	0.2 ± 7.8 (0.0-5.8)	1.0 ± 3.1 (0.0-32.2)
Proportion of agricultural areas (%)	10.0 ± 19.2 (0.0-96.3)	39.8 ± 40.2 (0.0-100.0)	13.4 ± 20.2 (0.0-95.8)	39.3 ± 36.5 (0.0-100)	16.3 ± 20.5 (0.0-92.6)	0.386 ± 0.332 (0.000-1.000)
Proportion of forests (%)	29.6 ± 31.7 (0.0-100.0)	16.9 ± 27.6 (0.0-100.0)	26.8 ± 28.2 (0.0-98.3)	16.3 ± 23.9 (0.0-100.0)	25.7 ± 24.9 (0.0-91.6)	15.9 ± 20.6 (0.0-95.3)
Proportion of open forests (%)	57.8 ± 34.3 (0.0-100.0)	41.1 ± 38.6 (0.0-100)	57.8 ± 30.7 (0.0-100)	41.9 ± 34.6 (0.0-100)	56.2 ± 28.3 (0.0-100.0)	42.6 ± 31.2 (0.0-100.0)
Proportion of water bodies (%)	2.6 ± 5.3 (0.0-25.2)	1.7 ± 9.0 (0.0-100)	1.7 ± 3.2 (0.0-14.2)	1.6 ± 8.3 (0.0-95.4)	1.6 ± 2.7 (0.0-17.3)	1.6 ± 7.2 (0.0-0.86.4)
Distance to the nearest Bonelli’s eagle nest (m)	8767.6 ± 6602.6 (3270.3-45507.9)	3501 ± 1641 (1256-10453)	8768 ± 6603 (3270-45508)	3501 ± 1641 (1256-10453)	8768 ± 6603 (3270-45508)	3501 ± 1641 (1256-10453)

Table S2a - Summary of the model selection procedure to evaluate the factors influencing nesting site selection by Bonelli’s eagles in southern Portugal at the 250-m buffer scale. Models are ranked by decreasing value of AICc. For each model we provide the variables included, the degrees of freedom (df) the log-likelihood (logLik), the Aikaike Information Criteria corrected for small sample sizes (AICc), the variation in AICc in relation to the top ranking model, and the Aikaike weight (wi). The 95% set of models used in model averaging are underlined in grey.

Model ID	**Model parameters (250 m)**	**df**	**logLik**	**AICc**	**ΔAICc**	***wi***
20	PC1, PC2, D_NEST	3	-14.552	35.100	0.000	0.337
24	PC1, PC2, PC3, D_NEST	4	-13.748	35.500	0.390	0.277
32	PC1, PC2, PC3, PC4, D_NEST	5	-13.031	36.100	0.960	0.209
28	PC1, PC2, PC4, D_NEST	4	-14.216	36.400	1.330	0.174
22	PC1, PC3, D_NEST	3	-20.296	46.600	11.490	0.001
30	PC1, PC3, PC4, D_NEST	4	-19.361	46.700	11.620	0.001
18	PC1, D_NEST	2	-22.584	49.200	14.060	0.000
26	PC1, PC4, D_NEST	3	-21.955	49.900	14.810	0.000
31	PC2, PC3, PC4, D_NEST	4	-21.617	51.200	16.130	0.000
23	PC2, PC3, D_NEST	3	-26.137	58.300	23.170	0.000
27	PC2, PC4, D_NEST	3	-26.334	58.700	23.560	0.000
19	PC2, D_NEST	2	-29.077	62.200	27.050	0.000
29	PC3, PC4, D_NEST	3	-30.433	66.900	31.760	0.000
21	PC3, D_NEST	2	-32.437	68.900	33.770	0.000
25	PC4, D_NEST	2	-34.393	72.800	37.680	0.000
17	D_NEST	1	-35.965	73.900	38.830	0.000
4	PC1, PC2	2	-73.981	152.000	116.860	0.000
8	PC1, PC2, PC3	3	-73.244	152.500	117.380	0.000
12	PC1, PC2, PC4	3	-73.965	153.900	118.830	0.000
16	PC1, PC2, PC3, PC4	4	-73.244	154.500	119.380	0.000
6	PC1, PC3	2	-85.285	174.600	139.470	0.000
14	PC1, PC3, PC4	3	-85.272	176.500	141.440	0.000
2	PC1	1	-88.176	178.400	143.250	0.000
10	PC1, PC4	2	-88.037	180.100	144.970	0.000
15	PC2, PC3, PC4	3	-133.999	274.000	238.890	0.000
7	PC2, PC3	2	-136.158	276.300	241.210	0.000
11	PC2, PC4	2	-141.582	287.200	252.060	0.000
3	PC2	1	-142.8	287.600	252.490	0.000
13	PC3, PC4	2	-151.359	306.700	271.610	0.000
5	PC3	1	-152.47	306.900	271.840	0.000
9	PC4	1	-160.183	322.400	287.260	0.000
1	Null	0	NA	NA	NA	0.000

Table S2b - Summary of the model selection procedure to evaluate the factors influencing nesting site selection by Bonelli's eagles in southern Portugal at the 500-m buffer scale. Models are ranked by decreasing value of AICc. For each model we provide the variables included, the degrees of freedom (df) the log-likelihood (logLik), the Aikaike Information Criteria corrected for small sample sizes (AICc), the variation in AICc in relation to the top ranking model, and the Aikaike weight (*wi*). The 95% set of models used in model averaging are underlined in grey.

Model ID	Model parameters (500 m)	df	logLik	AICc	ΔAICc	*Wi*
32	PC1, PC2, PC3, PC4, D_NEST	5	-15.534	41.100	0.000	0.338
24	PC1, PC2, PC3, D_NEST	4	-16.661	41.300	0.250	0.298
20	PC1, PC2, D_NEST	3	-18.116	42.200	1.160	0.189
28	PC1, PC2, PC4, D_NEST	4	-17.530	43.100	1.990	0.125
22	PC1, PC3, D_NEST	3	-20.293	46.600	5.520	0.021
30	PC1, PC3, PC4, D_NEST	4	-19.394	46.800	5.720	0.019
18	PC1, D_NEST	2	-22.794	49.600	8.520	0.005
26	PC1, PC4, D_NEST	3	-22.275	50.600	9.480	0.003
31	PC2, PC3, PC4, D_NEST	4	-21.487	51.000	9.910	0.002
23	PC2, PC3, D_NEST	3	-25.518	57.000	15.970	0.000
27	PC2, PC4, D_NEST	3	-28.026	62.100	20.980	0.000
19	PC2, D_NEST	2	-30.501	65.000	23.930	0.000
29	PC3, PC4, D_NEST	3	-29.923	65.800	24.780	0.000
21	PC3, D_NEST	2	-31.857	67.700	26.640	0.000
25	PC4, D_NEST	2	-34.273	72.500	31.480	0.000
17	D_NEST	1	-35.965	73.900	32.860	0.000
4	PC1, PC2	2	-78.898	161.800	120.730	0.000
12	PC1, PC2,PC4	3	-78.768	163.500	122.470	0.000
8	PC1, PC2, PC3	3	-78.852	163.700	122.640	0.000
16	PC1, PC2, PC3, PC4	4	-78.721	165.400	124.370	0.000
2	PC1	1	-92.697	187.400	146.330	0.000
6	PC1, PC3	2	-92.239	188.500	147.410	0.000
10	PC1, PC4	2	-92.425	188.800	147.780	0.000
14	PC1, PC3, PC4	3	-91.974	189.900	148.880	0.000
15	PC2, PC3, PC4	3	-135.271	276.500	235.470	0.000
7	PC2, PC3	2	-136.345	276.700	235.620	0.000
3	PC2	1	-141.945	285.900	244.820	0.000
11	PC2, PC4	2	-141.148	286.300	245.230	0.000
5	PC3	1	-155.154	312.300	271.240	0.000
13	PC3, PC4	2	-154.828	313.700	272.590	0.000
9	PC4	1	-160.564	323.100	282.060	0.000
1	Null	0	NA	NA	NA	0.000

Table S2c - Summary of the model selection procedure to evaluate the factors influencing nesting site selection by Bonelli's eagles in southern Portugal at the 1000-m buffer scale. Models are ranked by decreasing value of AICc. For each model we provide the variables included, the degrees of freedom (df) the log-likelihood (logLik), the Aikaike Information Criteria corrected for small sample sizes (AICc), the variation in AICc in relation to the top ranking model, and the Aikaike weight (*wi*). The 95% set of models used in model averaging are underlined in grey.

Model ID	Model parameters (1000 m)	df	logLik	AICc	ΔAICc	*Wi*
32	PC1, PC2, PC3, PC4, D_NEST	5	-12.623	35.200	0.000	0.602
28	PC1, PC2, PC4, D_NEST	4	-14.893	37.800	2.540	0.169
24	PC1, PC2, PC3, D_NEST	4	-15.491	39.000	3.740	0.093
20	PC1, PC2, D_NEST	3	-16.857	39.700	4.470	0.064
30	PC1, PC3, PC4, D_NEST	4	-16.192	40.400	5.140	0.046
22	PC1, PC3, D_NEST	3	-18.676	43.400	8.110	0.010
26	PC1, PC4, D_NEST	3	-18.757	43.500	8.270	0.010
18	PC1, D_NEST	2	-20.517	45.000	9.790	0.005
31	PC2, PC3, PC4, D_NEST	4	-19.615	47.200	11.980	0.002
23	PC2, PC3, D_NEST	3	-25.443	56.900	21.640	0.000
27	PC2, PC4, D_NEST	3	-25.688	57.400	22.130	0.000
19	PC2, D_NEST	2	-29.501	63.000	27.760	0.000
29	PC3, PC4, D_NEST	3	-28.682	63.400	28.120	0.000
21	PC3, D_NEST	2	-32.165	68.300	33.080	0.000
25	PC4, D_NEST	2	-32.676	69.400	34.110	0.000
17	D_NEST	1	-35.965	73.900	38.690	0.000
4	PC1, PC2	2	-76.684	157.400	122.120	0.000
8	PC1, PC2, PC3	3	-76.553	159.100	123.860	0.000
12	PC1, PC2, PC4	3	-76.597	159.200	123.950	0.000
16	PC1, PC2, PC3, PC4	4	-76.446	160.900	125.650	0.000
2	PC1	1	-89.391	180.800	145.540	0.000
6	PC1, PC3	2	-88.890	181.800	146.530	0.000
10	PC1, PC4	2	-89.390	182.800	147.530	0.000
14	PC1, PC3, PC4	3	-88.890	183.800	148.530	0.000
15	PC2, PC3, PC4	3	-130.406	266.800	231.570	0.000
7	PC2, PC3	2	-131.622	267.200	232.000	0.000
3	PC2	1	-135.918	273.800	238.590	0.000
11	PC2, PC4	2	-135.070	274.100	238.900	0.000
5	PC3	1	-154.512	311.000	275.780	0.000
13	PC3, PC4	2	-153.987	312.000	276.730	0.000
9	PC4	1	-160.420	322.800	287.600	0.000
1	Null	0	NA	NA	NA	0.000

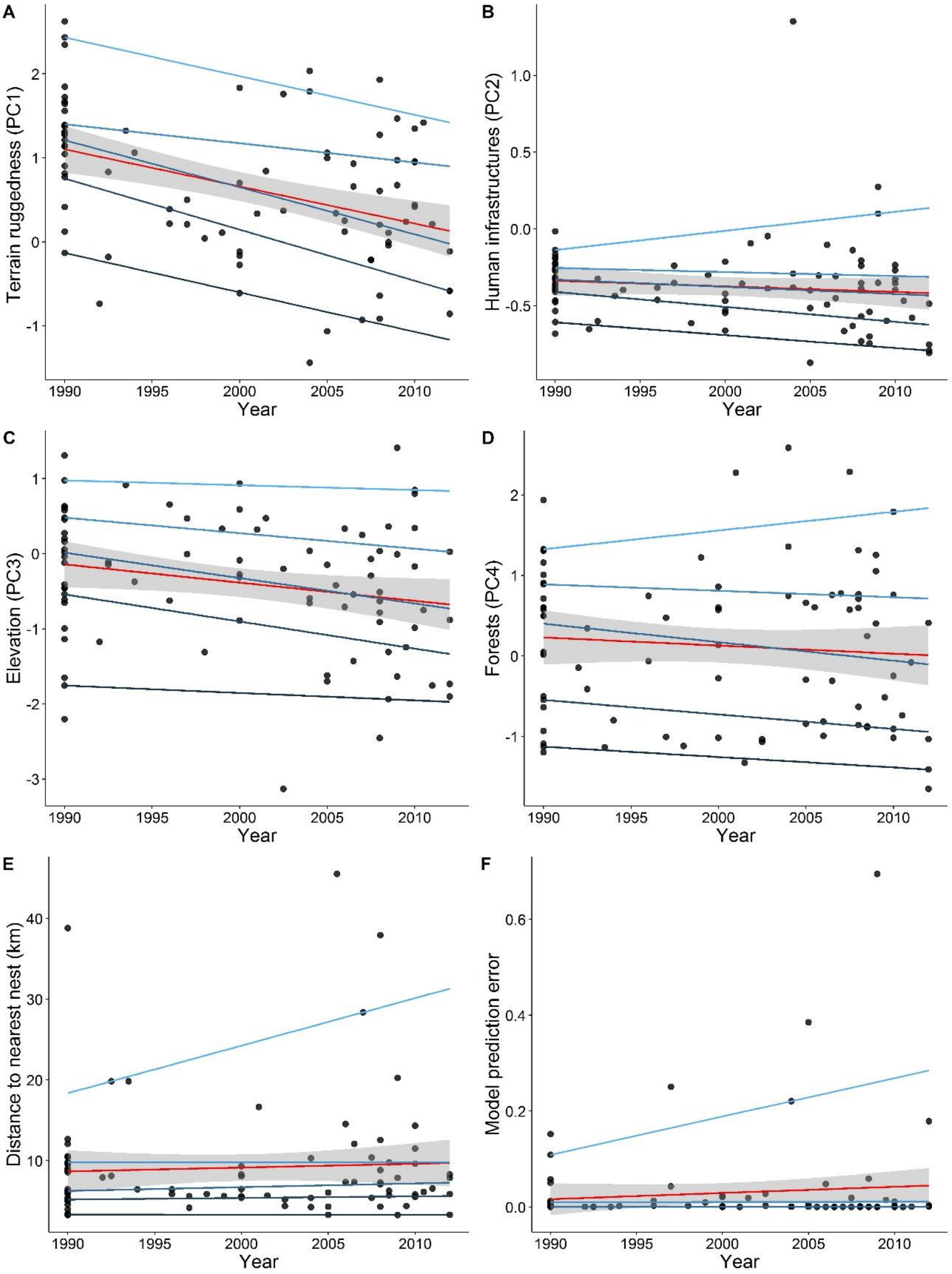

Figure S1 – Scatterplots showing trends in habitat conditions around Bonelli's eagle nests (250-m buffer) in relation to the year of territory establishment. Trends were estimated using ordinary least squares regression (red line, confidence intervals in grey) and quantile regression (light blue to dark blue lines), considering the habitat gradients extracted from a Principal Component Analysis (PC#), the distances to the nearest nest from a neighbouring territory, and the prediction error of the habitat model. The quantiles represented are 5% (dark blue), 25%, 50%, 75% and 95% (light blue).

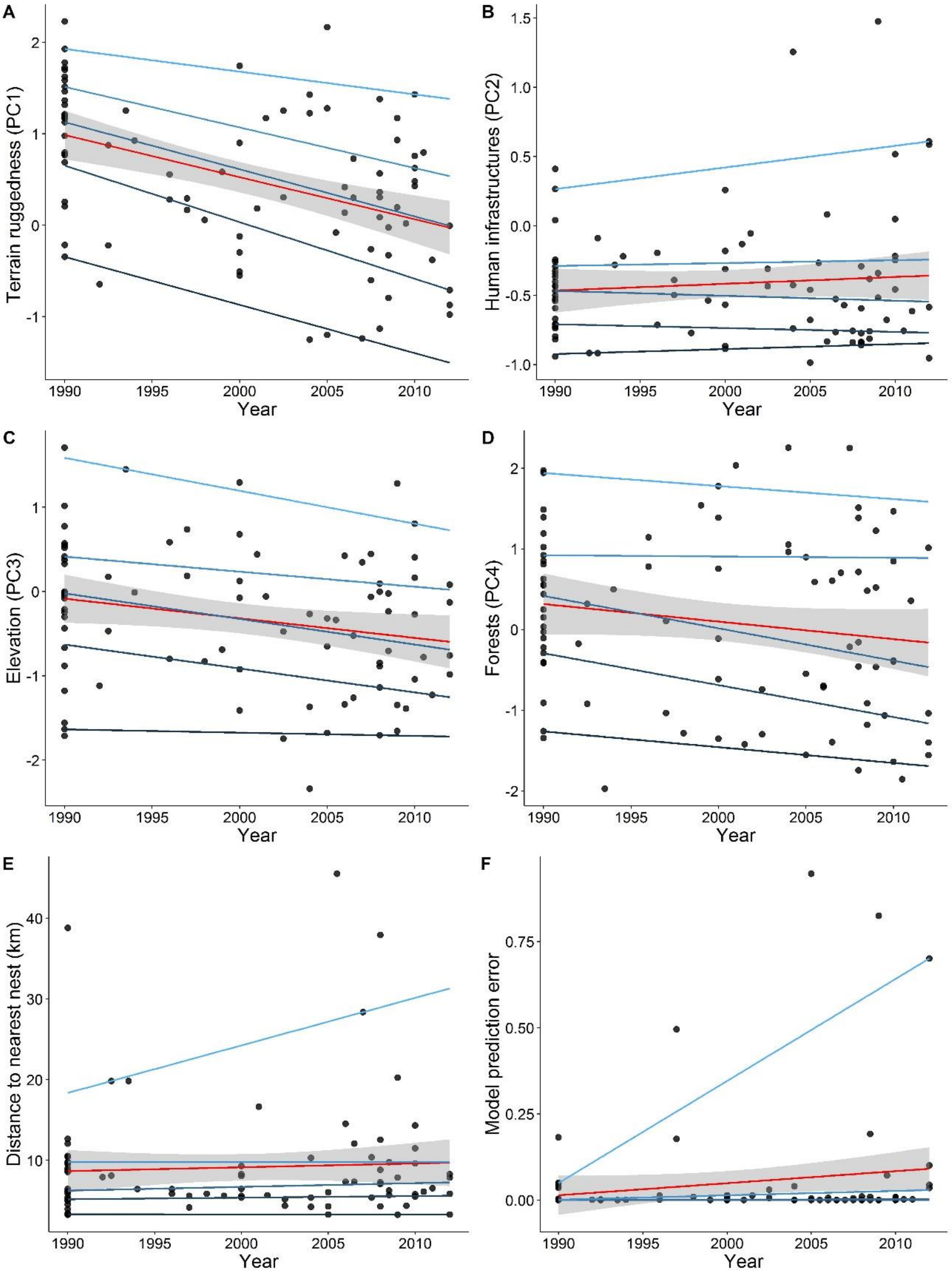

Figure S2 – Scatterplots showing trends in habitat conditions around Bonelli’s eagle nests (1000-m buffer) in relation to the year of territory establishment. Trends were estimated using ordinary least squares regression (red line, confidence intervals in grey) and quantile regression (light blue to dark blue lines), considering the habitat gradients extracted from a Principal Component Analysis (PC#), the distances to the nearest nest from a neighbouring territory, and the prediction error of the habitat model. The quantiles represented are 5% (dark blue), 25%, 50%, 75% and 95% (light blue).

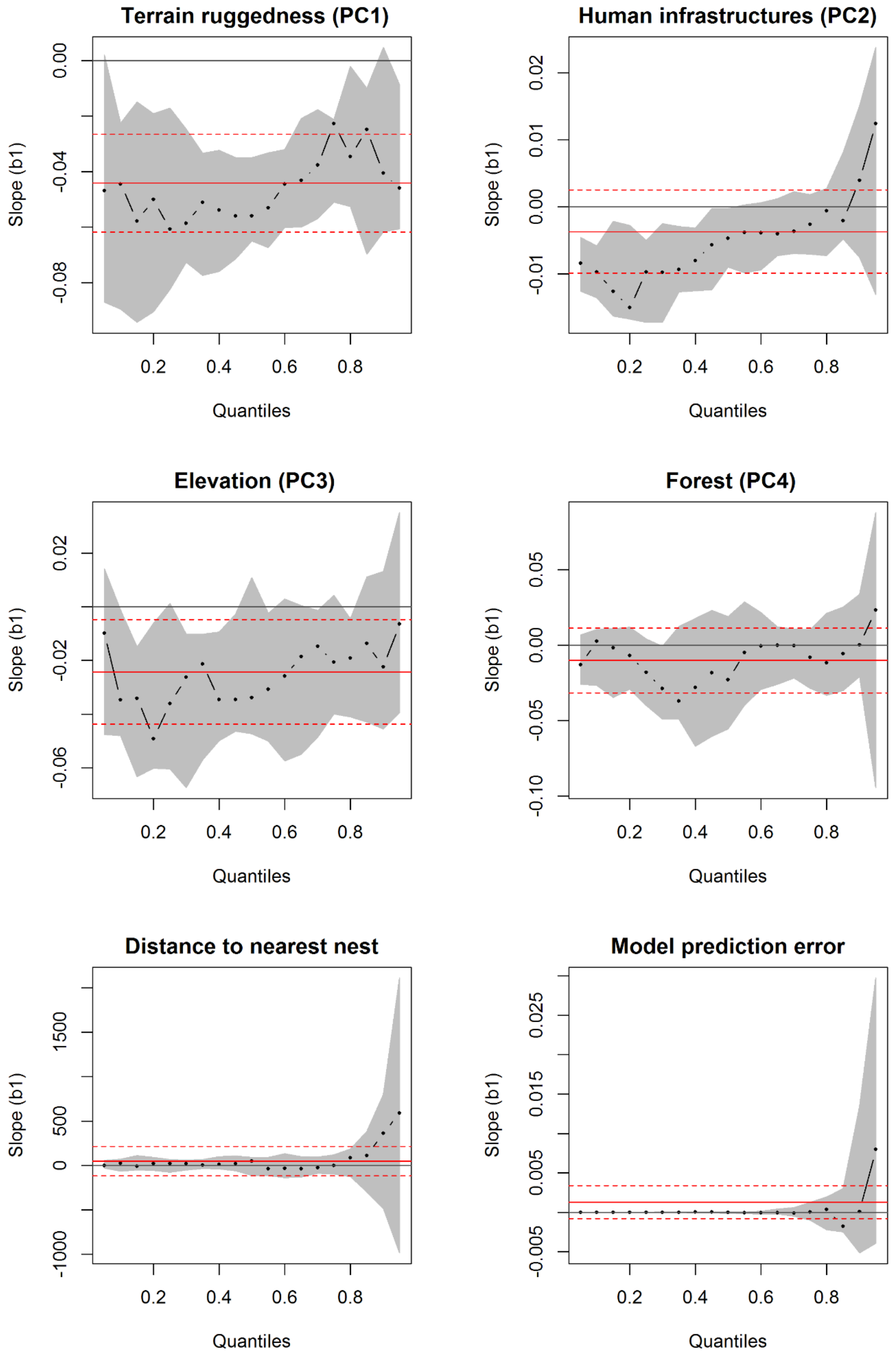

Figure S3 – Estimated slopes (black circles) and its 90% confidence intervals (grey area) for quantile regression models (5% to 95%, at 5% increments) relating habitat conditions around Bonelli’s eagle nests (250-m) to the year of territory establishment. We also provide the slope (red line) and confidence bounds (hatched red line) for the slope estimated with ordinary least squares regression.

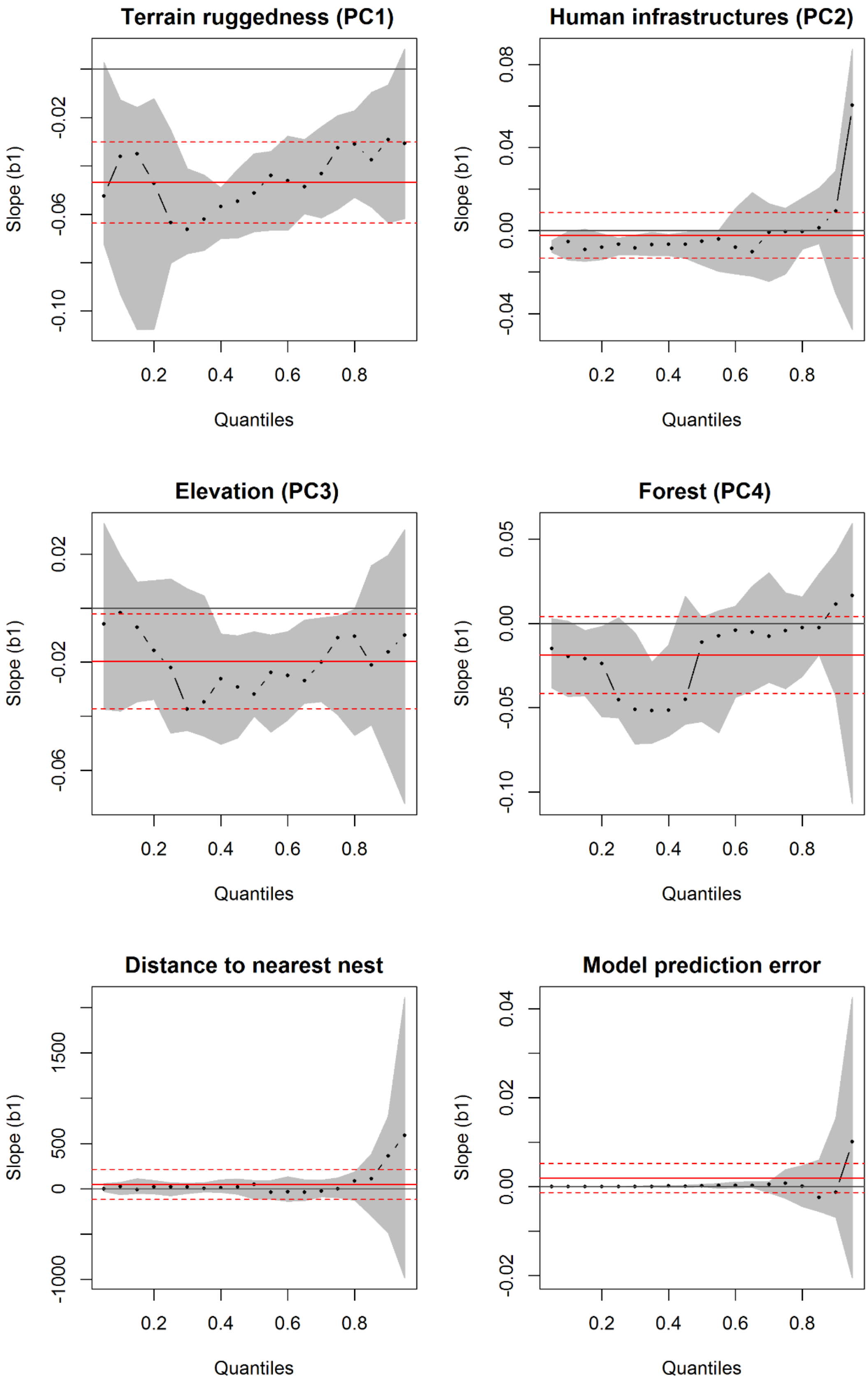

Figure S4 – Estimated slopes (black circles) and its 90% confidence intervals (grey area) for quantile regression models (5% to 95%, at 5% increments) relating habitat conditions around Bonelli’s eagle nests (500-m) to the year of territory establishment. We also provide the slope (red line) and confidence bounds (hatched red line) for the slope estimated with ordinary least squares regression.

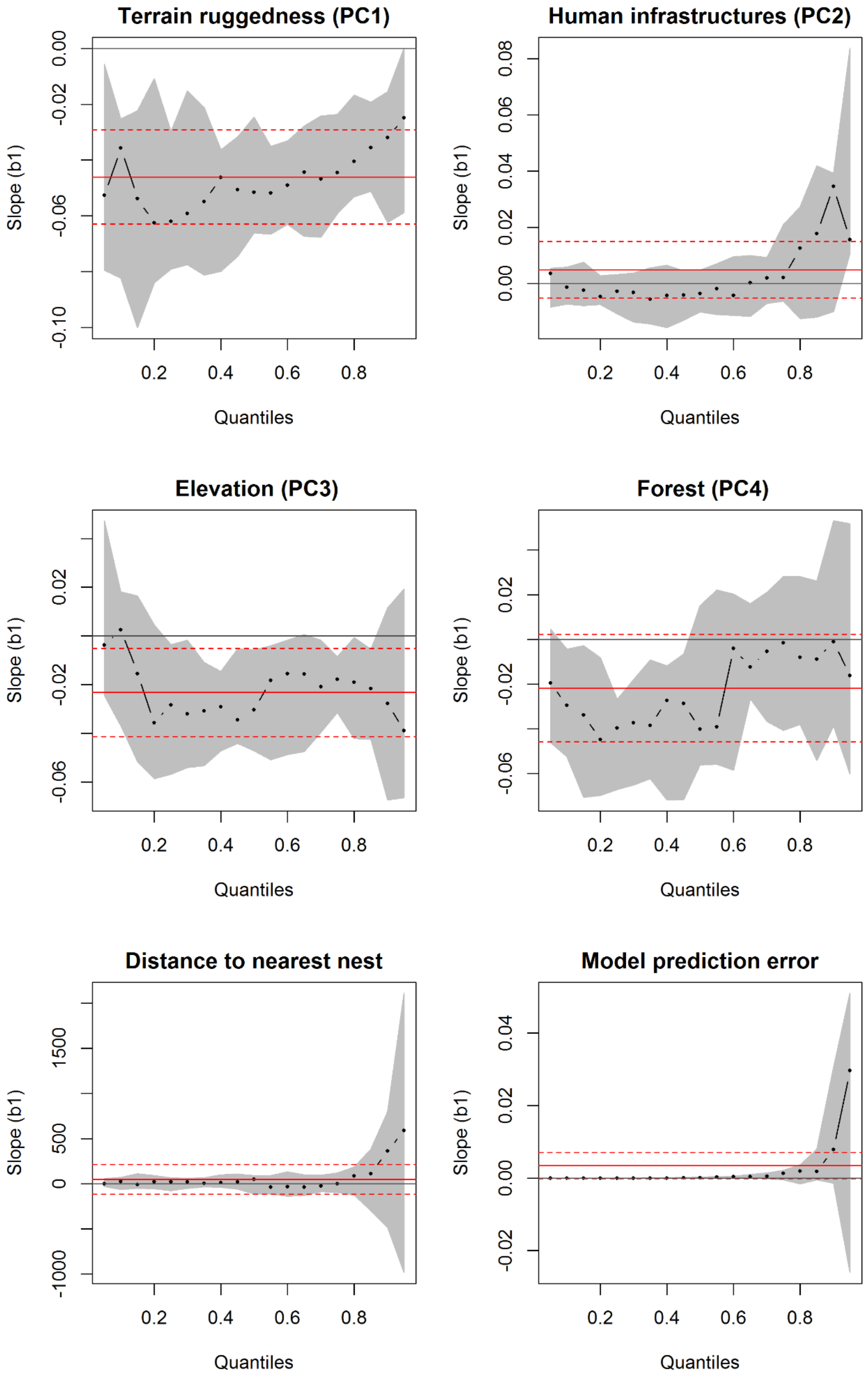

Figure S5 – Estimated slopes (black circles) and its 90% confidence intervals (grey area) for quantile regression models (5% to 95%, at 5% increments) relating habitat conditions around Bonelli's eagle nests (1000-m) to the year of territory establishment. We also provide the slope (red line) and confidence bounds (hatched red line) for the slope estimated with ordinary least squares regression.

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GENERAL DISCUSSION

The most exceptional feature of the Earth is the existence of life and the most extraordinary feature of this life is its diversity (Cardinale et al. 2012). The magnitude of the impact of human activities on global biodiversity has been documented at several organizational levels (Gaston et al. 2003). Today, strategies for preserving biodiversity mainly focus on the conservation of either species or ecosystems (Groom et al. 2006, Mace et al. 2007, Primack 2010).

Maintaining biodiversity is essential if the supply of ecosystem services is to continue and it is equally important to ensure their health and resilience (Pereira et al. 2013). To qualify as a biodiversity hotspot, a region must meet two strict criteria: 1) it must have at least 1,500 endemic vascular plants (*i.e.* a high percentage of plant life found nowhere else on the planet); and 2) it must have retained only 30% or less of its original natural vegetation, which is regarded as threatened (Marchese 2015).

The Mediterranean Basin is an example of a global biodiversity hotspot (Myers et al. 2000). These hotspots are said to be experiencing a major loss of habitats, as well as a decline in certain species such as birds of prey that play a key role in the ecological relationships of the system (Delibes-Mateos 2008). As a part of the species strategy, a focus on species whose conservation has implications for other ecosystem elements – the so-called umbrella species that need such large tracts of habitat that saving them will automatically save many other species (Simberloff 1998) – is often advocated (Caro and O'Doherty 1999; Branton and Richardson 2010). As a global conservation strategy, the focus on umbrella species including top predators is compatible with the preservation of key elements of all communities in Mediterranean ecosystems. Specifically, greater knowledge of the biological characteristics of a species, as well as of its biological role in ecosystems and the conservation problems that threaten it, help a focal species become a flagship species. From a strategic point of view, the presence of flagship species within biological communities (Simberloff 1998; Sergio et al. 2006) will often represent a very useful tool for conservationists and managers given that these species are generally greatly appreciated by people from all walks of life (Real 1991; Moleón et al. 2009).

In Mediterranean ecosystems, Bonelli's eagle is considered as an umbrella and flagship species (Real 1991; Moleón et al. 2009). It is long-lived and is found in a range that extends from south-east Asia and the Middle East to the western Mediterranean (del Hoyo et al. 1994). Territorial birds are found mainly in warm upland areas with rough terrain, normally crags and cliffs, and with variable degrees of vegetation cover: zones with extensive bush and shrub cover (*e.g.* maquis and garrigue) and sometimes with forests, but also barren slopes with virtually no vegetation. It occurs above all from sea-level to 1500 m in Europe, up to 2000 m in NW Africa, and up to 3750 m in Asia (Orta et al., 2016).

Considered of Least Concern worldwide and Near Threatened in Europe (BirdLife International 2015), in the Iberian Peninsula, however, Bonelli’s eagle is currently classified as Endangered (Madroño et al. 2004; Cabral et al. 2005). Its population status is an indicator of the health of the ecosystems in which it lives and its preservation is synonymous with the maintenance of biodiversity. Its conservation is linked to the general quality of its environment since it is a species that has suffered a marked decrease both in the number of birds and in the extension of its breeding range (López-López et al. 2012; BirdLife 2017). Despite a serious decline in its numbers since the 1970s, its populations have recently stabilized (del Moral 2006). Its regression has been especially intense in the northern half of the Iberian Peninsula and France, a decline that has been attributed to a demographic imbalance between survival and reproductive rates (Real and Mañosa 1997; Hernández-Matías et al. 2013) and, more specifically, to the increase and development of infrastructures such as electric power lines and communication routes that directly and indirectly affect this species’ survival, higher mortality rates, habitat destruction, and the isolation of populations (Pérez-García 2014; Ferrer 2012; Fahrig 2003). Despite the sharp decline in Bonelli’s eagles in the 1980s and 1990s due to increased adult and pre-adult mortality and habitat degradation, over the past 20 years the number of pairs has increased in southern Portugal, probably due to the increasing availability of habitat as the result of the human depopulation of rural areas that began in the first half of the twentieth century (Del Moral 2006).

Throughout its Mediterranean range, Bonelli's eagle is known to be primarily a cliff-nesting species, and only a fairly small percentage of breeding pairs nest in trees in this region (*e.g*. Muñoz et al., 2005). In 1991, however, in the south-west Portuguese uplands an almost entirely unknown tree-nesting Bonelli's eagle population was discovered (Palma et al. 1999), which has been expanding ever since (Palma 2013). It is one of the few birds of prey that can nest both on cliffs and in trees, thus this plasticity increases its potential distribution and ability to occupy habitat (del Moral, 2018).

Presumably, this tree-nesting population grew out of a few founding pairs in the south-west uplands and the neighbouring south-east lowlands that were present in the first half of the twentieth century (Mira 2006). This population has low genetic diversity but high genetic differentiation from other populations, which suggests that immigration is rare and that there is a certain degree of reproductive isolation. Imprinted tree-nesting behaviour may explain the strong preference for tree- as opposed to cliff-nesting, which may be one of the reasons for the observed genetic divergence (Mira 2006). This population acts as source whose dispersal sustains other populations, thereby preventing their decline (Hernández-Matías et al. 2013).

Specific morphological features of the tree-nesting population

The southern Portugal tree-nesting Bonelli's eagle population has divergent genetic features that allow us to compare its biometric measure with other European populations. Biometric measures are a useful tool in ornithology (Eck et al. 2011) and are valuable in conservation, ecology, biology, taxonomy and phylogenetic studies (Araóz et al. 2016). The comparison of the biometry of Bonelli's eagles from the Iberian Peninsula and France revealed differences between populations with different nesting habitats. The tree-nesting population had a generally larger body length, wingspan, head length and width, tarsus width, and tail length. This differentiation is matched by the previously described differences in diet (Palma et al. 2006, 2013), genetic structure (Mira et al. 2013) and nesting behaviour (Dias et al. 2017). For example, tails act as control devices that help maintain stability and as lifting surfaces that enhance manoeuvrability, agility and low-speed flight. Birds that require greater manoeuvrability generally have longer tails, for instance, to avoid collisions in cluttered environments (Thomas and Balmford 1995). This means that wing and tail structure may be related to vegetation density (Norberg 1990), which would seem to be the case of this tree-nesting Bonelli's eagle population, whose longer tails could be an adaptive feature related to habitat and prey selection. Another example of a parameter that could indicate differences in individuals and populations is body mass, an increase in which improves resistance to adverse environmental conditions and to food unpredictability, especially when birds face a fall in prey numbers (Hernández et al. 2011). Bonelli's eagles usually prey on European rabbits (*Oryctolagus cuniculus*) in Spain (Moleón et al. 2009, 2012; Caro et al. 2011) and France (Morvan 2010; Resano et al. 2012), where they are mostly cliff-nesters. Conversely, the tree-nesting Bonelli's eagles in SW Portugal have had to adapt to the decline of their staple prey and consume more birds. Geographical and temporal variations in body size are common phenomena in organisms whose principal predictors are food availability during growth periods and environmental temperatures.

Other environmental factors besides temperature such as humidity, seasonality and precipitation have been proposed as factors contributing to geographical variations in body size (Fan et al. 2019).

In this sense, animals that live at higher latitudes/elevations (*i.e.* at lower average temperatures) tend to have larger bodies (Bergmann's rule) and smaller appendages (Allen's rule) for thermoregulatory reasons. According to the heat conservation hypothesis, large body size and small appendage size help animals retain heat when subject to cold environmental temperatures, whereas small body size and large appendage size help them dissipate heat when necessary (Fan et al. 2019). There is no agreement about whether or not Bergmann's rule is general or valid. Empirical studies have found predicted patterns at both intraspecific and interspecific levels in mammals and birds, although animals that do not follow Bergmann's rule have also been reported (Fan et al. 2019). Within our study area, although latitudinal variation is insufficient to test Bergmann's rule directly, Bonelli's eagles do not show gradual size variations with annual mean temperature. Although French Bonelli's eagles are heavier and have larger claws (see also García et al., 2013), Bonelli's eagles from southern Portugal contradict Bergmann's latitudinal rule and have the highest values for most of the analysed biometric variables. Different biometrics could stem from adaptation to the forest environments in which this population nests. Within the geographical area considered, the biometric measurements of the Bonelli's eagle population are largely homogeneous, even though there are some important regional variations including the differentiation of the south-western tree-nesting population.

Taphonomy related to trophic relationships

Taphonomy means 'the laws of burial' (Behrensmeyer and Hill 1980) and is the field of study that describes and analyses the modifications that organisms undergo from the moment of death until they are unearthed at forensic, archaeological or palaeontological sites (Stiner 2008). Multidisciplinary studies such as the combination of taxonomy and ecology are of increasing relevance. Ecologists and palaeontologists (*i.e.* taphonomists) share a common interest in the natural cycles of life and death, even if their viewpoints on living organisms and the processes that recycle or preserve their remains are different. From studies of recent bone assemblages, taphonomists can gather information on diversity and abundance, animal behaviour, predator-prey interactions, habitat utilization, mortality (how and where animals die) and nutrient recycling. Although these studies were initially designed to improve paleontological understanding of the content and biases in the fossil record, the methods and findings of taphonomic research in modern ecosystems are also of potential value to ecologists. Both palaeontology and ecology benefit from the increased exchange of ideas and perspectives. The usefulness of taphonomy provides a potentially powerful tool for looking back in time for changes in community structure, species richness, habitat utilization and predator-prey interactions (Behrensmeyer and Miller, 2012).

We undertook the first ever taphonomic study of Bonelli's eagles via the analysis of pellets, which gave us an indication of the diet of tree-nesting Bonelli's eagle. Interestingly, it was found that the most-often consumed prey was the wild rabbit (*Oryctolagus cuniculus*) followed by the red-legged partridge (*Alectoris rufa*). However, analysis of samples showed that Bonelli's eagles in forest environments consume a greater diversity of birds besides partridges (*Columba* spp*., Garrulus glandarius,* *Corvidae, Ciconiiformes, Larus michaellis* and *Passeriformes*), while cliff-nesting Bonelli's eagles mainly consumed only *Columba* spp. and *Streptopelia* spp. (Lloveras et al., 2014). These findings are supported by other studies (Resano 2014; Real 1991; Moleón et al. 2009, 2012).

The presence of the remains of storks (Ciconiiformes) and yellow-legged gulls (*Larus michahellis*) may be due to the fact that one of the Bonelli's eagle pairs has a landfill in its territory, where these prey items, which Benelli's eagles have been seen hunting, feed in great abundance. Pairs situated near the coast also feed on gulls. The detection of a fragment of fish (Cyprinidae) was a surprise, although it could have come from the stomach of a gull.

Another curiosity of this study was the damage inflicted by Bonelli's eagles on Leporidae and bird bones, which differs greatly from the damage caused by other predators; this allows the presence of this eagle to be confirmed in archaeological sites. This taphonomy study will make reveal whether abandoned raptor nests were once occupied by Bonelli's eagles or other birds of prey.

Recently, at the Neolithic site of WF16 in Faynan (Jordan), fragments of bird bones from archaeological excavations (2008–2010) were compared with skeletons in a reference collection. This enabled the birds present at this site between 12,000 and 10,000 years ago to be identified. Bonelli's eagles are depicted in artwork throughout the history of Jordan and are notably present in the culture of the Nabataean Kingdom, which controlled parts of the southern Levant, northern Arabia and the Sinai Peninsula around 2,000 years ago. This illustrates the connection that has always existed between man and this species of eagle (Mithen et al. 2019).

A novel tree-nesting habitat that favours population expansion

The geographical range of a species is dynamic and will contract, expand or otherwise change as a response to a whole range of environmental and demographic drivers (Gaston, 2003). It is very important to understand the contribution made by patterns of habitat selection to population expansion. The behavioural plasticity inherent in many animal species leads to the appearance of new capacities that allows them to cope with and re-adapt to new environments in light of changes provoked by, for instance, climate change and human action (*e.g.* changes in land use) (Ghalambor et al. 2007; Wright et al 2010). Accordingly, the capability of a species to shift or develop a new specific behaviour and thereby face up to a fresh disturbance is a way of increasing its effectiveness and survival possibilities (Sih et al. 2004; Yeh and Price 2004). Knowledge of the causes behind this type of novel behaviour can be crucial when defining conservation strategies. Nevertheless, knowledge of the advantages (and disadvantages) that animal species have when facing up to environmental change and its effects on their persistence are still largely lacking.

Artificial nesting substrates in the region of the tree-nesting population consist of huge eucalypt trees isolated in valley bottoms, possibly as a result of seed dispersal from trees planted beside houses on the tops of hills to identify human dwellings when access was poor. Due to the scarcity of such trees and the difficulty to access them, they are of no economic interest and are seldom cut down. This allows them to grow over the years and provide appropriate and fairly secure nest supports for large birds such as Bonelli's eagle. After the abandonment of cereal cultivation from the middle of the twentieth century onwards, eucalypt (*Eucalyptus globulus*) plantations rapidly expanded across the mountains of south-west Portugal (Krohmer and Deil 2003); in addition, European Community-funded afforestation programs promoted the planting of conifers (Louro 1999; Costa et al. 2003). These pine stands are also used by eagles to build their nests. Commercial eucalyptus plantations are also sometimes used as nest sites, albeit much less often than the largely isolated eucalypts described above. The increasing use of large eucalypts and pines for nesting as a response to the current decline in the quality and availability of native trees is also striking (Ferreira 2010). The decline in native cork oaks for nesting is probably due to the extensive morbidity and mortality observed in cork oak stands, coupled with their degradation due to unsustainable forestry activities. This use of allochthonous trees foments the colonising of these novel ecosystems and, as the Earth becomes ever-more transformed by human actions, such ecosystems will increase in importance, even though yet they are relatively little studied (Hobbs et al. 2006).

This tree-nesting population appeared relatively recently and has exploited an unusual breeding niche, thereby making its study a key part of management actions. It is also important because it allows the species to occupy cliff-less habitats and thus expand throughout a large area that it otherwise would not be able to occupy (Palma, 2013).

Much of the evidence on behavioural plasticity allowing for the exploration and colonization of novel habitats and landscapes is provided by exotic invasive species (*e.g.* Duncan et al 2003; Wright et al. 2010). However, such evidence may be sought amongst native populations if opportunities arise for them as a result of habitat changes mediated by human activities. Several examples of species' behavioural plasticity when faced with new environments have already been studied (*e.g.* Slabbekoorn and den Boer-Visser 2006; Bouchard, Goodyer and Lefebvre 2007; Levey et al. 2009).

The tree-nesting Bonelli's eagle population in southern Portugal has undergone a three-fold increase over the past 30 years, which has led to the rapid colonization of large expanses of formerly vacant habitats beyond its core area. This is due to its ability to nest in trees, which underscores the adaptive advantage of behavioural plasticity. Apart from a few other local populations (Bergier and Naurois 1985; Kassinis 2010) in the Mediterranean region, Bonelli's eagles are largely cliff-nesting (*e.g.* Cramp and Simmons 1980; Hagemaijer and Blair 1997) and seem constrained by their restricted choice of habitat (Muñoz et al. 2013). As Ghalambor et al. (2007) stated, adaptive plasticity will persist in populations if the fitness cost of its maintenance is not too great. Given that throughout their global range Bonelli's eagles use cliffs or trees as nesting substrates depending on the availability of tree cover – and of tall trees in particular – and that tree-nesting is predominant in some regions such as southern Asia (*e.g.* Naoroji 2006; Zheng 1987), it seems plausible that the study population has retained some of the original ecological plasticity of the species within its core range, in which both cliff and tree-nesting territories co-existed before the onset of its expansion into the new habitats (Palma et al. 2013). However, in much of the Mediterranean area – possibly due to profound human-driven habitat changes in otherwise potential habitat – this has not occurred. While modelling Bonelli's eagles' responses to predictable climatic changes in Iberia, Muñoz et al. (2013) took into account behavioural plasticity – *i.e.* the ability of the species to switch to tree-nesting to exploit new favourable areas created by climatic changes that were devoid of nesting cliffs – as a major factor determining the increment in habitat availability (Muñoz et al. 2015). This shows the importance of correctly describing species' habitat preferences in novel habitats to accurately determine their capacity for adaptive responses to future ecological scenarios.

Although the patterns of space use and habitat selection have been extensively studied in cliff-nesting Bonelli's eagles (*e.g.* Ontiveros 1999; Carrete et al. 2002; Gil-Sánchez et al. 2004), there is barely any information available for tree-nesting populations. Our study introduced a temporal dimension into habitat selection patterns that had never been considered before. Bonelli's nesting sites are associated with the most rugged areas within territories, which may be related to the presence of suitable nesting trees and less human disturbance (Palma et al. 2013; Real et al. 2016); as well, rugged areas are less affected by forest management (Real et al. 2016; Santana et al. 2011). This preference for nesting in rugged areas may be a conservative characteristic of Bonelli's eagles that they have maintained in different geographical regions and nest site typologies. Tree-nesting Bonelli's eagles are associated with areas with low densities of roads and powerlines. They avoid disturbances that may arise near (< 1 km) nesting sites. Our study also suggests that new Bonelli's eagle pairs chose habitats that are structurally comparable to those of the founder population nucleus, which may be a consequence of the imprinting of natal habitat conditions on young birds.

The expansion of the tree-nesting Bonelli's eagle population in southern Portugal consists essentially of a colonization of extensive areas that gradually began to offer the minimum required conditions, that is, little or no disturbance, food availability, and the presence of nesting sites, which were non-existent a few decades ago. This increase in favourable habitat stems from the rural exodus that took place in the latter half of the twentieth century, the recent increase prey availability associated with new hunting regulations, and, above all, the crucial existence of large trees in sufficient quantity and quality to safeguard the novel nesting behaviour that makes these populations so different from any other in Europe (Palma 2009). The fixation of this tree-nesting behaviour means that individuals from this population will be more likely to breed with birds from the same population than with birds from neighbouring cliff-nesting populations in Extremadura and Andalusia, thereby reducing the genetic flow between them and leading to a marked genetic differentiation in the Portuguese tree-nesting population.

Although currently growing quickly and demographically, the tree-nesting Bonelli's eagle population is still threatened both directly and indirectly by forestry, which has been intensifying and spreading over the past two decades and is affecting significantly the quality of the vegetation cover, including the availability of trees suitable for nesting and the serenity and security these birds require. To these factors can be added the high mortality of these trees due to climatic factors and the major fires occurring in recent years, as well as growing pressure in the mountainous south-west from infrastructures such as power lines, wind farms and dams. The lack of knowledge of several aspects of the biology of these tree-nesting eagles and the poor general awareness of the threats to this species remain important obstacles to its conservation (Palma 2009).

The plasticity and adaptability of this species, which enables it to breed on different substrates, is a positive element in its conservation. Given that the most important role of a nest is to protect the eggs, chicks and even the adults themselves, it seems that cliff nests are more inaccessible to land predators than a tree, largely because mammals can climb. Therefore, nest sites have to be inaccessible to terrestrial predators; however, the potential enemies of these tree-nesting Bonelli’s eagles do include other large birds of prey such as eagle owls and, to a lesser extent, imperial and golden eagles, as well as anthropic disturbance and threats.

On the other hand, the use of trees for nesting extends this species’ range into areas without adequate cliffs or even into areas where suitable cliffs are already occupied by other species (*e.g.* the griffon vulture colonies that saturate nesting areas, or golden eagles and eagle owls).

Implications for conservation

Nowadays, the main threats to the tree-nesting Bonelli’s eagles in SE Portugal are the risks associated with forestry activities. Tree-nesting occurs in both forested and semi-steppe habitats, and its conservation depends above all on the preservation of the few available tall mature trees. Preventing these risks warrants specific conservation measures to be included in forestry projects.

Notwithstanding the many threats that this population is having up to face up to, in this thesis we only comment on those that directly threaten their tree-nesting substrate.

1) Forestry activities - when they coincide with nesting areas, logging, planting and sowing, land preparation, deforestation, etc., can all severely disrupt nesting, often leading to breeding failure. In particular, forestry work that takes place during the most sensitive periods of the breeding calendar (*i.e.* nest reoccupation, laying and incubation at the beginning of the breeding season, and the period immediately after the juvenile's departure) are the most harmful.

2) Wind farms and electrical power line construction - electric power lines constructed in the vicinity of the nests can contribute to the degradation of breeding habitat and also to the abandonment of local nesting. In the case of wind farms, they can cause birds to desert the areas they frequent, due not only to the placing of the wind turbines but also to the electric power lines, access roads and human presence.

3) Rural roads and tracks - although Bonelli's eagle is relatively tolerant of anthropogenic habitat change, it still selects, especially for breeding sites, the least accessible areas that are furthest from roads and tracks (*e.g.* Carrascal and Seoane 2008). Roads and tracks also improve human access to nesting and refuge areas, thereby constituting a potential for habitat degradation.

4) Opening and maintaining paths/accesses – the opening and maintaining of roads and tracks associated with forestry operations aim to facilitate the access of people and machinery to extraction sites (*e.g.* wood, cork). In addition, they provide access, for example, for hunting and recreational activities and grazing, thereby increasing the disturbance to Bonelli's eagle.

5) Grove degradation – the nests of this population face problems of tree degradation in certain species. In the case of cork oaks, several causes have been highlighted to explain mortality, from soil degradation due to poor management to physiological stress caused by water deficit associated with decreased rainfall (Rodrigues de Sousa 2007). In large eucalypts of the species *Eucalyptus globulus*, water stress also appears to be the

cause of mortality. Wide-ranging mortality in maritime pines is due to infestation by a pine nematode, *Bursaphelenchus xylophilus* (Sousa et al. 2001; Mota and Vieira, 2004), whose vector is the Coleoptera *Monochamus galloprovincialis*. Large forest fires have also had an important impact on nesting conditions (in 2003 and 2004 fires affected around 100 000 ha and vital areas for 11 pairs). On a smaller scale, ungulates (wild boar and deer) are a further factor affecting conifers as they graze on the bark of tree trunks and stems, which can lead to the death of trees that hold nests. This exaggerated dependence of the species on large nesting trees is a limiting factor on their use as breeding sites. Trees selected to nest are predominantly large and the cutting down of these trees is a severe threat as there is a great shortage of such trees in undisturbed places. The availability of these trees may be a limiting factor to the installation of new pairs in this population and an obstacle to its further expansion.

6) <u>Nest collapse</u> – the collapse of tree nests is more likely than nests on cliffs due to the breaking of support branches, high winds, etc. Although the collapse of the whole nest is infrequent, a total or partial (more frequent) collapse can cause the loss of eggs or chicks.

One of the most important conservation measures for the tree-nesting Bonelli’s eagle population is a reduction in the disturbance caused by forestry activities. Habitat management contracts need to be signed with the owners of nesting sites to ensure the maintenance of nesting habitat quality and tranquillity during the breeding season. These contracts should include restrictions on the impact of forestry activities and, above all, long-term preservation of the large trees used as nesting sites. It is also important to provide forest landowners and managers with technical support that consists of advice on habitat-friendly management measures and the monitoring of their implementation (for example, seasonal restrictions on forestry activities in the vicinity of nests during the critical periods of reproduction to prevent disturbance at nest sites and favour good breeding success). It is likewise important to provide regular assistance to energy and environmental assessment companies aiming to mitigate the potential impact on Bonelli’s eagles of new powerlines and wind farms, and of road accesses in areas near nests. In the case of the pine nematode, healthy pines should be left that will provide alternative nesting sites. If a pine with a nest is affected and has to be cut down, and if there are no other large healthy pines that could act as alternatives, other nesting solutions should be contemplated including the construction of artificial nests in healthy trees (preferably in tree species not susceptible to the nematode). The reinforcement of nests with wooden stakes and natural branches can improve nest stability. The construction of artificial nests using flexible iron bars and wooden poles, filled with vegetation, provides sturdy nests for pairs with poor breeding success or in highly disturbed territories.

In this thesis we show how a population starting from a few individuals and changing its type of traditional nesting substrate from cliffs to trees has expanded its range and colonized new areas. In the Iberian Peninsula and, specifically, in Spain, where this eagle species is threatened and only 8% of pairs are known to nest trees (Del Moral, 2005 and 2018), the possibility of having alternative nesting sites may favour the colonization of new areas, promote an expansion, and improve the conservation status of the species.

This unusual behaviour (tree-nesting) has enabled Bonelli’s eagles to colonize habitats that would otherwise have been unviable, thereby helping the species to improve its response to ongoing climatic and land use changes (Hernández-Matías et al., 2013; Muñoz et al., 2013; Palma et al., 2013). These characteristics could be of great use for recovery programs using reintroductions since it has been demonstrated that this species can nest in trees (GREFA, Pers. Comm. and Viada, pers. comm.).

It is essential to continue studying this population, monitored since the beginning of 1990s, and to try to understand the mechanisms behind its expansion. Genetic studies can help verify assumptions related to the origin, dynamics and chronology of its demographic expansion and clarify its isolation from neighbouring populations.

As it is an endangered and umbrella species, it is necessary to preserve this population of Bonelli’s eagle as an evolutionary unit with its particular genetic characteristics that could provide greater genetic heterogeneity within the Iberian population. Its nesting behaviour allows it to adapt to different habitats, thereby stimulating it to occupy sites where it would otherwise not breed and enabling its population to expand.

CONCLUSIONS

- Bonelli's eagle is an umbrella species and its conservation implies the maintenance of its ecological food web and the habitats and ecosystems in which it lives. Consequently, its presence is a good ecological indicator of Mediterranean ecosystems.

- In the main part of its distribution, Bonelli's eagles nest on cliffs. However, an almost exclusively tree-nesting population was discovered in southern Portugal in the 1990s. This trend towards tree-nesting is increasing in this population and in other areas of its range in the Iberian Peninsula.

- The plasticity of its nesting behaviour and the fact that its diet is more diverse (birds, medium-sized mammals and sometimes reptiles) enables it to adapt better to different environments.

- Individuals from the studied tree-nesting Bonelli’s eagle population did not show any gradual variation in size related to environmental temperatures, although there are some features that do have statistical significance in tree-nesting Bonelli's eagles (greater body length, wingspan, length and width of the head, tarsal width and tail length).

- Taphonomic studies of Bonelli's eagles were carried out for the first time and this type of approach can enrich our overall knowledge of this species. According to other studies of the diet of this species, compared to cliff-nesting Bonelli's eagles, forest-nesting eagles consume a greater diversity of birds.

- The way that Bonelli's eagles consume and break up Leporidae and birds’ bones is different from that of other predators and, as a result, their former presence at archaeological sites can be detected, and it is possible to know whether abandoned nests were once occupied by Bonelli's eagles or other species of bird of prey.

- The tree-nesting population of Bonelli's eagles in southern Portugal occupies a novel ecosystem that contains new combinations of species and landscapes that have emerged thanks to human action, namely the planting of eucalypts. Knowledge of the causes behind such novel behaviour is crucial when defining conservation strategies.

- Bonelli's eagle nesting areas are associated with the most rugged terrain within their territories, as well as with the presence of adequate trees for nesting and little human disturbance. These areas are also less affected by forest management. This preference for nesting in the most rugged areas is a conservative characteristic of Bonelli's eagle and is maintained in different geographical regions, regardless of whether it is a cliff- or tree-nesting population.

- This tree-nesting population is associated with areas with fewer roads and power lines. The species avoids disturbance at a distance of up to 1 km from its nesting sites.

- Our study also suggests that new colonising Bonelli's eagle pairs choose habitats that are structurally similar to those of the initial population nucleus, which may be a consequence of the imprinting of the original habitat conditions on young birds.

- It has been shown that Bonelli's eagles can breed in trees in habitats that are very different from those that it usually frequents; in other words, they will breed in forested or semi-steppe habitats if there are trees, even if they are few and far between, or just grow in small stands. This gives them the ability to expand their distribution into hitherto unoccupied areas and therefore improve the species' conservation status. Nuclei that are demographically self-sufficient can act as sources for the colonization of new areas with different habitat features. It is possible that the different morphological characteristics of this eagle's population in southern Portugal has contributed to this ability to colonize.

- The main conservation measures for this population should include forest management to promote the availability of suitable trees for nest building and the protection of the environment to ensure the preservation of the behavioural diversity and reproductive plasticity of the species. In summary, just as conservation measures for the tree population must be put into practice, it is vital to ensure that habitats maintain the necessary conditions for the presence of Bonelli's eagles. Correct habitat management should be encouraged throughout the area where the species is found, with a particular view to conserving large trees, reducing mortality and habitat degradation caused by power lines and wind farms, and to guaranteeing less disturbance from forestry activities.

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APPENDIX

BIOMETRIC DIFFERENCES BETWEEN CLIFF-NESTING AND TREE-NESTING BONELLI'S EAGLES AQUILA FASCIATA

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BIOMETRIC DIFFERENCES BETWEEN CLIFF-NESTING AND TREE-NESTING BONELLI'S EAGLES *AQUILA FASCIATA*

DIFERENCIAS BIOMETRICAS ENTRE ÁGUILAS PERDICERAS *AQUILA FASCIATA* RUPÍCOLAS Y ARBORÍCOLAS

Andreia Dias[1], Víctor García[2], A. Márcia Barbosa[3], Hernán Mayoral[4] and Joan Real[1]

1 Equip de Biologia de la Conservació, Departament de Biologia Evolutiv, Ecologia i Ciències Ambientals and Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Catalonia, Spain.

2 Deputy General Directorate on Nature. Ministry of Agriculture, Food and Environment. Pza. San Juan de la Cruz s/n., E-28071 Madrid, Spain.

3 Spatial Biology Lab, CICGE – Centro de Investigação em Ciências Geo-Espaciais, Faculdade de Ciências da Universidade do Porto, Vila Nova de Gaia, Portugal.

4 Calle los Álamos, 1 40197. San Cristóbal de Segovia, Spain.

Capsule -Tree-nesting Bonelli´s eagle from Southern Portugal have different biometric measurements when compared to the cliff-nesting populations from the rest of the Iberian Peninsula and France.

Aims - Test if biometric variance within populations of a species could be associated with behavioural differences.

Methods - Between 1998 and 2020, several biometric variables were measured (by the same observer) from 256 Bonelli's eagles captured across Spain, Portugal and southern France

Results - Bonelli´s eagles did not show gradual size variations in space (latitudinally, longitudinally or diagonally), but the tree-nesting population from southern Portugal showed larger body length, wingspan, head length and width, tarsus width, and tail length than the remaining, cliff-nesting populations.

Conclusion – This could indicate a difference in flight morphology, most probably dictated by a combination of different factors. Longer tails in tree-nesting Bonelli's eagles could be an adaptive feature related to habitat and prey selection. Our results corroborate that, in the geographic area considered, Bonelli's eagle' populations are largely homogeneous, also concerning biometric parameters, but show significant regional variations, such as a differentiation of the south-western tree-nesting population. Along with previously shown behavioural and genetic differences, this supports the notion that this population could be a distinct evolutionary unit.

INTRODUCTION

Biometric measurements such as lengths, weights or proportions are basic tools in ornithology (Eck et al. 2011). Some applications of biometry in the study of birds can be sex determination, differences in size among populations, wing morphology and body mass/body size relationship (Hernández et al. 2011). These measurements can be useful in conservation, ecology, biology, taxonomy and phylogenetic studies (Araóz et al. 2016).

Body size variation is one of the most used biometric parameters in endothermic animals, and it has been the subject of many studies (Hernández, et al., 2011). A hypothesis put forward to explain this variation is Bergmann's rule, which establishes that body size varies inversely with ambient temperature, so that body size increases with latitude on a global scale. This has been supported by some studies (Ashton, 2002; Meiri & Dayan, 2003), but not by others (Yom-Tov & Yom-Tov, 2005; Rodríguez et al., 2008). Global warming experienced over the last decades may also influence the variation in body size of birds, through changes in factors such as environmental variability (Jakober & Stauber, 2000). However, there are also studies that show the difficulty of finding a relationship between global warming and body size variation (Guillemain et al., 2005; Moreno-Rueda & Rivas, 2007), which seems to be influenced by other factors apart from climate, such as feeding ecology (Toïgo et al., 2006).

It is not uncommon, within a single species, for the size of individuals within populations to vary along their geographical distribution. The analysis of biometric differences between populations enables to relate them to environmental parameters and infer possible causes that may explain them (Hernández et al., 2011).

Comparison of measurements, if they have been collected over a long time or on a large geographical scale in a standardised manner, allows inferences about the response of individuals to changes environmental factors (Zink & Remsen, 1986; Eck, 2011). The study of morphological variation of species along geographical gradients can be useful for testing hypotheses about the factors determining their distribution and biology (Zink & Remsen 1986; Ricklefs & Miles, 1994). Nonetheless, biometric differences within a single species can be found in more reduced geographical areas, such as the Iberian Peninsula and the British Isles (Wyllie & Newton, 1994).

Bonelli´s eagle (*Aquila fasciata*) provides a good opportunity to explore species' biometry variations, due to its wide geographical distribution and available data concerning biometric measurements. It is a large resident bird of prey, whose most important numbers in Europe are found in the Iberian Peninsula and on the Mediterranean coast of France (Cramp & Simmons, 1980). In Europe, the species is considered "Near Threatened", and it has a population estimated with 1100 – 1200 pairs (BirdLife International 2015).

In the Iberian Peninsula, the species was in decline in the mid-1980s (Real & Mañosa, 1997; Real, 2004). Nowadays, the population size remains stable or is increasing lightly in some areas, although some populations at the northern and western extremes of the distribution range, continue to show some decline (Del Moral, 2018).

In a study which showed that Bonelli’s eagle females were generally larger than males, García et al. (2013) also noted that individuals from Portugal were generally larger than those from Spain and France. While this analysis did not fit biogeographical patterns, as Bonelli’s eagle populations are not divided by national borders (fig. 1), it hinted on biometric differences among western Mediterranean populations of this species.

In western Europe, Bonelli's Eagles most frequently nest in cliffs (Arroyo et al., 1995), except in south-western Portugal, where the population is almost exclusively tree-nesting (Dias et al., 2017). It is not known whether this population, which shows both genetic and behavioral differences (Mira et al, 2013; Palma et al., 2013, Dias et al., 2017), also has biometric differences. If these differences are found with this study, it would reinforce the notion that this population could represent a distinct evolutionary unit. The study area, which includes de Iberian Peninsula and southwestern France, provides an interesting biogeographic scenario for the study of morphological variation in Bonelli´s eagle.

In this context, we aimed to test two alternative hypotheses: 1) Bonelli's eagle individual size varies with annual mean temperature; 2) the size of Bonelli's eagles differs between the tree-nesting and cliff-nesting populations.

If significant differences are found, this information can provide a useful tool for researchers and conservation workers, for example with regard to the decision to reintroduce or translocate individuals within reintroduction/conservation projects.

METHODS

The study area spanned de Iberian Peninsula (which comprises the mainland territories of Portugal and Spain) and south-western France (fig. 1). Across this region, 256 wild Bonelli´s eagles were live-trapped and measured, encompassing three representative population areas of the species: 1) *Southern Portugal* (n = 19 individuals) (Baixo Alentejo and Algarve); 2) *Center* (n = 208) (provinces of Badajoz, Cáceres, Ciudad Real, Salamanca, Toledo and Zamora in Spain, and Trás-os-Montes e Alto Douro, Alto Alentejo and Alqueva region in Portugal); Mediterranean area, which includes Languedoc Roussillon (France) and the Spanish provinces of Girona, Barcelona, Tarragona, Teruel, Castellon, Valencia, Alicante, Albacete and Cuenca; Aragón and inland central Spain, including Cuenca, Guadalajara, Madrid, Toledo and Zaragoza; and Upper Ebro river, located in the provinces of Álava, Burgos, Huesca, La Rioja, Navarra and part of Zaragoza and 3*) SE France* (n = 29) in Provence and Languedoc Roussillon, Côte d´Azur and Rhone – Alpes.

This population nuclei were defined according on species distribution, considering the two marginal populations (southwest Portugal (Palma et al., 2013) and north-western of the French Mediterranean area (Lieury et al., 2015) and the rest of the population.

This work was performed within the framework of different research and conservation projects for which technical assistance from the Spanish Ministry of the Environment was required. The trapping of Bonelli’s eagles was carried out in areas occupied by territorial pairs but avoided the period, generally from February to April, when the birds were incubating and chicks were not yet well feathered (García et al., 2013). Baits were used along with remote-controlled floor net traps, built and patented by Víctor García Matarranz (patent number: ES2355778B1) activated by a field technician.

Birds were handled always with falconry hoods in order to reduce stress. Claws were wrapped with veterinary bandaging tape to prevent accidents for both the bird and the handler. All measures were gathered as quickly as possible before the birds were released back into the wild, and they were taken always by one of the authors, Víctor García, between 1998 and 2020, using a Pesola© scale, tape meter (accuracy 0.5 cm) and digital callipers (± 0.01 mm). After biometric measurements were recorded, all individuals were released in perfect condition.

Biometric variables

Body mass (weigh) - was determined using a 5000g Pesola© scale. Whether the individual had a full or empty crop was taken into account. In those cases in which there was a large amount of food in the crop, 100g were subtracted; **tarsus** (Tarsus_DV - dorsoventral width of tarsus-metatarsus; Tarsus_L - Lateral width of tarsus-metatarsus (L – Left leg and D - right leg) - in order to measure both the lateral and the dorsoventral width, we have looked for the bulge presented by the tarsometatarsus on the proximal edge of the metatarsal fossa, taking the measurement at the point located in the narrowing that follows this protuberance; **wing chord** - measured from the carpal joint to the tip of the 7th primary, which is the longest in this species, following the natural curvature of the wing by its upper or dorsal part; **wing ventral** – the same as "wing chord", but for the ventral part of the wing, in this case the contour is not followed but the shortest distance is taken between the two mentioned points; **7th primary** – has been named the fourth feather, if we start to count the feathers from the outermost wing part. If instead we numbered the wingtip feather as number one, we would have measured the 4th primary. It is measured from the calamus insertion to the end of the feather. For this, the end of the tape measure is inserted between the calamus of the 7th and 8th primaries until it touches the base of the feather, and from there the measurement is taken to the end of the 7th primary; **forearm** – measured from the junction of the proximal ends of the ulna and the radius with the distal end of the humerus, to the distal ends of the ulna and the radius at their junction with the carpus; **tail length** – from the uropigeal gland to the end of the central rectrix; **rectrix** – from the base of the central rectrix to its end; **wingspan** – the distance between the column and the end of the longest feather, taken with the wing fully extended. Since it is a manoeuvre that requires violent manipulation for the bird, it has been preferred to do it this way instead of opening the two wings, which would place more stress on the bird; **body length** – birds were placed ventrally on a tape measure, lengthening the neck with their head stretched. The distance between the rectrices is measured, with the tail together, to the end of the bill; **bill length -** from the end of the bill to the junction of the bill with the skull, on the cranial suture; **bill height** – the perpendicular is measured from the distal edge of the wax to the point at the base of the mandible below it; **bill width** – the line between the two points where the wax of the bill ends at the edge of the upper mandible; **head length** - the distance between the end of the beak and the cerebellar prominence of the skull; **head width** – the distance in the widest part of the skull behind the orbicular zone; **claw -** the distance between the point where the upper surface of the claw emerges from the skin at the tip of the toe to the end of the claw as measured across its arc.

Statistical analysis

To test the first hypothesis (biometric variation with ambient temperature), we performed bivariate general linear regressions, using the 'lm' function in R version 4.0 (R Core Team, 2020), between each of the biometric variables (across individuals) and annual mean temperature. The latter was obtained from the WorldClim 2.0 database on a ~1 km^2 resolution (Fick & Hijmans, 2017), using the ‘extract’ function of the ‘raster’ R package (Hijmans, 2020). The coefficients of determination (R-squared values) of these regression models were used for assessing the extent to which ambient temperature could account for the variation in biometric variables.

To test the second hypothesis (biometric differentiation between tree-nesting and cliff-nesting populations), we compared the biometric variables of the individuals of Southern Portuguese (tree-nesting) population against those of the remaining (cliff-nesting) populations combined. For this propose, we used box plots with notches; if the notches of two boxplots do not overlap, this is considered strong evidence that the two medians are different (Chambers et al. 1983). We also performed Mann-Whitney-Wilcoxon tests of the differences in each variable. This non-parametric test is appropriate when the variables are not normally distributed. Given that Bonelli’s eagle shows sexual dimorphism (García et al. 2013), we also performed these analyses separately for males and females. We also used box plots for a visual comparison of the biometric variables among all six populations, although the generally small samples sizes prevented more detailed statistical tests.

RESULTS

According to moult patterns and general coloration (Forsman, 2007; Caro, 2010), among the 256 live-trapped Bonelli´s eagles, there were 5 juveniles (first-second calendar year), 15 subadults (third-fourth calendar year) and 236 adults (fifth or more than fifth calendar year). Since all these age classes have the same biometry, all individuals were included in the analysis.

None of the biometric variables showed a gradual variation with temperature, which accounted for only 0 to 6.6% of the biometric variation (Supplementary Figure S1). However, when comparing the tree-nesting (“southern Portugal”) population with the remaining (cliff-nesting) populations, both boxplot notches and one-tailed Mann-Whitney-Wilcoxon tests showed that these differences were significant for several biometric variables (Table 1; Figure 2). These included total body length, wingspan, and measurements of the head (length and width), tarsus (lateral width), and tail (length and rectrix size).

The differences in body length, head width, wingspan, tail length and rectrix remained significant when comparing only females among tree-nesting and cliff-nesting populations (Supplementary Figure S2). For males only, the small sample size of the tree-nesting population prevented the detection of significant differences (Supplementary Figure S3).

When visually comparing the values of each biometric variable among the south-western Portuguese, the central (Spanish and Portuguese border) populations, and the easternmost French population, the results were similar to when comparing the tree-nesting nucleus against all cliff-nesting nuclei together: body length, head width and tail length, in both females and males, are visibly higher in tree-nesters (Supplementary Figure S3 and S4).

Wingspan and head length are also larger in Southern Portuguese females (Supplementary Figure S3). Males from Southern Portugal have the smallest measurement for claw and 7th primary; however, we have to take into account that to evaluate this measurement, we had a very small number of samples (n = 5 and n = 6, respectively) (Supplementary Figure S5).

DISCUSSION

Biometry has seen many interesting applications in the field of ornithology, and it has important potential applications in biology, ecology, taxonomy, phylogeny and conservation (e.g. Hernández et al. 2011; Araóz et al. 2016). Biometric variation has been related to factors such as environmental variability, including global warming (Jakober & Stauber 2000), or to ecological aspects such as feeding habits (Toïgo et al. 2006). Our study revealed biometric differences between Bonelli’s eagle populations with different nesting habitats, however, it does not have enough data to assess the effect of global warming.

It is well known that in birds of prey in general (Newton 2010), and Bonelli´s eagles in particular (Forsman 2007; García et al. 2013), females are larger than males. In a previous study that involved some of the same individuals used in this paper, García et al. (2013), found not only that females were larger than males regarding most variables analysed, but also that individuals from Portugal were also generally larger than those from Spain and France, which pointed to biometric differences among western Mediterranean populations of Bonellis' eagles. However, this analysis by country did not fit biogeographical patterns, as northern and eastern Portuguese populations are continuous with Spanish populations (see fig. 1).

The present study took a more ecologically meaningful approach by comparing biometrics among populations rather than among countries – particularly, among the tree-nesting population from Southern Portugal and the cliff-nesting populations from the remaining study area (Fig. 1). Size differences between populations could reflect adaptive variation in response to conditions in their habitats and/or nesting sites (Laiolo & Rolando 2001; Tieleman et al. 2003).

The tree-nesting Bonelli´s eagle population showed generally larger body length, wingspan, head length and width, tarsus width, and tail length. This could indicate a difference in flight morphology, most probably dictated by a combination of different factors such as flight behaviour, habitat selection, size of prey and display flight. It is known that even small morphological variations can reflect different behaviour and ecology (e.g. Norberg 1990, Chapter 12).

The relative importance of these different functions will, in turn, determine both the size and shape favored by natural selection. For example, tails act as control devices maintaining stability and as lifting surfaces to enhance manoeuvrability, agility, and low-speed flight. Birds that need high manoeuvrability, for instance, to avoid collisions in cluttered environments, generally have longer tails (Thomas & Balmford 1995). This means that wing and tail structure may also be related to vegetation density (Norberg 1990). This seems to be supported by the tree-nesting Bonelli´s eagle population, where longer tails could be an adaptive feature related to habitat and prey selection (Palma et al. 2006; García et al. 2013).

Body mass increase favours the resistance to adverse environmental conditions and to food unpredictability, especially when birds face a reduction in prey numbers (Hernández et al. 2011). Usually, Bonelli´s eagles prey on European rabbits (*Oryctolagus cuniculus*) in Spain (Moleón et al. 2009, 2012; Caro et al. 2011) and France (Morvan 2010; Resano et al. 2012), where populations are mostly cliff-nesters. In the peculiar population of SW Portugal, Bonelli´s eagles had to adapt to the decline of their staple prey (Palma et al. 2013), like in the Cyprus population, where they nest in Calabrian Pine *Pinus brutia* forests and use birds as their main prey (Iezekiel et al. 2010). The Southern Portuguese population feeds about 70% on Rural Pigeons *Columba livia*. Racing Pigeons *Columba livia* and Domestic Fowl *Gallus gallus* are also consumed frequently (Palma et al. 2006).

As well related to body size, geographical and temporal variations are common phenomena among organisms and may evolve within a few years. Yom-Tov and Geffen (2010) argue that body size acts much like a barometer, fluctuating in parallel with changes in the relevant key predictors, and that geographical and temporal changes in body size are actually manifestations of the same drivers. Commonly, the principal predictors of body size are food availability during the period of growth, and ambient temperature, which often affects food availability. It is a challenge to find which particular environmental factors determine food availability and, in turn, changes in animal body size. It is possible that recent changes in body size are phenotypic, but in some cases, they are partly genetic (Yom-Tov & Geffen 2010). Other environmental factors besides temperature, such as humidity, seasonality and precipitation, have been proposed as contributing to geographic variations in body size (Fan et al. 2019).

Globally, animals that live at higher latitudes/elevations (i.e., at lower average temperatures) tend to have a larger body size (Bergmann’s rule) and a smaller appendage size (Allen’s rule) for thermoregulatory reasons. According to the heat conservation hypothesis, large body size and small appendage size help animals retain heat under cold ambient temperatures, while small body size and large appendage size help them dissipate heat under warm temperatures (Fan et al. 2019). There is no agreement about whether Bergmann’s rule is general or valid. Empirical studies have found the predicted pattern at both the intraspecific and interspecific levels in mammals and birds, although animals that do not follow Bergmann’s rule have also been reported (Fan et al. 2019). Within our study area, while latitudinal variation is insufficient to test Bergmann’s rule directly, Bonelli´s eagles do not show gradual size variations with annual mean temperature (se Figures S1 in Supplementary Information).

In our study, although French Bonelli´s eagles (males and females) are heaviest and have larger claws (see also García et al. 2013), Bonelli´s eagles from Southern Portugal contradict Bergmann’s latitudinal rule, presenting the highest values of most of the analysed biometric variables. These different biometrics could stem from adaptation to the forest environments where this population nests.

Climate warming has also been linked with changes in the spatiotemporal distribution of species and the body size structure of ecological communities (Evans et al. 2019). It may influence the variation in body size of birds through changes in factors such as environmental variability (Jakober & Stauber 2000). Body size is a major factor influencing animal morphology, physiology, ecology, evolution and extinction probability (Schmidt-Nielsen 1984; Cardillo et al. 2005).

In general, our study found significant though not very strong differences between the biometric measurements of tree-nesting versus cliff-nesting Bonellis´s eagles. The relatively small sample sizes of some populations, particularly the tree-nesting population of SW Portugal, likely hampered the detection of stronger biometric differences. Some values may also be underestimated – for example, males from SW Portugal showed the smallest sizes for claw and 7th primary, but with reduced sample sizes of n = 5 and n = 6, respectively. Further analysis including larger numbers of individuals might add strength to the observed patterns. However, it must be taken into account that the current sample size already implied countless hours (across years) of field work, including the capture, meticulous measurement and release of hundreds of individual specimens, plus thousands of kilometres travelled to cover all the studied populations (fig. 1).

Despite the necessarily limited sample size, the current data show significant differences for several biometric measurements between tree-nesting and cliff-nesting Bonelli's eagles. Furthermore, this differentiation is matched by the previously described differences in diet (Palma et al. 2006, 2013), genetic structure (Mira et al. 2013) and nesting behaviour (Dias et al. 2017). All of this points to a distinctive character of the SW Portuguese population of Bonelli's eagles, which should consequently be treated as a distinct biogeographic and evolutionary unit.

The observed expansion of tree-nesting Bonelli's eagles from southern Portugal, possibly was facilitated by the tree-nesting behavior, which allowed the colonization of areas without cliffs (Dias et al., 2017). This idea is reinforced by genetic studies which showed that these population had the lowest genetic diversity but a marked differentiation from others (Mira et al., 2013). This is also corroborated with demographic modelling where it was likely the main source of colonists throughout the expansion process. This population, like the ones from south of Iberian Peninsula, act as sources that thanks to dispersal sustain all populations (Hernández- Matías et al., 2013).

It should be noted that this study did not include biometric data on the Bonelli's eagle population from Andalusia, which serves as the main source of the species in the Iberian

Peninsula (Muñoz et al., 2005; De las Heras & Garrido R., 2018). In addition, the Andalusian population has been supplying specimens in recent years to reinforce other Spanish populations, likely causing a mixture of individuals in the studied populations (Life Bonelli, 2017).

Our results help corroborate the fact that Bonelli's eagle populations are largely homogeneous in the geographic area considered, also with regard to biometrics, but there are potentially important regional variations, such as a differentiation of the south-western tree-nesting population. This must be taken into account when making decisions about research, conservation and management of this endangered species, for example with regard to the decision to reintroduce or translocate individuals within reintroduction/conservation projects. In European Mediterranean ecosystems, Bonelli’s eagle is regarded as an umbrella species, as it is one of the top avian predators found in these natural systems (Real 1991, Moleón et al. 2009) and moreover plays a key role in shaping the structure of the endangered biotic communities that these systems contain.

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Variable	**W**	***p* value**
Body mass	1896.5	0.144
Body length	426.5	0.000
Head length	627.5	0.024
Head width	389	0.000
Bill length	762.5	0.288
Bill width	866.5	0.352
Bill height	843	0.294
Claw	907.5	0.481
Tarsus L width L	1380.5	0.024
Tarsus L width R	1614.5	0.121
Tarsus DV width L	1617	0.128
Tarsus DV width R	1482.5	0.056
Wingspan	1254	0.032
Wing width	43	0.598
Wing length D	1187.5	0.103
Wing length V	1414	0.077
Primary 7	1401.5	0.354
Forearm	1326	0.128
Tail length	1041	0.001
Rectrix	1168	0.022

Legend to figures

Figure 1. Locations of collected samples distributed in the six study areas: 1 - Southern Portugal; 2 - Center; 3 - SE France. Dots represent locations where samples were taken.

Figure 2 Box plots comparing the values of each biometric variable between tree-nesting and cliff-nesting populations of Bonelli's eagle. Asterisks indicate variables for which the Mann-Whitney-Wilcoxon test result was significant (Table 1).

Figure S1. Bonelli's eagle biometric differentiation, spatial trend for ambient temperature.

Figure S2. Bonelli's eagle biometric differentiation – boxplot females.

Figure S3. Bonelli's eagle biometric differentiation – boxplot males.

Figure. S4. Box plots comparing values of each Bonelli's eagle´s (females) biometric variable, between geographic nuclei (1 - Southern Portugal; 2 - Center; 3 - SE France).

Figure. S5. **-** Box plots comparing values of each Benelli's eagle´s (males) biometric variable, between geographic nuclei (1 - Southern Portugal; 2 - Center; 3 - SE France).

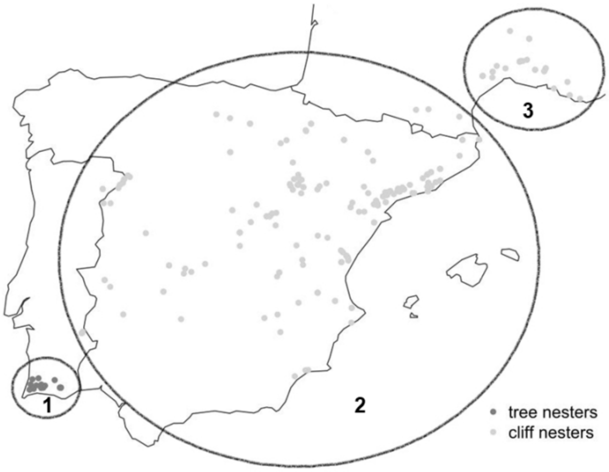
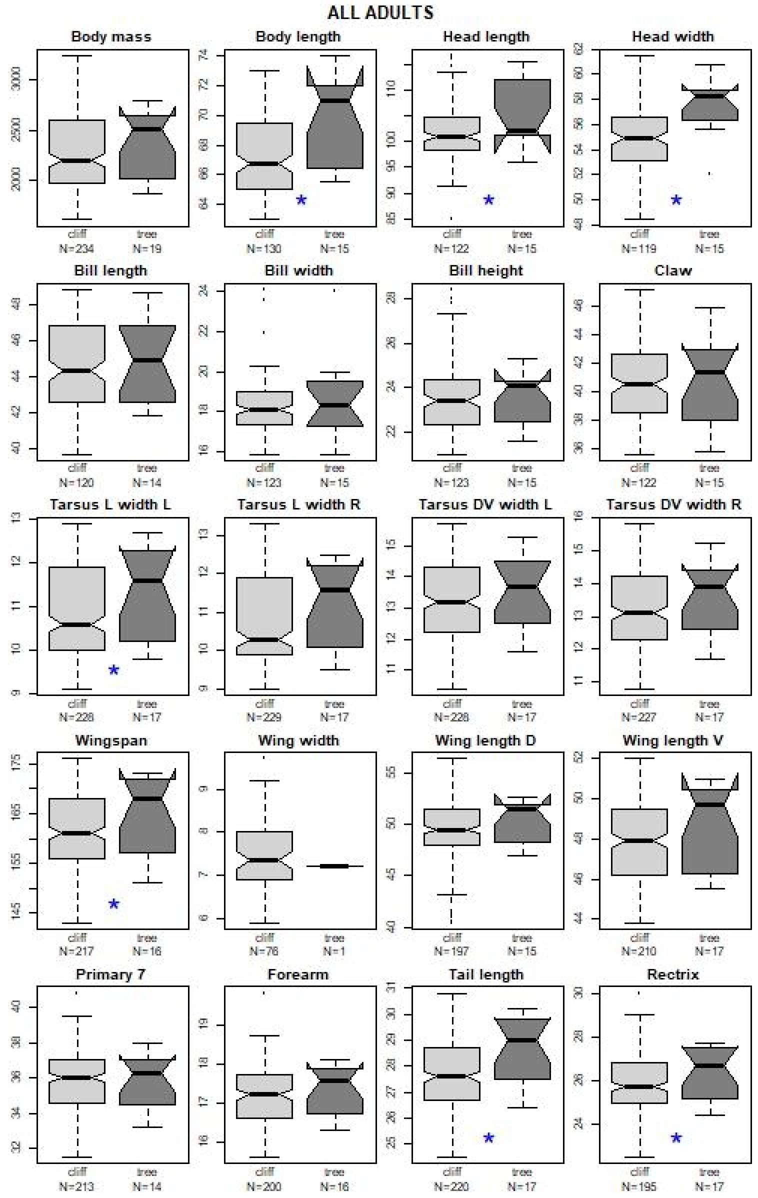


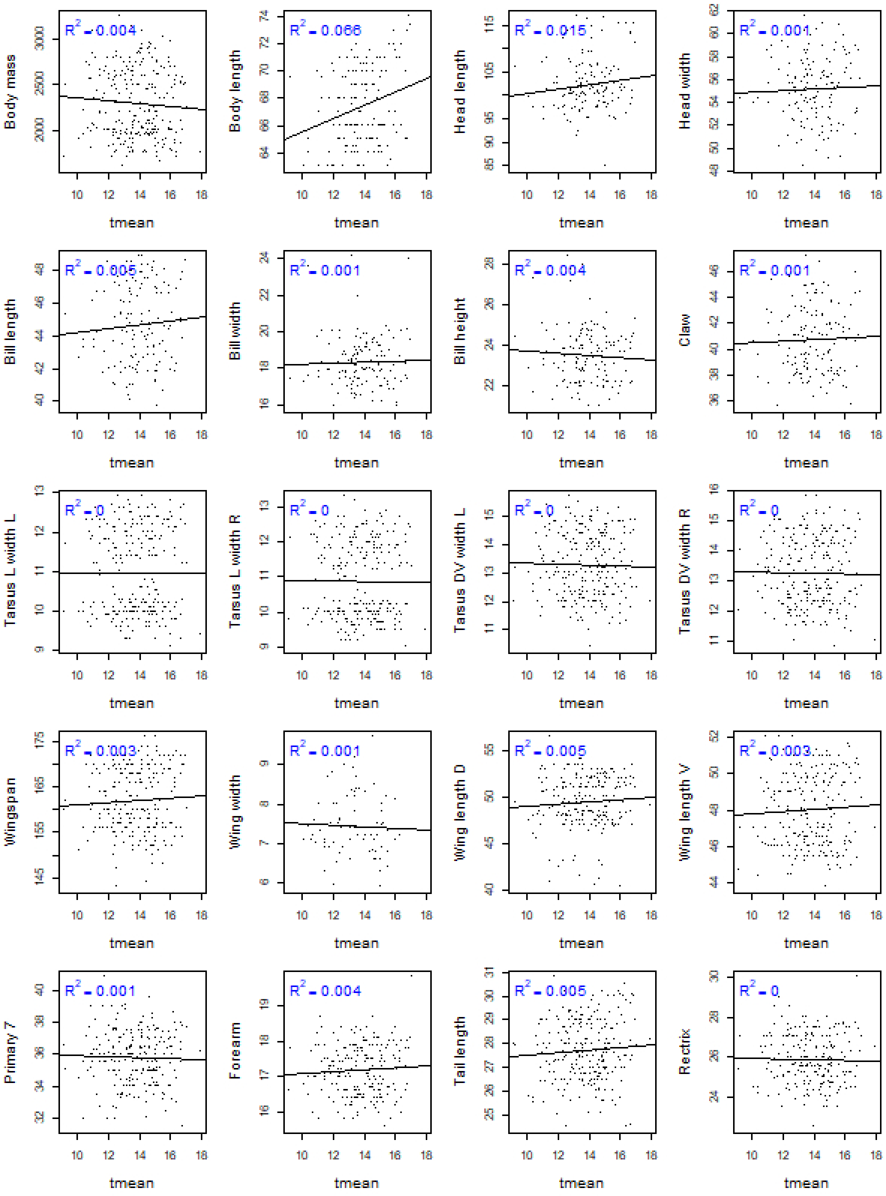
Figure 1. Locations of collected samples distributed in the six study areas: 1 - Southern Portugal; 2 - Center; 3 - SE France. Dots represent locations where samples were taken.

338x190mm (96 x 96 DPI)

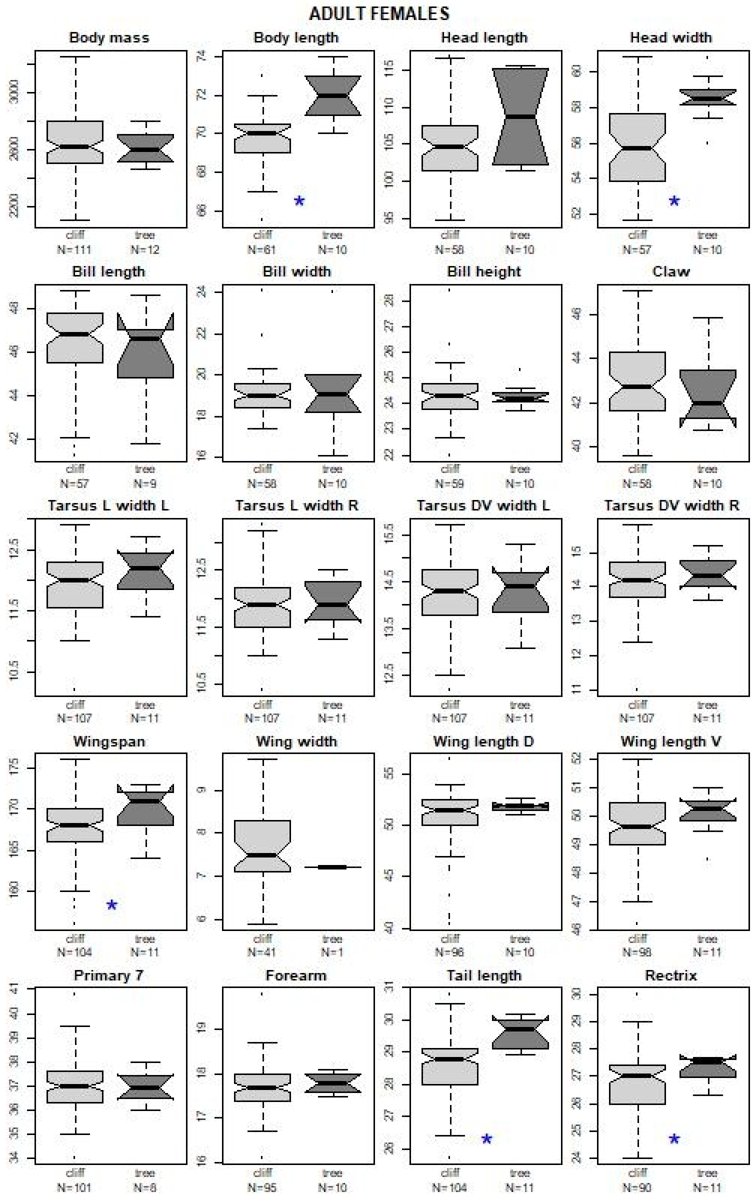


Box plots comparing the values of each biometric variable between tree-nesting and cliff-nesting populations of Bonelli's eagle. Asterisks indicate variables for which the Mann-Whitney-Wilcoxon test result was significant (Table 1).

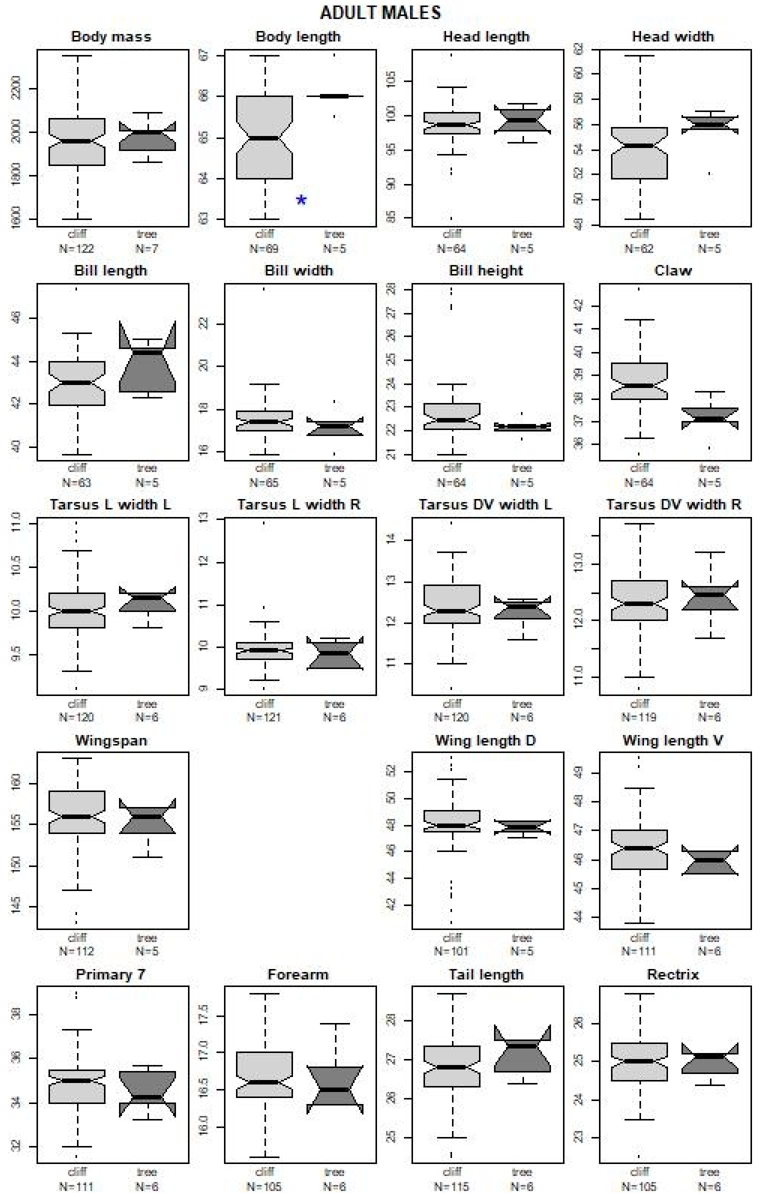
176x282mm (72 x 72 DPI)



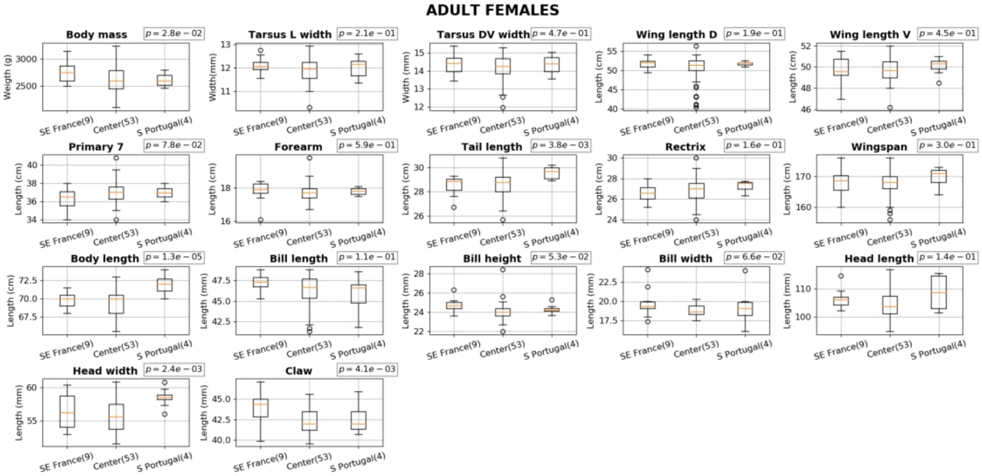
211x282mm (72 x 72 DPI)

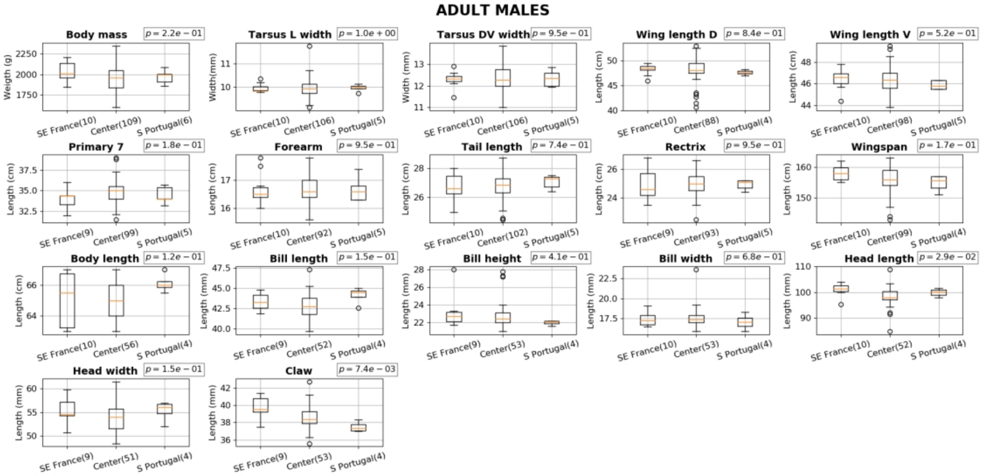


176x282mm (72 x 72 DPI)



176x282mm (72 x 72 DPI)


ADULT FEMALES
Body mass
$p = 2.8e-02$
Weigth (g)
3000
2500
Tarsus L width
$p = 2.1e-01$
Width(mm)
13
12
11
Tarsus DV width
$p = 4.7e-01$
Width (mm)
15
14
13
12
Wing length D
$p = 1.9e-01$
Length (cm)
55
50
45
40
Wing length V
$p = 4.5e-01$
Length (cm)
52
50
48
46
Primary 7
$p = 7.8e-02$
Length (cm)
40
38
36
34
Forearm
$p = 5.9e-01$
Length (cm)
18
16
Tail length
$p = 3.8e-03$
Length (cm)
30
28
26
Rectrix
$p = 1.6e-01$
Length (cm)
30
28
26
24
Wingspan
$p = 3.0e-01$
Length (cm)
170
160
Body length
$p = 1.3e-05$
Length (cm)
72.5
70.0
67.5
Bill length
$p = 1.1e-01$
Length (mm)
47.5
45.0
42.5
Bill height
$p = 5.3e-02$
Length (mm)
28
26
24
22
Bill width
$p = 6.6e-02$
Length (mm)
22.5
20.0
17.5
Head length
$p = 1.4e-01$
Length (mm)
110
100
Head width
$p = 2.4e-03$
Length (mm)
60
55
Claw
$p = 4.1e-03$
Length (mm)
45.0
42.5
40.0
SE France(9)
Center(53)
S Portugal(4)


ADULT MALES
Body mass
$p = 2.2e-01$
Weigth (g)
2250
2000
1750
SE France(10)
Center(109)
S Portugal(6)
Tarsus L width
$p = 1.0e+00$
Width(mm)
11
10
SE France(10)
Center(106)
S Portugal(5)
Tarsus DV width
$p = 9.5e-01$
Width (mm)
13
12
11
SE France(10)
Center(106)
S Portugal(5)
Wing length D
$p = 8.4e-01$
Length (cm)
50
45
40
SE France(10)
Center(88)
S Portugal(4)
Wing length V
$p = 5.2e-01$
Length (cm)
48
46
44
SE France(10)
Center(98)
S Portugal(5)
Primary 7
$p = 1.8e-01$
Length (cm)
37.5
35.0
32.5
SE France(9)
Center(99)
S Portugal(5)
Forearm
$p = 9.5e-01$
Length (cm)
17
16
SE France(10)
Center(92)
S Portugal(5)
Tail length
$p = 7.4e-01$
Length (cm)
28
26
SE France(10)
Center(102)
S Portugal(5)
Rectrix
$p = 9.5e-01$
Length (cm)
26
24
SE France(9)
Center(93)
S Portugal(5)
Wingspan
$p = 1.7e-01$
Length (cm)
160
150
SE France(10)
Center(99)
S Portugal(4)
Body length
$p = 1.2e-01$
Length (cm)
66
64
SE France(10)
Center(56)
S Portugal(4)
Bill length
$p = 1.5e-01$
Length (mm)
47.5
45.0
42.5
40.0
SE France(9)
Center(52)
S Portugal(4)
Bill height
$p = 4.1e-01$
Length (mm)
28
26
24
22
SE France(9)
Center(53)
S Portugal(4)
Bill width
$p = 6.8e-01$
Length (mm)
22.5
20.0
17.5
SE France(10)
Center(53)
S Portugal(4)
Head length
$p = 2.9e-02$
Length (mm)
110
100
90
SE France(10)
Center(52)
S Portugal(4)
Head width
$p = 1.5e-01$
Length (mm)
60
55
50
SE France(9)
Center(51)
S Portugal(4)
Claw
$p = 7.4e-03$
Length (mm)
42
40
38
36
SE France(9)
Center(53)
S Portugal(4)

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Understanding the taphonomic signature of Bonelli's Eagle (*Aquila fasciata*)

Lluís Lloveras [a], [b], [*], Richard Thomas [a], Rui Lourenço [c], Jesús Caro [d], [e], Andreia Dias [f]

[a] School of Archaeology and Ancient History, University of Leicester, University Road, Leicester LE1 7RH, UK
[b] SERP, Departament de Prehistòria, Història Antiga i Arqueologia, Universitat de Barcelona, Montalegre 6-8, 08001 Barcelona, Spain
[c] ICAAM – Instituto de Ciências Agrárias e Ambientais Mediterrânicas, LabOr – Laboratório de Ornitologia, Universidade de Évora, Núcleo da Mitra, Ap. 94, 7002-554 Évora, Portugal
[d] Departmento de Zoología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain
[e] Instituto de Investigación en Recursos Cinegéticos – IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, 13071, Ciudad Real, Spain
[f] Departament de Biologia Animal, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Catalonia, Spain

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ABSTRACT

Bonelli's eagle (*Aquila fasciata*) is a large bird of prey that breeds in warm regions of the Palearctic. In Europe, it is mainly found in the Mediterranean region, in open or partially-open landscapes in mountainous areas. They normally feed on mammals, up to the size of a hare, medium-sized birds and large reptiles.

The remains of Bonelli's eagles have been found at Pleistocene archaeological sites, raising the possibility that they were active bone accumulating agents in caves and shelters, a practice evidenced by contemporary studies that show their nests are usually located on rocky cliffs.

Taphonomic studies on prey remains consumed by these raptors do not exist and their role in bone accumulations at archaeological sites is not understood. We analyse non-ingested bone remains and pellets recovered at well-known Bonelli's eagle nests situated in the south of Spain and Portugal with the aim of characterising their accumulations. Specifically, we detail taxonomic and anatomical representation, bone breakage, beak marks and digestion damage. Results show that European wild rabbit (*Oryctolagus cuniculus*), red-legged partridge (*Alectoris rufa*) and pigeons (*Columba* spp.) are the dominant prey. The taphonomic pattern varies depending on the type of prey and the origin of skeletal materials (non-ingested versus pellets). Comparisons with other agents of bone accumulation (birds of prey and terrestrial carnivores) suggest that the taphonomic signature of Bonelli's eagle differs from most other predators.

1. Introduction

Bonelli's eagles (*Aquila fasciata*) are widespread raptors, with a range extending from the Iberian Peninsula and NW Africa across southern Europe, the Middle East and the Arabian Peninsula through Afghanistan to India, south China and Indonesia. Western Palaearctic populations are distributed mainly in the Mediterranean area, generally in fairly warm and dry regions (Cramp and Simmons, 1980; Ferguson-Lees and Christie, 2001; Real, 2003).

They inhabit open or partially-open landscapes often in hilly areas and prefer short or sparse vegetation, such as garrigue, dry grassland and rocky habitats; however, its habitat can be highly variable including forests and parkland as well as bushes and scrub. It is also often found in open habitats with non-intensive crops, vineyards, olive groves, small woodlands and pastures (Cramp and Simmons, 1980; Tucker and Heath, 1994).

Despite a marked decline in numbers since the early 1980s, Bonelli's eagle is still present in most of the Iberian Peninsula with the exception of the Cantabrian region and in the north-western quarter of Spain (Cabral, 2008; Del Moral, 2006). Pairs are primarily distributed in the Mediterranean regions (from southern Portugal to Catalonia), in the mountainous areas with a Mediterranean climate characterized by hot summers and low precipitation (Muñoz et al., 2005; Ontiveros and Pleguezuelos, 2003; Palma et al., 1996; Real and Mañosa, 1997).

Bonelli's eagles are large birds of prey (55–67 cm in length and a mass of 1.5–2.5 kg [Cramp and Simmons, 1980]) that feed on medium-sized mammals, birds and reptiles. Previous feeding

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[*] Corresponding author. School of Archaeology and Ancient History, University of Leicester, University Road, Leicester LE1 7RH, UK.
E-mail address: lluislloveras@ub.edu (L. Lloveras).

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studies have shown that rabbits, partridges and pigeons are the preferred game but they also take hares, squirrels, rodents, corvids and lizards among others (Caro et al., 2011; Del Amo et al., 2008; Ontiveros and Pleguezuelos, 2000; Ontiveros et al., 2005; Palma et al., 2006; Real, 1996; Valkama et al., 2005). Rabbits seems to be the favourite prey of the eagle in terms of weight and energetic value, but when they are scarce, the eagle preys upon a wider range of species that are more difficult to capture and offer lower calorific returns (Arroyo and Ferreiro, 1997; Moleón et al., 2009).

While Bonelli's eagles do nest in trees (particularly in south Portugal, although less than 4% of the Spanish population do it), breeding is normally in holes in cliffs rock shelters of variable size (Del Moral, 2006; Palma et al., 2006). Pellets and leftover prey remains accumulate on the surface of the nest and under roosting sites and perches of the surrounding area (Real, 1996). Pleistocene-aged remains of Bonelli's eagles have been found in archaeological deposits at Gruta da Figueira Brava (Portugal), Brechas de la Cantera de l'Altissent (Spain) and Devil's Tower and Gorham's Cave (Gibraltar) (Tyrberg, 2008), raising the possibility that they were active bone-accumulating agents in prehistoric caves and shelters. Their nests can therefore occur in the same spaces frequented by prehistoric hunter-gatherers populations and the food remains of both may become intermingled. Establishing the taphonomic signature of this diurnal raptor is necessary to distinguish between human and eagle accumulations.

In recent years, assessment of the origin of small prey bone accumulations from archaeological sites has become an important line of taphonomic research. In order to identify the agent responsible for accumulations of small prey, several actualistic studies have been conducted for terrestrial carnivores (e.g. Alvarez et al., 2012; Cochard, 2004a; Lloveras et al., 2008a, 2012a; Mallye et al., 2008; Mondini, 2002; Rodríguez-Hidalgo et al., 2013; Sanchis, 2000; Sanchis Serra and Pascual Benito, 2011; Schmitt and Juell, 1994; Stiner et al., 2012) and nocturnal and diurnal raptors (Bochenski, 2005; Bochenski et al., 1997, 1999, 2009; Cochard, 2004b; Hockett, 1989, 1991, 1995; 1996; Laroulandie, 2002; Lloveras et al., 2008b, 2009, 2012b, 2014a; Sanchis, 2000; Sanchis et al., 2013; Schmitt, 1995; among others). Information provided by these taphonomic studies is necessary to understand the formation processes at archaeological and palaeontological sites, and distinguish human and other animal agents of accumulation. The aim of our study is to elucidate the taphonomic patterns of prey remains recovered from modern nests and pellets of Bonelli's eagles and to establish diagnostic features that can be used to evaluate their role as contributors of bone accumulations in archaeological assemblages.

2. Materials and methods

We analysed osteological remains of prey from nine Bonelli's eagle nests located in two areas in the south of the Iberian Peninsula (Fig. 1): six nests from the Algarve and Alentejo regions (south of Portugal) and three nests from the Sistema Bético (south of Spain).

All materials were collected by the authors (AD, RL and JC) between 2007 and 2012 after the breeding season to avoid disturbing the birds. Each sample comprises non-ingested remains and pellets collected on the surface of nests and in the surrounding areas beneath them (Fig. 2). Feeding behaviour studies of Bonelli's eagles show that these raptors usually remove uneaten prey remains from the nest; only a low proportion of remains are left on the surface (Real, 1996). For this reason, most non-ingested bones can be found on perches or on the floor around nests.

Pellets were disaggregated while dry to separate the osteological material and bones and teeth were sorted under a magnifying glass to prepare for analysis. Skeletal remains were anatomically determined, sided, and identified to taxon whenever possible.

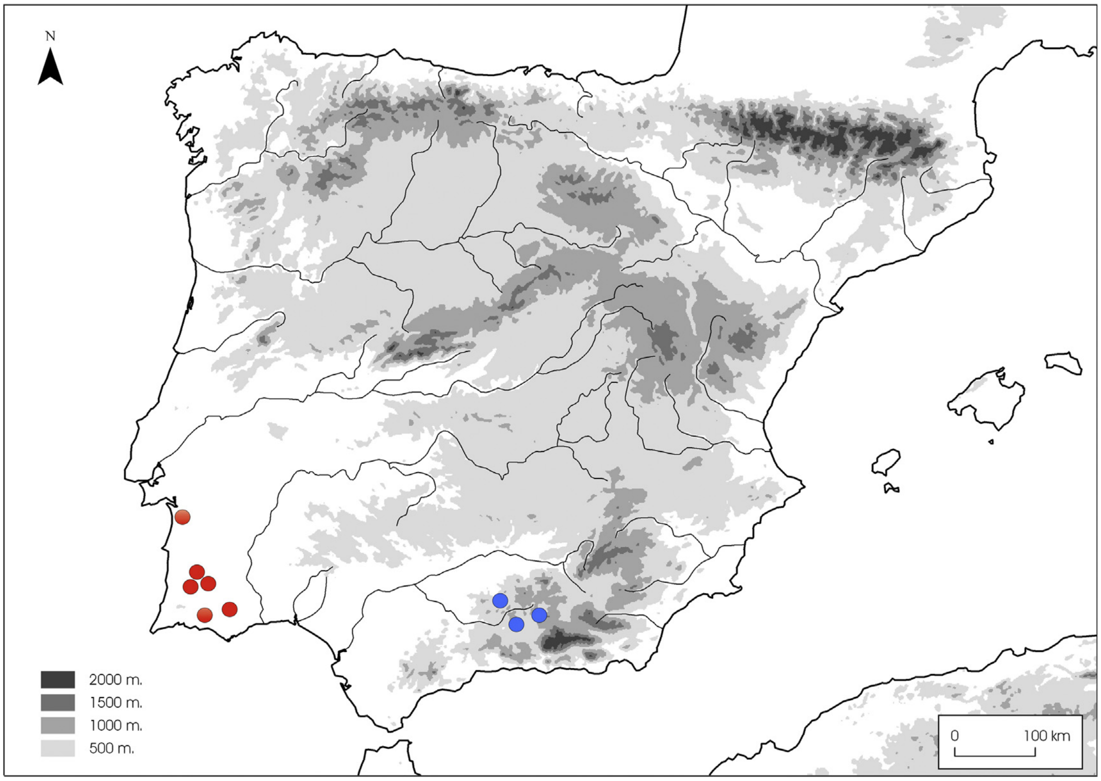

Fig. 1. Locations from which Bonelli's eagles nests samples were collected. In red: Portuguese samples. In blue: Spanish samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. Examples of pellets and non-ingested materials recovered from Bonelli's Eagle nesting areas.

Identifications were carried out using the animal bone reference collection of the School of Archaeology and Ancient History Bone Laboratory, University of Leicester. The Number of skeletal elements (N), Number of Identified Specimens Present (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were calculated as well as relative frequencies.

Determination of the age at death of the prey mammals was only possible for rabbits and was estimated taking into account the epiphyseal fusion state of long bones (humeri, femora and tibiae), metapodials, scapulae, calcanei and innominates (Rogers, 1982; Taylor, 1959). Only two age categories were considered, adult and immature.

To facilitate comparison of the taphocoenosis of Bonelli's eagle with other predators, the analytical methodology follows the same criteria applied in previous works (Lloveras et al., 2008a, 2008b, 2009, 2012a, 2014a):

2.1. Anatomical representation

Relative abundance was calculated using the formula advocated by Dodson and Wexlar (1979):

$$RA_i = MNE_i/MNI \times E_i$$

(RA_i = the relative abundance of element i; MNE_i = the minimum number of skeleton element i; MNI = the minimum number of individuals based on the highest number of any single element in the assemblage; E_i = the number of element i in the prey skeleton).

In addition, proportions of skeletal elements in mammalian prey were evaluated using the following ratios (Andrews, 1990):

(a) PCRT/CR – the total number of postcranial elements (limb elements, vertebrae and ribs) compared with the total number of cranial elements (mandibles, maxillae and teeth).
(b) PCRAP/CR – the total number of limb elements (long bones, scapulae, innominates, patellae, metapodials, carpals, tarsals and phalanges) compared with the total number of cranial elements (mandibles, maxillae and teeth).
(c) PCRLB/CR – the total number of postcranial long bones (humeri, radii, ulnae, femora and tibiae) compared with the total number of cranial elements (mandibles and maxillae).

Loss of distal limb elements was shown by two indices (Lloveras et al., 2008a):

(d) AUT/ZE – autopodia (metapodials, carpals, tarsals and phalanges) compared with zygopodia and stylopodia (tibiae, radii, ulnae, humeri, femora and patellae);
(e) Z/E – zygopodia (tibiae, radii and ulnae) compared with stylopodia (femora and humeri).

A further index compared anterior to posterior limb elements:

(f) AN/PO – scapulae, humeri, radii, ulnae and metacarpals compared with innominates, femora, tibiae and metatarsals.

The following ratios were calculated for birds:

(a) To assess the differential representation of wings and legs (following Ericson, 1987), the number of wing elements (humeri, ulnae, carpometacarpi) was divided by the sum of wing and leg elements (femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.
(b) To evaluate the presence of proximal and distal elements (Bochenski and Nekrasov, 2001), the number of proximal elements (scapulae, coracoids, humeri, femora, tibiotarsi) was divided by the sum of proximal and distal fragments

(ulnae, radii, carpometacarpi, tarsometatarsi), and expressed as a percentage.

(c) To appraise the proportions of core and limb elements (Bochenski, 2005), the number of core elements (sterna, pelves, scapulae, coracoids) was divided by the sum of core and limb elements (humeri, ulnae, radii, carpometacarpi, femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.

All the ratios were calculated using the MNE.

Chi-square test and *Z*-test were used to evaluate the significance of differences in survivorship of particular skeletal elements or their fragments.

2.2. Breakage

The breakage pattern was described by the maximum length of all identified skeletal elements. Percentages of complete elements, isolated teeth (for mammals) and articulated elements were also calculated (Andrews, 1990). Fragmentation of bones was analysed using separate categories for mammals and birds. For all mammals, bone fragments were categorised depending on bone type:

- Patellae, carpals, tarsals and ribs were classified as complete (C) or fragmented (F).
- Phalanges were recorded as complete (C), proximal (P) or distal (D) fragments. When the distinction between proximal or distal was not possible, they were recorded as fragment (F).
- Vertebrae were registered as complete (C), vertebral body (VB), vertebral epiphysis (VE) or spinous process (SP).
- Breakage of teeth was calculated separately for isolated and *in situ* elements (Fernández-Jalvo and Andrews, 1992) and they were classified as complete (C) or fragmented (F).
- Breakage categories for long bones, metapodials, mandibles, crania, scapulae and innominates follow those proposed by Lloveras et al. (2008a) and applied in subsequent studies (Lloveras et al., 2008b, 2009, 2012a, 2014a).

Breakage of bird bones was analysed using the methodology proposed by Bochenski et al. (1993). The ratio of proximal and distal portions of long bones (Bochenski, 2005) was calculated to observe the differences between whole bones and proximal and distal parts.

2.3. Digestion

Damage to the bone surface was observed under light microscope (×10–×40 magnification). Different categories of digestion damage were applied to bones and teeth (Fernández-Jalvo and Andrews, 1992; Lloveras et al., 2008a, 2008b, 2014b). Five categories of digestion were distinguished: null (0); light (1); moderate (2); heavy (3); and extreme (4).

2.4. Beak/talon marks

Damage to bone surfaces caused by beaks were noted and counted. Following the methodology used in previous studies (Lloveras et al., 2008a, 2008b, 2009, 2012a, 2014a) beak marks were classified as scoring, notches, tooth punctures/tooth pits and crenulated/fractured edges (Andrews, 1990; Binford, 1981; Brain, 1981). Punctures and pits were also classified by their number (isolated or multiple) and distribution (unilateral – i.e. located on one surface – or bilateral) (Sanchis Serra et al., 2013).

3. Results

A total of 826 skeletal fragments was analysed, 321 from south Portugal and 505 from south Spain. For analytical purposes the data from all nest sites have been combined and analysed as a single assemblage. Since the accumulating agent is the same for each sample it was assumed that the taphonomic pattern would be identical.

3.1. Taxonomic representation

The taxa recovered from the samples are presented in Table 1. The leporid sample was exclusively European wild rabbit (*Oryctolagus cuniculus*). Two unidentified small mammal bone fragments were also present. The birds included red-legged partridge (*Alectoris rufa*), pigeon (*Columba* spp.), dove (*Streptopelia* spp.), Eurasian jay (*Garrulus glandarius*), yellow-legged gull (*Larus michahellis*) and unidentified corvids, Ciconiiformes and passerine remains. Fish were represented by a single specimen attributed to Cyprinidae (carps, true minnows, and their relatives).

The most abundant taxon was European rabbit, which made up 53% of the total sample, followed by birds (46.6% – red-legged partridge (21.5%), pigeon (16.3%) and dove (3.4%)), small mammals (0.2%) and fish (0.1%) (Table 1, Fig. 3). The most abundant taxa when quantified by MNI were European rabbit (9), red-legged partridge (8) and pigeon (7).

Table 1 separates the taxonomic abundance for the Portuguese and Spanish samples. In both regions rabbits, red-legged partridges and pigeons were clearly the most numerous species. However, rabbits and pigeons were better represented in the Spanish sample. Partridges were more common in the Portuguese sample, which also included a greater diversity of taxa.

3.2. Age at death

Age at death was only estimated for rabbits and revealed a preponderance of immature individuals ($N = 34$, 58.6%).

3.3. Taphonomic analysis

All body parts were represented in the samples, though their presence and frequency varied by taxonomic group. Observation of

Table 1
NISP (Number of Identified Specimens), MNE (Minimum Number of Elements) and MNIs (Minimum Number of Individuals) by taxon recovered in Portuguese and Spanish samples.

	Portuguese sample		Spanish sample		Whole sample			
TAXA	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**MNE**	**MNIs**
Leporids								
Oryctolagus cuniculus	140	43.6	298	59	438	53	385	9
Small mammals								
Unidentified	–	–	2	0.4	2	0.2	2	1
Birds								
Alectoris rufa	116	36.1	62	12.3	178	21.5	147	8
Columba spp.	31	9.7	104	20.6	135	16.3	125	7
Streptopelia spp.	–	–	28	5.5	28	3.4	28	2
Garrulus glandarius	7	2.2	–	–	7	0.8	7	1
Corvidae	1	0.3	–	–	1	0.1	1	1
Ciconiiformes	12	3.7	–	–	12	1.5	12	1
Larus michahellis	5	1.6	–	–	5	0.6	5	1
Passeriformes	7	2.2	–	–	7	0.8	7	1
Unidentified	1	0.3	11	2.2	12	1.5	12	1
Fish								
Cyprinidae	1	0.3			1	0.1	1	1
Total	321		505		826		732	

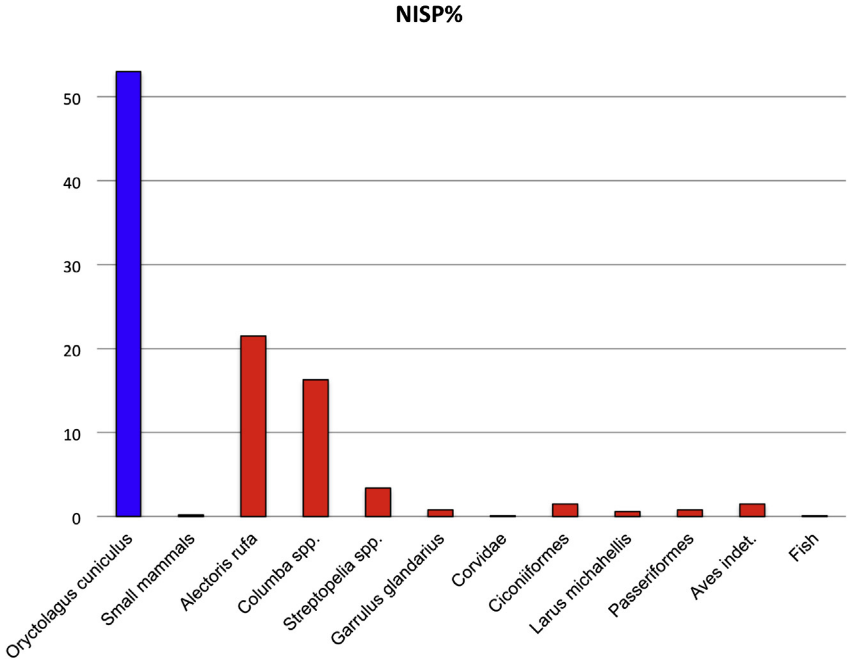

Fig. 3. Relative abundance of prey taxa (%NISP).

breakage patterns reveals that prey remains were moderately fragmented with an average percentage of complete bones of 62.6%. Additionally, a total of 43.4% of the remains measured less than 10 mm in length, 38.7% of bones were articulated and 62.7% of teeth remained *in situ*. Damage from digestion affected 44.7% of the remains and most (49.2%) showed a heavy degree of corrosion. Beak or talon marks occurred on 34 remains (4.1%), crenulated edges (41.9%) and beak punctures (27.9%) were the most common form.

Henceforth, the taphonomic analysis for leporids and birds is treated separately given the potential for different groups of taxa to exhibit different taphonomic signatures.

3.3.1. Leporids

The total number of recovered leporid remains was 438, 245 were non-ingested remains and 193 were extracted from pellets.

3.3.1.1. Anatomical representation. The anatomical composition of the identified remains in the leporid sample is presented in Table 2. The entire skeleton was represented – upper molars (22.4%), vertebrae (18%), phalanges (15.1%) and cranial remains (8.9%) were the most numerous elements (N%). The relative abundance of skeletal elements (RA%) is also shown in Table 2 and Fig. 4. The mean value (28.5%) was very low indicating an important loss of

Table 2

Leporid skeletal elements recovered from Bonelli's Eagle nest accumulations. Key: *N* – number of skeletal elements; *N*% – percentage of skeletal elements; MNE – minimum number of elements; RA% – relative abundance. Abbreviations: cra – cranium; man – mandible; inc – incisors; u mol – upper molar; l mol – lower molar; sc – scapula; hum – humerus; rad – radius; uln – ulna; mtc – metacarpal; inn – innominate; fem – femur; pat – patella; tib – tibia; mts – metatarsal; cal – calcaneum; ast – astragalus; c/t – carpal/tarsal; phal – phalanges; ver – vertebrae; rib – rib.

LEPORIDS	Whole sample (MNI = 9)					Non-ingested (MNI = 8)				Pellets (MNI = 4)			
	N	*N*%	MNE	RA%	MNI	*N*	*N*%	MNE	RA%	*N*	*N*%	MNE	RA%
cra	39	8.9	9	100	9	15	6.1	7	87.5	24	12.4	2	50
man	4	0.9	4	22.2	2	0	0	0	0	4	2.1	4	50
inc	24	5.5	24	44.4	5	19	7.8	19	39.6	5	2.6	5	20.8
u mol	98	22.4	98	90.7	9	61	24.9	61	63.5	37	19.2	37	77.1
l mol	10	2.3	10	11.1	1	0	0	0	0	10	5.2	10	25
sc	6	1.4	4	22.2	2	3	1.2	2	12.5	3	1.6	2	25
hum	4	0.9	3	16.7	2	2	0.8	2	12.5	2	1	1	12.5
rad	6	1.4	5	27.8	3	2	0.8	2	12.5	4	2.1	3	37.5
uln	4	0.9	3	16.7	2	2	0.8	2	12.5	2	1	1	12.5
mtc	4	0.9	4	4.4	1	0	0	0	0	4	2.1	4	10
inn	18	4.1	16	88.9	8	14	5.7	13	81.3	4	2.1	3	37.5
fem	8	1.8	7	38.9	4	6	2.4	5	31.3	2	1	2	25
pat	2	0.5	2	11.1	1	2	0.8	2	12.5	0	0	0	0
tib	7	1.6	4	22.2	3	4	1.6	3	18.8	3	1.6	1	12.5
mts	19	4.3	15	20.8	2	8	3.3	8	16.7	11	5.7	7	21.9
cal	3	0.7	3	16.7	2	2	0.8	2	12.5	1	0.5	1	12.5
ast	2	0.5	2	11.1	1	2	0.8	2	12.5	0	0	0	0
c/t	23	5.3	23	10.6	2	10	4.1	10	5.2	13	6.7	13	13.5
phal1/2	42	9.6	42	13.7	2	16	6.5	16	5.9	26	13.5	26	19.1
phal3	24	5.5	24	14.8	2	8	3.3	8	5.6	16	8.3	16	22.2
ver	79	18	73	17.6	2	62	25.3	62	16.8	17	8.8	11	6
rib	12	2.7	10	4.6	1	7	2.9	6	3.1	5	2.6	4	4.2
Total	438		385			245		232		193		153	

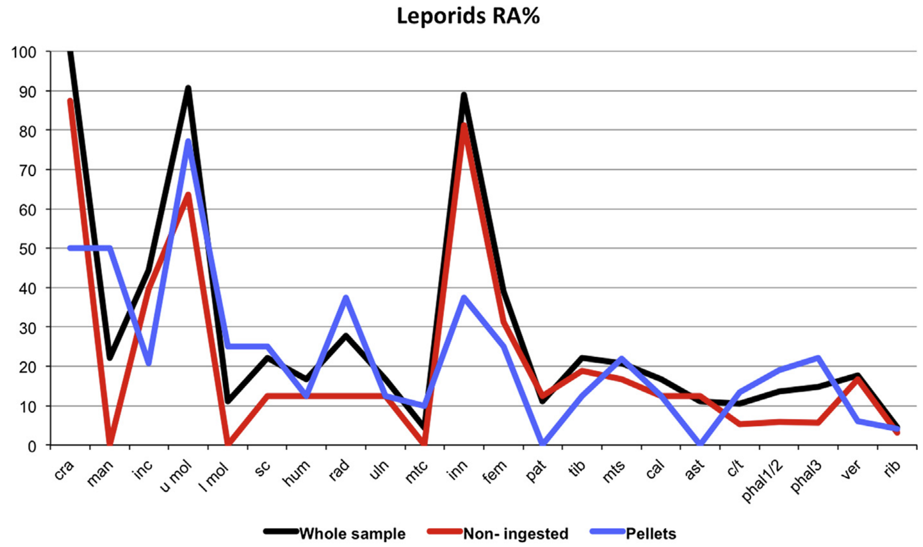

Fig. 4. Relative abundance of different parts of the skeleton for leporid remains. For abbreviations see the caption for Table 2.

bones in the assemblage. The best-represented elements were the cranium (100%), upper molars (90.7%) and the innominate (88.9%), whilst metacarpals and ribs were rare (4.4% and 4.6% respectively).

Relative proportions of skeletal elements are shown in Table 3. Results indicate that there was a deficiency in the numbers of:

- postcranial compared to cranial remains;
- lower compared to upper limb elements, indicating an important loss of distal elements (specially the smallest ones, i.e., third phalanges and carpal/tarsal bones) and;
- anterior compared to posterior limb elements.

Analysis of the leporids by the origin of remains (non-ingested and pellets), reveals that the absolute numbers of cranial remains, metapodials and phalanges were higher in pellets, whereas vertebrae and innominates were better-represented in non-ingested remains (Table 2). Relative abundance profiles were similar in both samples (Table 2, Fig. 4), but long bones, mandibles and phalanges were more abundant in pellets, and crania and innominates predominated in non-ingested remains. This difference is statistically significant ($\chi^2 = 187.9$, $P < 0.01$, df = 21).

3.3.1.2. Breakage. The size of leporid bone fragments ranges between 1.7 and 89.6 mm; the average maximum length was 19.7 mm and 54.9% of the rabbit remains had length values under 10 mm. The percentage of complete elements was 74.7%. Values vary according to bone size, with the highest percentages obtained for the smallest bones: carpals/tarsals; patellae; calcanei; astragali; phalanges; and teeth (Table 4). Long bones were complete in 51.7% of cases.

A total of 172 (39.3%) remains within the entire leporid sample were articulated and 63.6% of teeth were recovered *in situ.*

Table 3
Proportions of different parts of the skeleton for leporids.

Indices %	Leporids sample
PCRT/CR	32.1
PCRAP/CR	30.4
PCRLB/CR	48.6
AUT/ZE	57.7
Z/E	80
AN/PO	35.2

Breakage categories (Table 5) show that:

- crania were complete in only 2.6% of cases and their fragments were mostly identified by parts of the neurocranium (NC) and maxilla (M);
- mandibles were never complete, their fragments were represented by body portions (including MB and MBB);
- teeth located *in situ* were always complete and isolated teeth were complete in 91.8% of cases;
- vertebrae were complete in 79.7% of cases, their fragments were mainly represented by the vertebral body (VB); there were a few instances of vertebral epiphyses (VE) and spinous processes (SP);
- innominates were complete in 55.6% of cases, fragments were represented by portions containing the acetabulum (AISIL, AIL, AIS);

Table 4
Numbers (*C*) and percentages (*C*%) of complete skeletal remains of leporids. For abbreviations see the caption for Table 2.

LEPORIDS	Whole sample		Non-ingested		Pellets	
	C	*C*%	*C*	*C*%	*C*	*C*%
cra	1	2.6	1	6.7	0	0
man	0	0	–	–	0	0
inc	23	95.8	19	100	5	80
u mol	97	99	61	100	36	97.3
l mol	8	80	–	–	9	90
sc	0	0	0	0	0	0
hum	2	50	2	100	0	0
rad	3	50	2	100	1	25
uln	2	50	2	100	0	0
mtc	4	100	–	–	4	100
inn	10	55.6	10	71.4	0	0
fem	5	62.5	4	66.7	1	50
pat	2	100	2	100	–	–
tib	3	42.9	3	75	0	0
mts	12	63.2	8	100	4	36.4
cal	3	100	2	100	1	100
ast	2	100	2	100	–	–
c/t	23	100	10	100	13	100
phal1/2	40	95.2	16	100	23	88.5
phal3	24	100	8	100	16	100
ver	63	79.7	61	98.4	2	11.8
rib	0	0	0	0	0	0
Total	327	74.7	213	86.9	115	59.6

Table 5
Numbers and percentages of parts of the skeleton included in each breakage category for leporids. **Long bones**, **metacarpal** and **metatarsal** bones were classified as: complete (C); proximal epiphysis (PE); proximal epiphysis + shaft (PES); shaft (S); shaft + distal epiphysis (SDE); and distal epiphysis (DE). **Mandible** as: complete (C); incisive part (IP); mandible body + incisive part (MBI); mandible body (MB); mandible body + branch (MBB); and condylar process (CP). **Cranium** as: complete (C); incisive bone (IB); incisive bone + maxilla (IBM); maxilla (M); zygomatic arch (ZA); and neurocranium (NC). **Innominate** as: complete (C); acetabulum (A); acetabulum + ischium (AIS); acetabulum + ischium + ilium (AISIL); acetabulum + ilium (AIL); ischium (IS); and illium (IL). **Scapula** as: complete (C); glenoid cavity (GC); glenoid cavity + neck (GCN); neck + fossa (NF); and fossa (F). **Vertebrae** as: complete (C); vertebral body (VB); vertebral epiphysis (VE); and spinous process (SP). **Phalanges** as: complete (C); proximal fragment (P); distal fragment (D); and fragment (F). **Patella, carpal/tarsal, calcaneum, astragalus, ribs and teeth** as: complete (C); and fragment (F).

Leporids sample – breakage categories

Long bones and metapodial	**C**		**PE**		**PES**		**S**		**SDE**		**DE**	
	N	**%**	***N***	**%**	***N***	**%**	***N***	**%**	***N***	**%**	***N***	**%**
Humerus	2	50	1	25	0	0	1	25	0	0	0	0
Radius	3	50	0	0	0	0	0	0	1	25	1	25
Ulna	2	50	0	0	0	0	0	0	1	16.7	2	33.3
Femur	5	62.5	1	12.5	1	12.5	0	0	1	12.5	0	0
Tibia	3	42.9	1	14.3	0	0	2	28.6	0	0	1	14.3
Metacarpus	4	100	0	0	0	0	0	0	0	0	0	0
Metetarsus	12	63.2	0	0	0	0	0	0	3	15.8	4	21.1

Mandible	***N***	**%**	**Cranium**	***N***	**%**	**Innominate**	***N***	**%**	**Scapula**	***N***	**%**
C	0	0	C	1	2.6	C	10	55.6	C	0	0
IP	0	0	IB	2	5.1	A	1	5.6	GC	0	0
MBI	0	0	IBM	3	7.7	AIS	1	5.6	GCN	2	33.3
MB	3	75	M	8	20.5	AISIL	3	16.7	NF	2	33.3
MBB	1	25	ZA	3	7.7	AIL	2	11.1	F	2	33.3
PC	0	0	NC	22	56.4	IS	0	0			
						IL	1	5.6			

Vertebrae	***N***	**%**	**Ribs**	***N***	**%**	**Phalanges 1/2**	***N***	**%**	**Phalanges 3**	***N***	**%**
C	63	79.7	C	0	0	C	40	95.2	C	24	100
VB	10	12.7	F	12	100	P	2	4.8	F	0	0
VE	2	2.5				D	0	0			
SP	4	5.1									

Patella	***N***	**%**	**Car/tar**	***N***	**%**	**Cal**	***N***	**%**	**Ast**	***N***	**%**
C	2	100	C	23	100	C	3	100	C	2	100
F	0	0	F	0	0	F	0	0	F	0	0

Teeth	**“in situ”**						**Isolated**					
	Incisors		**Upper molars**		**Lower molars**		**Incisors**		**Upper molars**		**Lower molars**	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
C	19	100	64	100	1	100	5	83.3	33	97.1	7	77.8
F	0	0	0	0	0	0	1	16.7	1	2.9	2	22.2

- scapulae were never complete and most fragments comprised the glenoid cavity (GC, GCN);
- all breakage categories were found on the limb bones, which were mostly complete; the majority of radius and ulna fragments included the distal epiphysis;
- metapodials were well preserved; metacarpals and metatarsals were complete in 100% and 63.2% of cases respectively.

Non-ingested remains were clearly less affected by breakage than bones from pellets. The size of the leporid remains differs noticeably; in the non-ingested remains sample the average maximum length was 43.1 mm and only 6.8% of the rabbit remains had length values under 10 mm, whereas those in the pellets had an average maximum length of 8.3 mm and 78.1% of remains had length values under 10 mm. The percentage of complete elements was also distinct: 86.9% in non-ingested remains compared with 59.6% in pellets. Differences were mostly concentrated in large skeletal elements (Table 4) such as: long bones (88.3% *vs* 15%); innominates (55.6% *vs* 0%); and metatarsi (100% *vs* 36.4%).

3.3.1.3. Digestion and beak/talon marks. Digestion damage was present in 31.2% of the overall leporid sample (Fig. 5). Different degrees of digestion damage were observed on the surface of rabbit remains; specifically, 2.3% of the skeletal elements were altered by a light degree, 7.9% by a moderate degree, 14.4% by a heavy degree and 6.5% by an extreme degree of corrosion.

No digested remains were recovered in the non-ingested sample. Considering the pellet sample, the percentage of remains affected by digestion was considerably higher (72%). In this sample, the percentage of elements included in each degree of digestion damage was: 5.4% light, 18.3% moderate, 33.3% heavy and 15.1% extreme (Fig. 6 and Table 6). Different skeletal elements were altered in different proportions: vertebrae, scapulae, skull remains, humerus and tibia were more corroded than the remains of autopodia (carpals/tarsals, metapodials and phalanges) (Table 6). Whole surfaces of bones were often affected by digestive corrosion, the most altered areas were fractured or articular surfaces. A high proportion of teeth (92%) were corroded (Table 6).

Beak marks were observed on ten specimens (2.3% of the sample); all occurred on non-ingested remains (4.1% of the sample) and were mostly situated on the innominates (5) and scapulae (2), although crania (1), vertebrae (1) and femora (1) were also affected. The most common form of damage was crenulated edges (36.4%), followed by notches (27.3%), punctures (18.2%), pits (9.1%) and fractured edges (9.1%) (Fig. 5). Pits and punctures were always isolated and limited to a single surface (i.e. not opposed). Some of the recorded marks may have been inflicted by talons, however, there are no reliable criteria by which these might be separated.

3.3.2. Birds

The total number of recovered bird remains was 385, of which 57 came from non-ingested remains and 328 were from pellets.

3.3.2.1. Anatomical representation. All parts of the avian skeleton were recovered (Table 7). Phalanges (36.9%) showed the highest values. Vertebrae (7%), crania (6.2%), tarsometatarsi (4.9%),

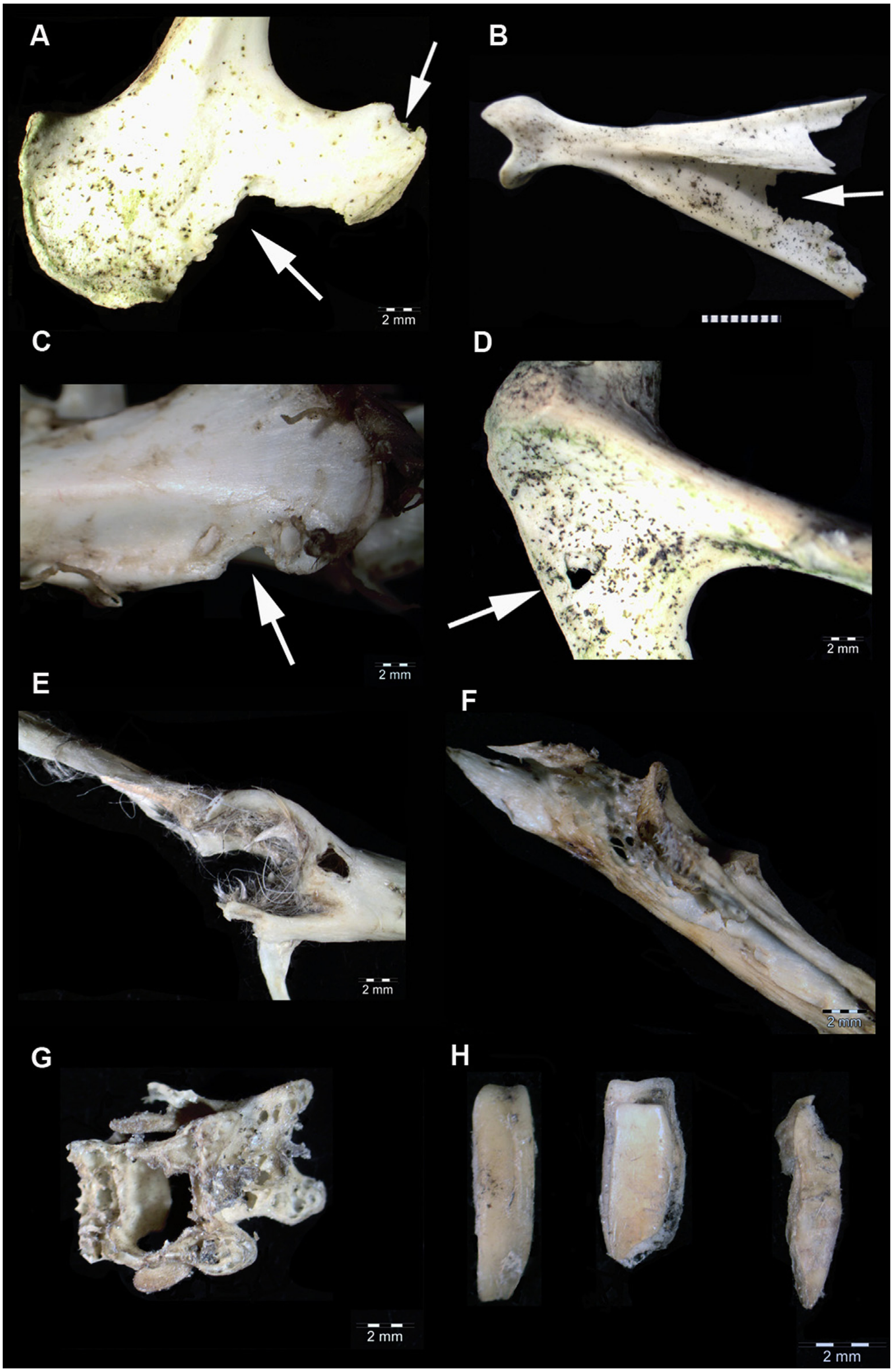

Fig. 5. Examples of leporid bones and teeth displaying beak marks (A–D) and digestion damage with extensive corrosion ($E = 4$, $F = 3$, $G = 4$ and $H = 3$) caused by Bonelli's eagles.

tibiotarsi (4.4%) and scapulae (4.2%) were also common. Relative abundance varied by skeletal element (Table 7, Fig. 7): fragments of the trunk (sternum and pelvis) were the best represented (100% and 91.7% respectively) followed by cranial remains (75%). Pectoral arch (scapula, coracoid and clavicle), wing and leg bones were also well represented: most displayed values over 50% (Table 7, Fig. 7). Vertebrae and ribs showed the lowest percentages (6.9% and 3.1% respectively).

Relative abundance was calculated separately for *Columba* spp. and red-legged partridge because these were the best represented taxa. Results show that anatomical representation is similar in both taxa; however, the pelves and crania were the most frequent elements for red-legged partridge whereas sterna and scapulae dominated the *Columba* spp. assemblage (Table 7, Fig. 7). Differences in the relative abundance of both taxa were statistically significant ($\chi^2 = 213.4$, $P < 0.01$, df $= 16$).

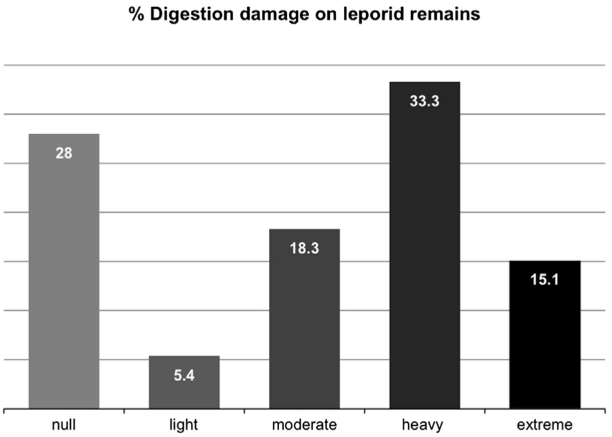

Fig. 6. Percentage of leporid remains from the pellets sample included in each digestion category.

Wing bones account for 45.8% of the sum of wing and leg bones evidencing a slightly higher representation of leg bones. The deviation from the expected 50% (1:1 proportion) is not statistically significant ($Z = 0.53$, $p > 0.05$). The ratio of proximal to distal portions was almost equal (53.2%). Deviation from the expected percentage (50%) is not statistically significant ($Z = 0.05$, $p > 0.05$). The ratio of the core to limb elements was 36.6%, the predominance of limb elements is highly statistically significant ($Z = 2.54$, $p < 0.01$).

Separate analysis of the sample by origin (non-ingested *vs* pellets) reveals that sterna and pelves were the most common elements in the non-ingested sample, with poor representation or absence of other elements. In contrast, crania, pectoral arch and most wing and leg bones (including phalanges) were abundant in pellets and sterna and pelves were rare, demonstrating that Bonelli's eagles do not normally ingest these skeletal elements. Vertebrae and ribs were very scarce indicating almost total loss of these elements (Table 7, Fig. 7). Differences in anatomical representation in both samples were statistically highly significant ($\chi^2 = 424.8$, $P < 0.01$, df = 12).

Table 6
Numbers and percentage of leporid bones and teeth included in each digestion category. For abbreviations see the caption for Table 2. The number of bones considered was 186, a total of 7 bones from pellets were not used because surface damage could not be observed, therefore no digestion corrosion category could be attributed.

Digestion damage on leporid remains (pellets sample)

	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
cra	0	0	0	0	7	29.2	10	41.7	7	29.2
man	0	0	0	0	0	0	2	66.6	1	33.3
inc	0	0	0	0	2	40	2	40	1	20
u mol	4	11.4	4	11.4	11	31.4	14	40	2	5.7
l mol	0	0	2	20	1	10	7	70	0	0
sc	0	0	0	0	0	0	1	33.3	2	66.7
hum	0	0	0	0	0	0	1	50	1	50
rad	2	50	0	0	1	25	1	50	0	0
uln	1	50	0	0	1	50	0	0	0	0
mtc	4	100	0	0	0	0	0	0	0	0
inn	0	0	0	0	0	0	4	100	0	0
fem	1	50	0	0	0	0	1	50	0	0
pat	0	0	0	0	0	0	0	0	0	0
tib	0	0	0	0	0	0	3	100	0	0
mts	5	45.5	1	9.1	2	18.2	3	27.3	0	0
cal	0	0	0	0	0	0	1	100	0	0
ast	0	0	0	0	0	0	0	0	0	0
c/t	11	84.6	0	0	0	0	2	15.4	0	0
phal1/2	17	65.4	3	11.5	4	15.4	1	3.8	1	3.8
phal3	7	58.3	0	0	2	16.7	3	25	0	0
ver	0	0	0	0	1	5.9	4	23.5	12	70.6
rib	0	0	0	0	2	40	2	40	1	20
TOTAL	52	28	10	5.4	34	18.3	62	33.3	28	15.1

The ratio of wing to leg elements varied in both samples (88.9% in non-ingested and 39.7% in pellets) indicating that leg bones were very scarce in non-ingested remains. The ratio of proximal to distal bones did not show great differences (58.8% and 46.4%), but the ratio of the core to limb elements (65.9% and 22.7%) pointed to a major presence of core elements in the non-ingested remains sample. Differences in survivorship of particular skeletal elements in both types of samples are statistically significant ($\chi^2 = 8.43$, $P = 0.014$, df = 2).

3.3.2.2. Breakage. The size of the recovered avian remains ranged between 2.3 mm and 90.4 mm (average maximum length 17.6 mm) and 35.4% of bones had length values under 10 mm.

The degree of fragmentation was moderate; on average 49.9% of the elements were complete, with the small bones such as carpals, ribs and phalanges being the least fragmented (Table 8). The tarsometatarsi and coracoids were the best preserved (26.3% and 23.1% respectively) limb/core bones, whereas the femur and tibiotarsus were never complete.

A notable number of skeletal remains was articulated ($N = 148$, 38.4%); most being leg bones (tarsometatarsi and phalanges, 55.4%).

Breakage categories (Table 9) show that:

- all breakage categories occurred on long bones, scapulae and coracoids; few bones were complete (14.4%), but proximal and distal ends and shaft (with missing articular ends) were well represented (35.6%, 22% and 28% respectively);
- most scapula, coracoid, radius and femur fragments were proximal ends; the best represented fragments of humeri and tarsometatarsi were distal ends; the tibiotarsi and ulnae were mostly shaft fragments and most carpometacarpi were complete;
- skulls were generally represented by brain case and beak fragments;
- most mandibles were represented by fragments of *pars symphysialis*;
- most pelves fragments included the synsacrum and ilium–ischium–pubis bones (50%), fragments of ilium-ischium-pubis bones were also abundant (35.7%);
- a high percentage of sternae fragments included the rostrum (91.6%), but most were less than half complete (58.3%).

Non-ingested remains were less affected by breakage than those from pellets. The average maximum length of uneaten remains was 43.9 mm and all bones were over 10 mm in length; the average maximum length in the pellets sample was 14.9 mm and 40.1% of remains had length values under 10 mm. The percentage of complete elements was very similar in both samples (around 50%, Table 8) because of the presence of high numbers of small elements (phalanges, carpals) in the pellets sample, which were normally complete. When long bones are considered in isolation, the percentage of complete elements decreases to 47.1% (in non-ingested remains) and 9.5% (in pellets).

3.3.2.3. Digestion and beak/talon marks. Digestion corrosion was evident in 60.4% of the whole bird sample (Fig. 8). Most bones showed heavy corrosion (30.8%) whereas it was light on only 3.3% of the elements. The percentage of elements recorded as being

Table 7
Bird skeletal elements recovered from Bonelli's Eagle nests. Key: N – number of skeletal elements; N% – percentage of skeletal elements; MNE – minimum number of elements; MNI – minimum number of individuals; RA% – relative abundance. Abbreviations: cra – cranium; man – mandible; fur – furcula; sc – scapula; cor – coracoid; hum – humerus; rad – radius; uln – ulna; cmc – carpometacarpus; c – carpal (carpi radial, carpi ulnare); di – wing digit; fem – femur; tbt – tibiotarsus; tmt – tarsometatarsus; str– sternum; pel – pelvis; phal – leg phalanges; ver – vertebrae; rib – rib.

BIRDS	Whole sample (MNI = 12)					*Columba* spp. (MNI = 7)				*Alectoris rufa* (MNI = 8)				Non-ingested (MNI = 10)				Pellets (MNI = 8)			
	N	*N*%	MNE	RA%	MNI	*N*	*N*%	MNE	RA%	*N*	*N*%	MNE	RA%	*N*	*N*%	MNE	RA%	*N*	*N*%	MNE	RA%
cra	24	6.2	9	75	9	2	1.5	2	28.6	21	11.8	6	75	1	1.8	1	10	22	6.7	8	100
man	4	1	4	33.3	4	0	0	0	0	3	1.7	3	37.5	1	1.8	1	10	3	0.9	3	37.5
fur	4	1	4	33.3	4	2	1.5	2	28.6	1	0.6	1	12.5	1	1.8	1	10	3	0.9	3	37.5
sc	16	4.2	14	58.3	8	10	7.4	8	57.1	3	1.7	3	18.8	3	5.3	3	15	13	4	11	68.8
cor	13	3.4	12	50	8	7	5.2	7	50	4	2.2	3	18.8	4	7	4	20	9	2.7	8	50
hum	10	2.6	7	29.2	7	3	2.2	2	14.3	5	2.8	3	18.8	3	5.3	3	15	8	2.4	4	25
rad	14	3.6	13	54.2	9	4	3	4	28.6	7	3.9	6	37.5	1	1.8	1	5	13	4	12	75
uln	12	3.1	11	45.8	8	3	2.2	3	21.4	6	3.4	5	31.3	2	3.5	2	10	10	3	9	56.3
cmc	17	4.4	15	62.5	9	3	2.2	3	21.4	9	5.1	7	43.8	3	5.3	3	15	14	4.3	12	75
c	11	2.9	11	–	4	1	0.7	1	–	5	2.8	5	–	3	5.3	3	–	8	2.4	8	–
di	9	2.3	9	–	3	0	0	0	–	5	2.8	5	–	4	7	4	–	5	1.5	5	–
fem	14	3.6	12	50	8	5	3.7	4	28.6	4	2.2	3	18.8	0	0	0	0	14	4.3	12	75
tbt	17	4.4	14	58.3	11	8	6	7	50	7	3.9	5	31.3	0	0	0	0	17	5.2	14	87.5
tmt	19	4.9	13	54.2	8	8	6	5	35.7	9	5.1	6	37.5	1	1.8	1	5	18	5.5	12	75
str	12	3.1	12	100	12	7	5.2	7	100	3	1.7	3	37.5	10	17.5	10	100	2	0.6	2	25
pel	14	3.6	11	91.7	11	1	0.7	1	14.3	11	6.2	8	100	12	21.1	10	100	2	0.6	1	12.7
phal	142	36.9	142	42.3	10	63	46.7	63	32.1	51	28.7	51	22.8	0	0	0	0	142	43.3	142	63.4
ver	27	7	25	6.9	2	6	4.4	4	1.9	21	11.8	21	8.8	5	8.8	5	1.7	22	6.7	20	8.3
rib	6	1.6	6	3.1	1	2	1.5	2	1.8	3	1.7	3	2.3	3	5.3	3	1.9	3	0.9	3	2.3
TOTAL	385		344			135		125		178		147		57		55		328		289	

affected by a moderate and extreme degree was 14.8% and 11.5% respectively.

No bones exhibiting digestion damaged were recorded in the non-ingested sample. Considering only the pellets sample, the percentage of digested remains was 71.4%. Heavy corrosion (36.4%) predominated, followed by moderate (17.5%) and extreme (13.6%) (Fig. 9 and Table 10).; light digestion was very low (3.9%).

Most skeletal remains exhibited substantial damage with long bones,, specifically humeri, ulnae, femora and tibiotarsi, exhibiting the highest degree of alteration (Table 10). Phalanges appeared to be less damaged, probably because they were ingested in anatomical connection and protected by the skin of the feet. Sterna and pelves were the least affected by digestion because these skeletal elements do not seem to be ingested regularly by Bonelli's eagles.

Traces left by beaks were observed on 24 bones, 6.2% of the sample (Fig. 8). Most of them occurred on the pelves (10) and sterna (9). The rest were located on crania (1), coracoids (1), scapulae (1), humeri (1) and femora (1). Crenulated edges (41.2%) were the most common form of damage, followed by punctures (32.3%), pits (20.6%) and fractured edges (5.9%). One coracoid and two pelves displayed two simultaneous pit/puncture marks; pits and punctures were isolated in all other specimens and they were always unilateral (not opposed).

Most elements affected by beak marks came from the non-ingested sample (*N* = 20; 35.1%), marks occurred on only four bone fragments from the pellets (1.2%).

4. Discussion

The prey taxa identified in our samples is characteristic of Bonelli's eagles. In most feeding studies, leporids and birds are the most abundant prey, with European rabbit, red-legged partridge and pigeons playing a major dietary role (Caro et al., 2011; Del Amo et al., 2008; Moleón et al., 2009; Ontiveros et al., 2005; Palma et al., 2006; Resano et al., 2011). Our observations support the reported diet of Bonelli's eagle, which appears to be adapted to the most abundant prey available in each region, with rabbits always predominating in regions where they are present (Moleón et al., 2009). This variation is evident in the slightly different relative composition of prey in each of our study areas. It is apparent, therefore, that prey diversity must be taken into account when analysing archaeological samples.

Body part representation at the Bonelli's eagle nests varied with taxonomic group or species. Real's (1996) study of prey consumption behaviour at nests of these raptors showed that the lowest weight class prey (red squirrel (*Sciurus vulgaris*), ocellated lizard (*Timon lepidus*), or corvids), were consumed whole in most cases and no remains were left in the nest. In the case of rabbits and pigeons, more than half of the individuals were not completely eaten. However, while rabbit remains were frequently removed from the nest by the eagles, one third of the pigeons were left. This behaviour undoubtedly affects the relative frequencies and anatomical representation of different prey types.

Our study shows that Bonelli's eagles often fragment the bones of their prey, although the degree of fragmentation varies markedly among prey species. The percentage of complete elements and complete long bones was clearly higher for rabbits (74.7% and 51.7%) than for birds (49.9% and 14.4%). Differences between taxa were also found in bone surface alterations. For example, birds were more affected by digestion corrosion than rabbits (60.4% vs 31.2%), which is related to the fact that fewer parts of the rabbit carcass were ingested by Bonelli's eagles. Beak marks were also more common on bird remains (6.2% vs 2.3%). It is manifest that the taphonomic pattern obtained is strongly related to the prey/predator size, to the type of prey and to the feeding behaviour of the predator.

4.1. The taphonomic signature of Bonelli's eagle on leporid remains

To facilitate comparisons, we present a summary of results obtained from different leporid predators, where the data have been collected using the same methods (Table 11). In relation to the age at death, we found that the majority of rabbits (58.6%) were immature. Palma et al. (2006) in their study of the feeding habits of Bonelli's eagle found that 86.2% of rabbits were adult. This suggests that the percentage of adult individuals can be variable. Lloveras et al. (2012b), observed a similar phenomena in their study of

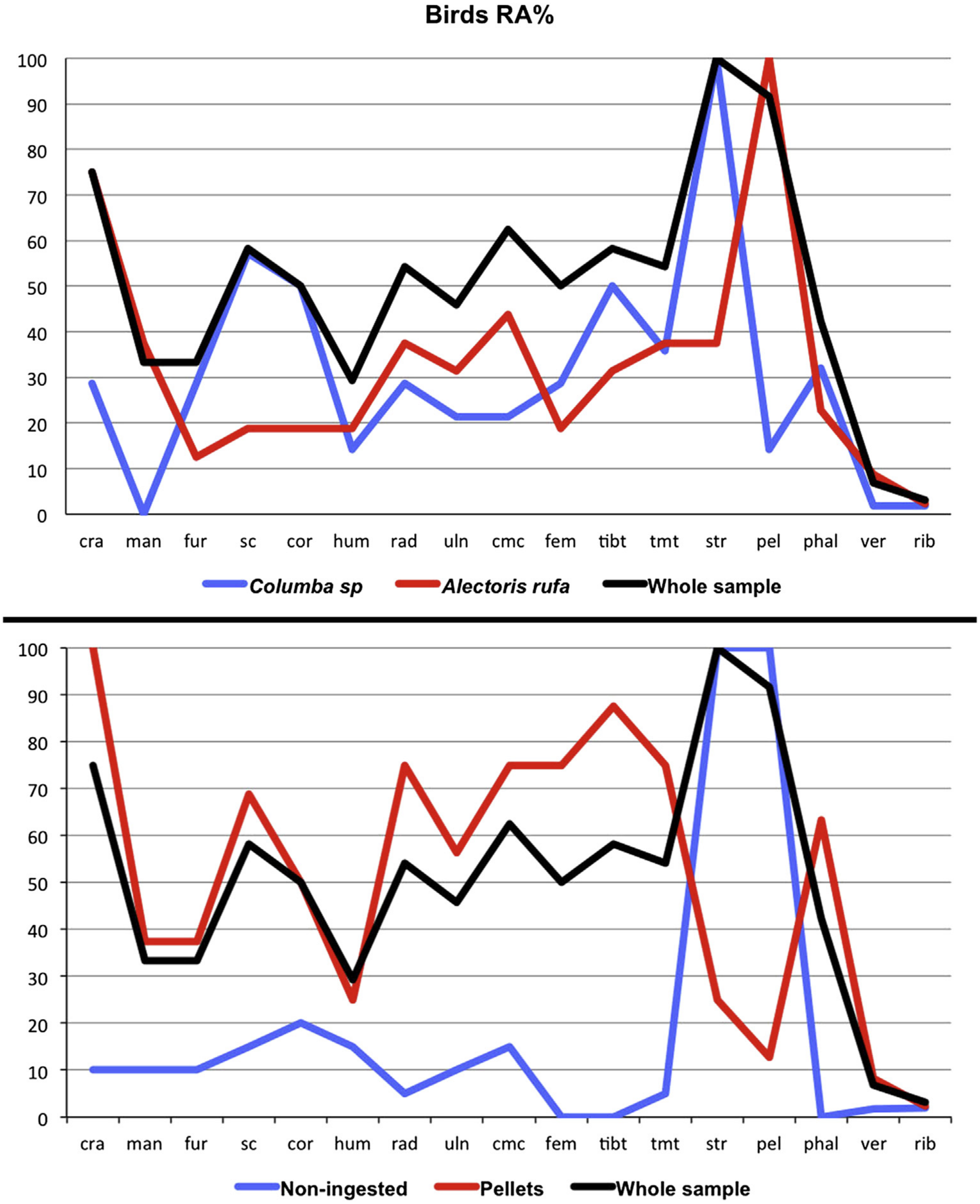

Fig. 7. Relative abundance of different parts of the skeleton in the bird remains samples. For abbreviations see the caption for Table 7.

eagle owl prey at nests. The implication is that leporid age may be an insufficiently distinctive character to separate accumulations generated by Bonelli's eagle and potentially other predators as well.

The main taphonomic features observed in the leporid sample point to anatomical representation characterized by an abundance of cranial remains and innominates, a low frequency of axial elements and autopodia and a greater presence of hindlimbs relative to forelimbs. While some differences were observed between non-ingested remains and pellets, these traits prevailed in both samples. Comparisons with other diurnal raptors reveal that the taphonomic signature of Bonelli's eagle leporid accumulations is distinctive. Hockett (1995, 1996) and Schmit (1995) reported that the most common skeletal elements in leporid assemblages accumulated by golden eagles (*Aquila chrysaetos*) were hindlimb bones, specifically tibiae and associated elements (calcanei and astragali) followed by femora. Cranial remains and innominates were also represented in their samples but in lower frequencies. In contrast, femora outnumbered tibiae in the Bonelli's eagle whole sample, whilst calcanei and astragali were rare. Comparison with the taphonomic signature of Spanish imperial eagle (*Aquila adalberti*) pellet samples also shows clear differences. This eagle tends to accumulate large numbers of tibiae, calcanei and phalanges (Lloveras et al., 2008b); all of which were scarce in our Bonelli's eagle pellet sample. Greater differences are found with nocturnal raptors, such as the European eagle owl (*Bubo bubo*), in which the anatomical profile is characterized by high percentages of postcranial remains, specifically long bones, innominates and autopodia (Cochard, 2004b; Lloveras et al., 2009; Sanchis, 2000). With regards to terrestrial carnivores, both Iberian lynx (*Lynx pardinus*) and red fox (*Vulpes vulpes*) leporid assemblages of non-ingested remains are characterised by low frequencies of cranial remains, with long bones and autopodia much more abundant than in our study (Lloveras et al., 2008a, 2012a; Rodríguez-Hidalgo et al., 2013). The scat accumulations of both carnivores display high percentages of cranial remains;

Table 8
Numbers (*C*) and percentages (*C%*) of complete skeletal remains of birds. For abbreviations see the caption for Table 7.

BIRDS	Complete elements					
	Whole sample		Non-ingested		Pellets	
	C	*C%*	*C*	*C%*	*C*	*C%*
cra	1	4.2	1	100	0	0
man	1	25	1	100	0	0
fur	1	25	1	100	0	0
sc	1	6.3	0	0	1	7.7
cor	3	23.1	3	75	0	0
hum	1	10	1	33.3	0	0
rad	1	7.1	1	100	0	0
uln	2	16.7	1	50	1	10
cmc	6	35.3	2	66.7	4	28.6
c	11	100	3	100	8	100
di	6	66.7	4	100	2	40
fem	0	0	–	–	0	0
tbt	0	0	–	–	0	0
tmt	5	26.3	0	0	5	27.8
str	0	0	0	0	0	0
pel	2	14.3	2	16.7	0	0
phal	135	95.1	–	–	135	95.1
ver	10	37	5	100	5	22.7
rib	6	100	3	100	3	100
Total	192	49.9	28	49.1	164	50

nevertheless long bones are far more abundant than in the Bonelli's eagles samples, especially those of the forelimbs (Lloveras et al., 2008a, 2012a).

As far as breakage patterns are concerned, the percentage of complete elements was surprisingly high in our study. Diurnal raptors have been defined as important bone destroyers compared to owls (Andrews, 1990). However, the 74.7% of complete bones recorded in the Bonelli's eagle whole sample is clearly higher than the 38–32.3% obtained with golden eagle accumulations (Schmit, 1995) and the 53.9–45.9% found in European eagle owl nest assemblages (Lloveras et al., 2009). In the pellets sample, the percentage of complete bones and complete long bones was 59.6% and 15.4%, again higher than the values recorded for Spanish imperial eagles (27% and 0%) or for terrestrial carnivore scat accumulations (Table 11). These results indicate that leporid bones accumulated by Bonelli's eagles are less-fragmented than those generated by other predators. This could be related to the size of the raptor, and more specifically to its beak size. Bonelli's eagle beaks are smaller than those of Spanish imperial eagles, golden eagles and European eagle owls (Cramp and Simmons, 1980), and are thus less capable of breaking the bones of large prey, such as rabbits and hares.

The percentage of digested remains in our Bonelli's eagle samples is lower than those recorded for other predators. Values obtained for the pellets sample (72%) are lower than those recorded for Spanish imperial eagle pellets (98%) and for Iberian lynx and fox scat accumulations (97.2% and 99.5%). Even in eagle owl nest accumulations, the percentage of digested remains is higher (Table 11). However, digested remains in our samples were damaged to a very high degree. This clearly distinguishes Bonelli's eagles from European eagle owls, which are characterised by high percentages of light corrosion. Digestion damage was also more pronounced than in Spanish imperial eagle pellets, where high percentages of moderate corrosion were recorded. The values for Bonelli's eagles are similar to those of terrestrial carnivores (Fig. 10).

The percentage of bones with beak marks is similar to those recorded in European eagle owl nest accumulations but clearly lower than those obtained for other raptors such as the Egyptian vulture (*Neophron percnopterus*), which reached values of 7.5%–10.4% (Lloveras et al., 2014a; Sanchis Serra et al., 2013). Beak marks were not found in pellet remains, but this type of damage was also rare in other raptors such as Spanish imperial eagles (0.5%, Table 10). Iberian lynx produces much less damage in non-ingested remains (0.9%), while the percentage of tooth damage in red fox leporid accumulations was much higher (9.5%). Nevertheless, the lack of gnawing and location of the puncture marks is not typical of the action of carnivores but of birds of prey (Sanchis Serra et al., 2013).

In summary, leporid assemblages accumulated by the Bonelli's eagles are characterised by:

- a body part representation with an abundance of cranial remains, upper molars and innominates, very few axial and autopodium elements and a greater abundance of hindlimbs relative to forelimbs;
- a moderate degree of breakage, with high percentages of complete bones;
- a moderate percentage of digested remains but mostly heavy and extreme corrosion;
- a large number of beak/talon marked bones;

Table 9
Numbers and percentages of parts of the skeleton included in each breakage category for birds.

Birds sample – breakage categories											
Mandible	*N*	%	Skull	*N*	%	Pelvis	*N*	%	Sternum	*N*	%
Whole	1	25	whole	1	4.2	Synsacrum + ilium–ischii–pubis	7	50	more 1/2 with rostrum	4	33.3
One branch	0	0	beak + brain case without back part	1	4.2	Ilium–ischii–pubis	5	35.7	less 1/2 with rostrum	7	58.3
Articular part	0	0	brain case without back part	0	0	synsacrum	1	7.1	fragment without rostrum	1	8.3
Pars symphysialis	3	75	brain case	15	62.5	acetabulum	1	7.1			
Middle part branch	0	0	beak	7	29.2						

	Whole		Proximal part		Distal part		Shaft			Complete		Fragment	
	N	%	*N*	%	*N*	%	*N*	%		*N*	%	*N*	%
Scapula	1	6.3	13	81.3	0	0	2	12.5	Phalanges	135	95.1	7	4.9
Coracoid	3	23.1	9	69.2	1	7.7	0	0	Vertebrae	10	37	17	63
Humerus	1	10	3	30	5	50	1	10	Ribs	6	100	0	0
Radius	1	7.1	7	50	1	7.1	5	35.7					
Ulna	2	16.7	1	8.3	2	16.7	7	58.3					
Carpometacarpus	6	35.3	4	23.5	2	11.8	5	29.4					
Femur	0	0	6	42.9	4	28.6	4	28.6					
Tibiotarsus	0	0	2	11.8	6	35.3	9	52.9					
Tarsometatarsus	5	26.3	2	10.5	8	42.1	4	21.1					

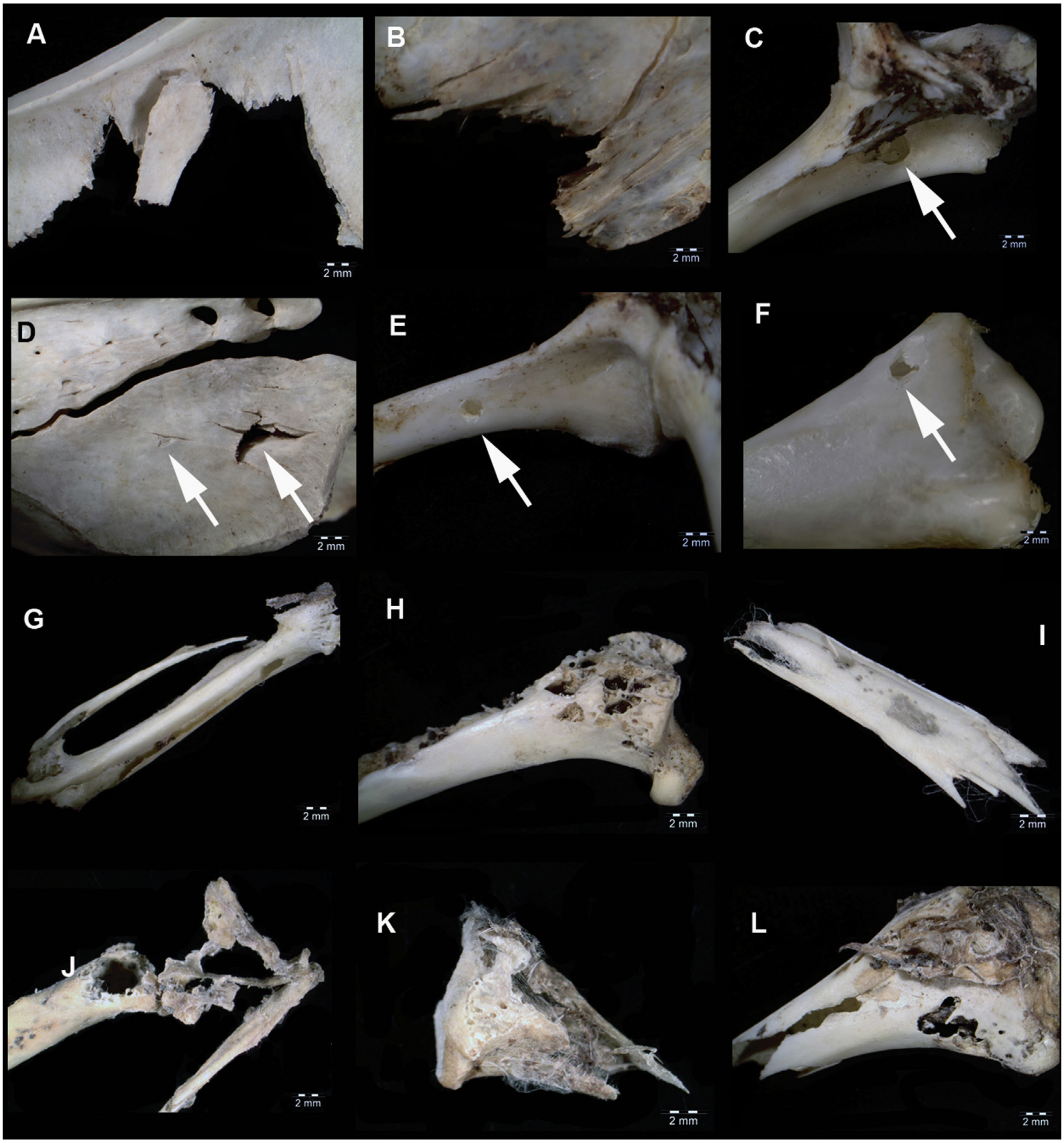

Fig. 8. Examples of bird bones displaying beak marks (A–F) and digestion damage with extensive corrosion (*G* = 3, H = 3, I = 4, *J* = 4, *K* = 4, *L* = 3) produced by the Bonelli's eagle.

Taken separately these features can be shared with other leporid predators, but together they form a distinctive taphonomic signature for Bonelli's eagle.

4.2. The taphonomic signature of Bonelli's eagle on bird remains

Among the bird remains recovered, sterna and pelves were the most abundant elements in the non-ingested sample. The sternum was also the best represented element in non-ingested assemblages from diurnal raptors such as Spanish imperial eagle, golden eagle, gyrfalcon (*Falco rusticolus*), crested caracara (*Caracara plancus*) and Egyptian vulture (Bochenski, 2005; Bochenski et al., 1998, 1999, 2009; Lloveras et al., 2014a; Montalvo et al., 2011; Sanchis Serra et al., 2013). In these studies, pelves were also abundant but they do not reach the values we found. Coracoids, scapulae, humeri and carpometacarpi were the best-represented long bones. Coracoids and humeri are the most frequent elements in non-ingested remains of diurnal raptors (Bochenski, 2005). In contrast, the tarsometatarsi or crania (or both) are the best-represented bones in pellet assemblages of diurnal and nocturnal raptors (Bochenski, 2005; Laroulandie, 2002). A similar pattern has been recorded for Bonelli's eagles; however, femora and radii were also abundant in our study whereas in other raptor assemblages they were consistently rare (Bochenski, 2005).

Results from the wing/leg ratio indicated a higher abundance of wing elements in non-ingested remains. When comparing these data with other studies (Bochenski, 2005; Bochenski et al., 1997, 1999; Laroulandie, 2002; Montalvo et al., 2011), it is clear that this is a feature shared with assemblages accumulated by other diurnal raptors. The preponderance of leg bones in the pellet

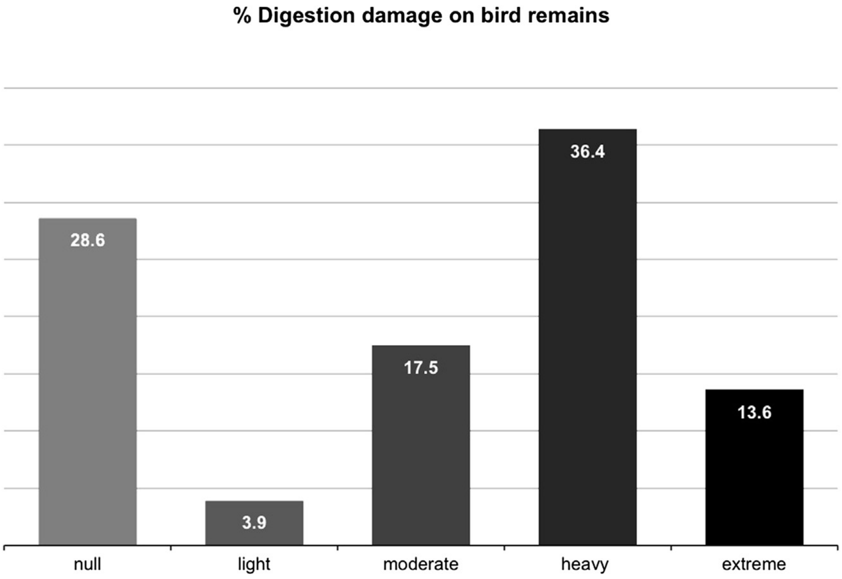

Fig. 9. Percentage of bird remains from the pellets sample included in each digestion category.

sample has only been recorded for Spanish imperial eagles (Bochenski et al., 1997). The ratio of proximal to distal elements permits the distinction of three groups of avian predators, namely: (I) pellets of diurnal birds of prey; (II) pellets of owl species and non-ingested remains of some diurnal raptors; and (III) non-ingested remains of golden eagles (Bochenski, 2005; Bochenski and Nekrasov, 2001). The present material falls into group II, in which proximal elements make up about 60% of the remains (Bochenski et al., 2009). The predominance of limb elements (versus core) observed in pellets has also been recorded for various owls and diurnal birds of prey. The abundance of core elements detected in non-ingested food remains is only shared with golden eagles (Bochenski, 2005; Bochenski et al., 1999).

Bonelli's eagles fragment bird bones to a similar extent to other diurnal birds of prey. However, the percentage of complete long bones was 47.1% for uneaten remains, which is comparable with values above 60% reported by Bochenski (2005) for diurnal raptors. This indicates that Bonelli's eagles break their victims' bones somewhat more frequently. In pellets, only 9.5% of long bones were complete. This percentage is consistent with the pattern exhibited in the pellets of diurnal raptors in which less than 30% of complete bones were registered (Bochenski, 2005). Particular skeletal elements differ in the degree of fragmentation: scapulae and tibiotarsi are the most affected and carpometacarpi, tarsometatarsi and coracoids are the best preserved. This is a feature related to the physical properties of these skeletal elements and it is common to all predators (Bochenski, 2005).

Table 10
Numbers and percentage of bird bones included in each digestion category. For abbreviations see the caption for Table 7. The number of bones considered was 308, a total of 20 bones from pellets were not used because surface damage could not be observed, therefore no digestion corrosion category could be attributed.

Digestion damage on bird remains (pellets sample)										
	Null		Light		Moderate		Heavy		Extreme	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
cra	3	14.3	0	0	3	14.3	12	57.1	3	14.3
man	1	33.3	0	0	2	66.7	0	0	0	0
fur	0	0	0	0	1	33.3	2	66.7	0	0
sc	0	0	0	0	3	25	7	58.3	2	16.7
cor	0	0	0	0	2	28.6	2	28.6	3	42.9
hum	0	0	0	0	1	14.3	5	71.4	1	14.3
rad	0	0	0	0	5	38.5	7	53.8	1	7.7
uln	0	0	0	0	0	0	9	90	1	10
cmc	0	0	0	0	2	13.3	10	66.7	3	20
c	3	37.5	0	0	3	37.5	1	12.5	1	12.5
di	0	0	0	0	0	0	4	80	1	20
fem	0	0	0	0	1	7.1	10	71.4	3	21.4
tbt	0	0	0	0	1	5.9	10	58.8	6	35.3
tmt	1	5.6	2	11.1	3	16.7	9	50	3	16.7
str	1	50	0	0	0	0	0	0	1	50
pel	0	0	0	0	0	0	2	100	0	0
phal	73	57.9	10	7.9	26	20.6	14	11.1	3	2.4
ver	4	18.2	0	0	0	0	8	36.4	10	45.5
rib	2	66.7	0	0	1	33.3	0	0	0	0
TOTAL	88	28.6	12	3.9	54	17.5	112	36.4	42	13.6

Few data exist on the digestion of bird remains (Bochenski, 1997; Bochenski et al., 1998; Laroulandie, 2002; Lloveras et al., 2014a; Montalvo et al., 2011). In Bonelli's eagle pellets more than 70% of total remains and practically 100% of long bones were digested. These values are clearly higher than those recorded for the European eagle owl (Laroulandie, 2002), Snowy owl (*Bubo scandiacus*) (Bochenski et al., 1997), crested caracara (Montalvo et al., 2011), Egyptian vulture (Lloveras et al., 2014a) and gyrfalcon (Bochenski et al., 1998). Moreover, most remains were digested with a heavy degree of damage (category 3 of damage defined by Bochenski (2005)).

The percentage of remains affected by beak marks was lower for Bonelli's eagle (6.2%) than for Egyptian vulture (28.3%, Lloveras et al., 2014a). The location of most beak marks on pelves (71.4%) and sterna (75%) is replicated on non-ingested assemblages left by other diurnal birds of prey. Bochenski et al. (2009) found punctures on 70% of sterna and 38% of pelves in white-tailed eagle (*Haliaaetus albicilla*) assemblages and punctures were observed on 39% of sterna, 51% of pelves in golden eagles. Our results show that Bonelli's eagles are closer to white-tailed eagles than golden eagles (Bochenski et al., 2009). Coracoids, scapulae, humeri and femora were the most affected long bones in our study. Similar results have also been recorded for other raptors (Bochenski et al., 2009).

In summary, the taphonomic signature observed on bird remains accumulated by Bonelli's eagles is characterised by:

- an abundance of sterna and pelves in non-ingested remains; and crania, pectoral arch and most of the wing and leg bones (including phalanges) in pellets;

Table 11
Anatomical representation, breakage, digestion and teeth/beak marks for leporid remains accumulated by different types of predators compared with the results obtained for Bonelli's eagles in the present study.

Leporid comparisons	Eagle owl		S. imperial eagle	Iberian lynx		Fox		Bonelli's eagle		
Reference	*Bubo bubo*		*Aquila adalberti*	*Lynx pardinus*		*Vulpes vulpes*		*Aquila fasciata*		
	Lloveras et al., 2009		Lloveras et al., 2008b	Lloveras et al., 2008a	Rodríguez-Hidalgo et al., 2013	Lloveras et al., 2012a		Present study		
Origin	Nest	Nest	Pellets	Scats	Non-ingested	Scats	Non-ingested	Whole sample	Non-ingested	Pellets
N	1808	1932	824	1522	9564	265	639	438	245	193
RA% >values	cal-inn-fem	cal-inn-tib	phal 3-u mol-tib	man-teeth-cra	tib-cal-mts	long bone-sc	mts-ast-tib	cra-u mol-inn	cra-inn-u mol	u mol-cra-man
RA% <values	mtc-c/t	rad-c/t-mtc	rib-fem-rad	c/t-ver-rib	sc-ver-hum	mtc-c/t-inn	cr-sc-rib	mtc-rib	man-l mol-mtc	ast-pat-rib
PCRT/CR	+postcranial	=	+cranial	+cranial	+postcranial	=	+postcranial	+cranial	+cranial	+cranial
P/D	+proximal	+proximal	+distal	+proximal	+distal	+proximal	+distal	+proximal	+proximal	+proximal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+forelimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+hindlimb
Complete elements %										
Mean value long bones	14.6	10.8	0	2.5	37.6	0	5.4	51.7	81.3	15.4
Mean value total	53.9	45.9	27	43	73.2	12	89.4	74.7	86.9	59.6
Length (in mm)										
Minimum	2.3	2.5	1.8	1.1	3	3	4	1.7	2.8	1.7
Maximum	86.3	90	36.1	30.1	69	26.8	86.2	89.6	89.6	78.7
%<10 mm	49	40	73	80	19.7	61	28	54.9	6.8	78.1
% Digested remains	68.8	65.6	98	97.2	–	99.5	–	31.2	–	72
% Digested long bones	88.9	83.9	100	100	–	100	–	31	–	69.2
Degree										
Null	31.2	34.4	2	2.8	–	0	–	68.8	–	28
Light	40.2	40.2	18.2	12	–	6	–	2.3	–	5.4
Moderate	19.8	19.8	46.8	22	–	26	–	7.9	–	18.3
Heavy	8	5.3	27.4	43.8	–	43	–	14.4	–	33.3
Extreme	0.7	0.15	5.6	19.3	–	25	–	6.5	–	15.1
Teeth/beak marks	2	1.34	0.5	0.26	0.9	3	9.5	2.3	4.1	0
Age – % of adults	50	50	–	21.4	–	87	–	41.4	–	–

- a moderate degree of breakage of non-ingested remains, with around 50% complete bones. A high degree of long bone breakage in pellets (less than 10% complete bones);
- a high percentage of digested remains, most of them to a heavy and extreme degree;
- a significant percentage of beak marked bones, most on pelves, sterna and long bones.

Comparisons show clear differences to nocturnal birds of prey. Although many features are shared with other diurnal raptors,

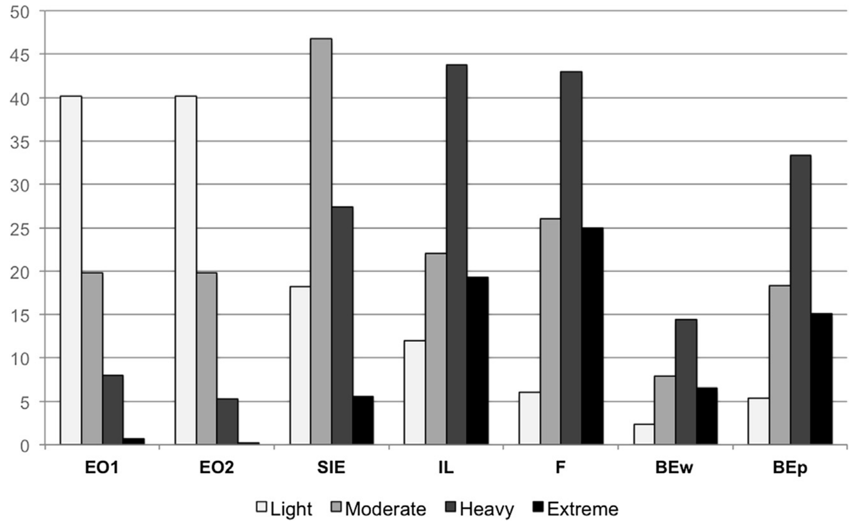

Fig. 10. Comparison of percentage of leporid remains included in each digestion category in accumulations produced by eagle owls (EO1 and EO2, Lloveras et al., 2009), Spanish imperial eagle (SIE; Lloveras et al., 2008b), Iberian lynx (IL; Lloveras et al., 2008a), red fox (F; Lloveras et al., 2012a) and Bonelli's eagle whole and pellets sample (BEw, BEp; present study).

especially with Spanish imperial eagles, differences are, apparent nevertheless. Some of the differences recorded could relate to different prey species accumulated in the samples analysed. Taphonomic data about avian prey accumulations are still scarce, especially regarding some variables such as digestion damage. Future studies are needed to provide more data that permit a deeper understanding of this variability.

5. Conclusions

This study provides the first detailed taphonomic observations on leporid and bird bones accumulated by Bonelli's eagles. Results from our analysis help to identify and classify the most important characteristics of bones accumulated by this raptor. Where rabbits, partridges and pigeons are abundant, they constitute a very high percentage of their diet. Both, non-ingested elements and bones from pellets are found in nest assemblages.

The observations and results obtained through this study showed that damage caused by Bonelli's eagles on leporids and birds differ sufficiently from other predators. Differences also exist in the character of leporid depending on the origin of the assemblage (i.e. non-ingested remains compared with pellets). The skeletal elements most abundant in non-ingested remains were scarce in the pellets and vice versa. The other taphonomic patterns observed also show divergent results. Non-ingested remains were less fragmented and beak/talons marks were more common, whereas pellet remains were affected by heavy and extreme digestion corrosion.

On archaeological grounds, assemblages of mixed origin are the most likely to be encountered. The criteria presented in this study for mixed samples can reveal the presence of this predator; however, results may vary depending on the relative proportion of remains derived from non-ingested accumulations and pellets. The use of the criteria presented in this study together with data on the geographical and biological background (i.e. location of the site and prey species composition of the deposit) can help to assess the potential contribution of Bonelli's eagles in accumulating small prey remains on archaeological sites.

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ORIGINAL RESEARCH

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The role of conservative versus innovative nesting behavior on the 25-year population expansion of an avian predator

Andreia Dias[1,2] | Luís Palma[2] | Filipe Carvalho[3,4] | Dora Neto[3] | Joan Real[1] | Pedro Beja[2,5]

[1]Equip de Biologia de la Conservació, Departament de Biologia Evolutiv, Ecologia i Ciències Ambientals and Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Catalonia, Spain

[2]CIBIO/InBio-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal

[3]CIBIO/InBIO-UE, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade de Évora, Évora, Portugal

[4]Department of Zoology and Entomology, School of Biological and Environmental Sciences, University of Fort Hare, Alice, South Africa

[5]CEABN/InBIO, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal

Correspondence
Pedro Beja, CIBIO/InBio-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Vairão, Portugal.
Email: pbeja@cibio.up.pt

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Abstract

Species ranges often change in relation to multiple environmental and demographic factors. Innovative behaviors may affect these changes by facilitating the use of novel habitats, although this idea has been little explored. Here, we investigate the importance of behavior during range change, using a 25-year population expansion of Bonelli's eagle in southern Portugal. This unique population is almost exclusively tree nesting, while all other populations in western Europe are predominantly cliff nesting. During 1991–2014, we surveyed nest sites and estimated the year when each breeding territory was established. We approximated the boundaries of 84 territories using Dirichlet tessellation and mapped topography, land cover, and the density of human infrastructures in buffers (250, 500, and 1,000 m) around nest and random sites. We then compared environmental conditions at matching nest and random sites within territories using conditional logistic regression, and used quantile regression to estimate trends in nesting habitats in relation to the year of territory establishment. Most nests (>85%, n = 197) were in eucalypts, maritime pines, and cork oaks. Nest sites were farther from the nests of neighboring territories than random points, and they were in areas with higher terrain roughness, lower cover by agricultural and built-up areas, and lower road and powerline densities. Nesting habitat selection varied little with year of territory establishment, although nesting in eucalypts increased, while cliff nesting and cork oak nesting, and terrain roughness declined. Our results suggest that the observed expansion of Bonelli's eagles was facilitated by the tree nesting behavior, which allowed the colonization of areas without cliffs. However, all but a very few breeding pairs settled in habitats comparable to those of the initial population nucleus, suggesting that after an initial trigger possibly facilitated by tree nesting, the habitat selection remained largely conservative. Overall, our study supports recent calls to incorporate information on behavior for understanding and predicting species range shifts.

KEYWORDS
Aquila fasciata, behavioral innovation, conditional logistic regression, conservation, habitat selection, quantile regression, range expansion

1 | INTRODUCTION

The geographic range of species is dynamic, often contracting, expanding, or otherwise changing its limits in relation to multiple environmental and demographic drivers (Gaston, 2003). In general, it is expected that a species range will track changes in the geographic distribution of favorable climates and habitats, under the constraints of dispersal limitation (Robillard, Coristine, Soares, & Kerr, 2015; Schloss, Nuñez, & Lawler, 2012; Sohl, 2014). This view has been used to forecast species range shifts in relation to climate and land use changes (Robillard et al., 2015; Schloss et al., 2012; Sohl, 2014) or to predict the ranges of exotic species introduced into new areas (Peterson, Papes, & Kluza, 2003; Veech, Small, & Baccus, 2011). Implicit within this idea, however, is that climatic and habitat niches are conserved during range shifts, which may not be warranted due for instance to evolutionary adaptations to changing conditions or the emergence of behaviors that facilitate the use of novel habitats (Broennimann et al., 2007; Van Dyck, 2012; Wright, Eberhard, Hobson, Avery, & Russello, 2010). Understanding these processes is essential to predict species responses to environmental changes (Lavergne, Mouquet, Thuiller, & Ronce, 2010).

Behavioral innovations, defined as the ability of animals to invent new behaviors or adjust old behavior to new problems (Overington, Griffin, Sol, & Lefebvre, 2011; Sol, Sayol, Ducatez, & Lefebvre, 2016), may be particularly important during range expansion, when species are bound to face novel environmental conditions (Keith & Bull, 2017). For instance, species colonizing landscapes modified by humans often show behavioral adaptations such as changes in the timing of breeding, adjustments of diel activity patterns, and the use of new food sources and foraging strategies (Lowry, Lill, & Wong, 2013; Martínez-Abraín & Jiménez, 2016). Innovations in breeding habitats include, for instance, avian nesting in human structures such as houses and electric pylons, which permit overcoming scarcity of natural nesting substrates (Martínez-Abraín & Jiménez, 2016). Likewise, increasing behavioral tolerance toward humans is normally considered a prerequisite for a species to colonize urban habitats and other heavily disturbed areas (Lowry et al., 2013). Despite these benefits of innovation, however, animal behavior may often be conservative rather than innovative, thereby restricting or at least delaying range expansion into potentially suitable habitats (Keith & Bull, 2017; Sol et al., 2016). For instance, imprinting of young to natal habitat characteristics is judged to strongly constrain breeding habitat selection when individuals reach maturity (Davis & Stamps, 2004). Overall, therefore, it is likely that species colonizing new geographic areas should be strongly affected by conservative versus innovative behaviors, although long-term studies examining this topic are lacking.

The Bonelli's eagle (*Aquila fasciata*) in southern Portugal provides a valuable opportunity to examine the role of behavior during a long-term process of expansion. The Bonelli's eagle is a medium/large bird of prey that is endangered in Europe, where it is largely confined to the Mediterranean region and its numbers have declined since the early 1980s (Hernández-Matías et al., 2013). In Western Europe, the Bonelli's eagle has a metapopulation-like structure with a source-sink dynamics, where the only growing populations are those of southern Spain and southern Portugal (Hernández-Matías et al., 2013). The population of southern Portugal is peculiar, because it is almost exclusively made up of tree nesting pairs (Figure 1) and is genetically divergent, whereas Bonelli's eagle populations in northern Portugal and elsewhere in the Iberian Peninsula and France are largely dominated by cliff nesters and well-connected demographically and genetically (Hernández-Matías et al., 2013; Mira, Arnaud-Haond, Palma, Cancela, & Beja, 2013; Palma, Beja, & Sánchez, 2013). This population has been closely monitored during the past 25 years, while it grew from about 25 to at least 110 breeding pairs (Beja & Palma, 2008; Palma et al., 2013). The original nucleus was largely confined to the uplands of the extreme south of the country, where the landscape is dominated by forests and scrubland, and human population density is low, while the current population occupies a much larger geographic area with a wide range of habitats and human occupation patterns (Palma et al., 2013). Evidence from demographic modeling and genetics suggests that population growth was sustained by the intrinsic demography of the original nucleus, rather than immigration (Hernández-Matías et al., 2013; L. Palma and R. Godinho Unpublished Data). Presumably, tree nesting behavior had an important role in this expansion, by allowing new pairs to establish in cliffless areas in a wide range of landscape types (Palma et al., 2013). It is uncertain, however, whether this expansion was associated with innovation in terms of new habitats occupied and increasing tolerance toward humans, or rather it was conservative by largely retaining the characteristics

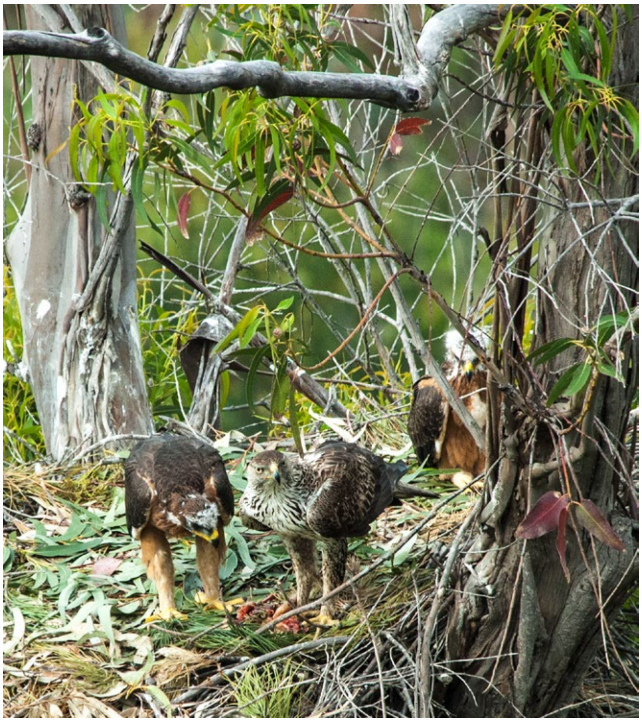


FIGURE 1 Bonelli's eagle (*Aquila fasciata*) nest in a eucalyptus tree, with one adult and two well grown chicks. Photograph by Joaquim Pedro Ferreira

of the original population nucleus in terms of nesting substrate and breeding habitats.

Here, we test these ideas by analyzing nesting habitat selection by the Bonelli's eagle, using territories established in southern Portugal from 1990 to 2014 and that were still active at the end of the study period. Specifically, we: (1) assessed the use of nesting substrates by the expanding population; (2) characterized environmental conditions within territories and around nests in terms of dominant habitat features and human occupation patterns; (3) quantified factors affecting nesting habitat selection within territories using conditional logistic regression; and used quantile regression to estimated trends in (4) nesting habitat conditions and in (5) the predictive ability of habitat selection models in relation to the year of territory occupation. If habitat selection was conservative, we expected that nesting substrates and the habitats around nesting sites should not change in relation to the year of territory establishment. Also, there should be no trends in the predictive ability of the nesting habitat model in relation to territory age, as it was calibrated considering all the territories occupied during the 25-year study period. In contrast, if behavior was innovative, we would expect the occurrence of changes in some of these descriptors, including temporal trends in the mean nesting habitat characteristics, or temporal increases in the variability of such habitats at the population level. Results were used to discuss the importance of innovative versus conservative behavior for the conservation management of Bonelli's eagles and other species of concern.

2 | METHODS

2.1 | Study area

The study was carried out in southern Portugal, encompassing an area of about 4×10^4 km^2. The climate is Mediterranean, with mean annual temperature of ≈17°C, and mean annual precipitation ranging from ≈500 to ≈1,000 mm (IM/AEMet, 2011). The landscape is dominated by an extensive peneplain (200–450 m a.s.l.) punctuated by residual elevations and bordered on its southern and southwestern ends by low altitude (<900 m a.s.l.) uplands. Land cover is varied, but it includes vast areas occupied by irrigated and rainfed annual crops, permanent crops (e.g. vineyards and olive groves), cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*) woodlands and agroforestry systems, Blue gum (*Eucalyptus globulus*) and pine (*Pinus* spp.) plantations, and scrublands of diverse structure and composition. Human density is low throughout much of the area, with most population concentrated along the coast and in urban centers in the hinterland.

2.2 | Study design

Bonelli's eagles are nonmigratory birds of prey, living in pairs that occupy exclusive territories, where there may be one or several alternative nests (Hernández-Matías et al., 2013; and references therein). The study was based on a long-term survey (1991–2014) of these breeding pairs and their territories in southern Portugal. For each territory, we estimated the approximate year of first occupation by the breeding pair, and we tried to locate all its nests. In the field, we recorded whether each nest site was built on a cliff or in a tree, and in the latter case, we recorded the nest tree species. Habitats around nests (250-m, 500-m and 1,000-m radius buffers) and random sites (see below) were characterized using variables extracted from GIS layers. We considered three buffers, because factors operating at different spatial scales may affect the selection of nesting habitats. The analysis of habitat selection was based on the comparison of habitat conditions at matching nest and random sites within territories. For each breeding pair, we retained in analysis all nests at >2,000 m from each other, to avoid overlapping buffers. For each group of nests at <2,000 m from each other, we retained the one used most frequently during the study period. Every nest site of each breeding pair was then matched with three points randomly located at >2,000 m from each other and from the nest site, within the corresponding territory boundary (Figure 2). The number of random points was a compromise between the need to avoid overlapping buffers, and to sample adequately the habitat available within each territory (e.g., Carvalho, Carvalho, Mira, & Beja, 2016). To avoid trivial results, random points falling within urban areas and water reservoirs were randomly relocated. To infer eventual behavioral changes during expansion, we estimated temporal trends in the mean and in the variability of nesting habitat conditions.

2.3 | Bonelli's eagle data

The methods used to collect comprehensive information on the breeding Bonelli's eagle population in southern Portugal have been detailed elsewhere (e.g., Beja & Palma, 2008; Hernández-Matías et al., 2013; Palma, Beja, Pais, & Cancela da Fonseca, 2006; Palma et al., 2013). Briefly, we conducted surveys throughout the region during courtship, nest building and breeding to locate Bonelli's eagle territories, focusing primarily on areas with potentially suitable habitats. In addition, surveys were directed toward areas with historical information on breeding sites, and areas with observations of individuals reported by other researchers and birdwatchers. Repeated observations of one or two adults or subadults within circumscribed areas were used to identify potentially breeding territories, which were then thoroughly surveyed until nests were found. A breeding territory was considered to be present in a given area when at least one nest was located, and there was at least one breeding attempt (i.e., at least nest building or repair) in at least 1 year. The year of territory establishment was estimated from a combination of information sources, including mainly the history and spatial pattern of Bonelli's eagle observations in the area, and enquiries to key informers such as shepherds and game managers. Frequently, estimates were made in terms of a likely time interval, for which we used the mid-point in subsequent analysis. Breeding data were collected for the active nests located each year in each territory, based on observations carried out using binoculars and telescopes (20–60×) from a distance to minimize disturbance.

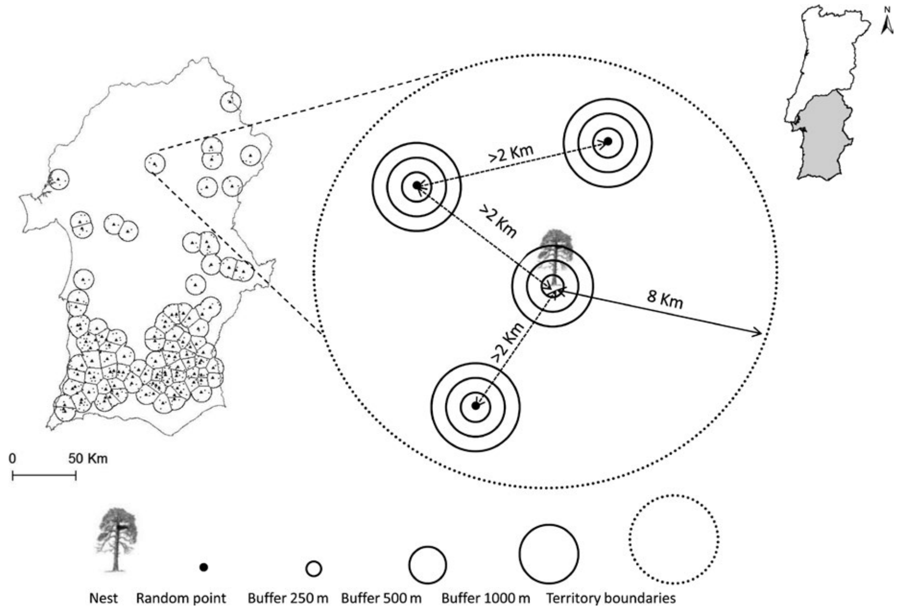


FIGURE 2 Location of the study area in southern Portugal showing the Bonelli's eagle breeding territories and nests considered in this study (1990–2014), and schematic representation of the study design (see text for details)

To match nest sites with random locations within the same territory, we defined the territory boundary of each breeding pair as an 8-km radius buffer around its central point, which was estimated as the geographic centre of all the nests of the breeding pair (Palma et al., 2006). When the centers of neighboring territories were at <16 km from each other, the territory boundaries were defined using Dirichlet tessellation (Schlicht, Valcu, & Kempenaers, 2014). These assumptions were similar to those taken in a previous study where we found a good matching between diets and food resources across territories (Palma et al., 2006), and they were based on home range data from satellite tracking of ten breeding adults in our study area (L. Palma, unpublished data). Therefore, we believe that these territories provided a reasonable approximation to select random points and thus estimate the habitats available to each breeding pair, although it does not account for eventual variations in territory sizes and shapes (e.g., Bosch, Real, Tintó, Zozaya, & Castell, 2010; Mure, 2003).

2.4 | Environmental variables

The buffers around nest sites and random points were characterized from 15 variables reflecting topography, human disturbance, land cover, and potential intraspecific interactions (Table 1, Table S1), which were expected to influence Bonelli's eagles (e.g., Carrascal & Seoane, 2008; Di Vittorio, Sarà & López-López, 2012; Muñoz & Real, 2013; Real, Bosch, Tintó, & Hernández-Matías, 2016). All variables were extracted on a GIS from digital thematic layers, using ArcMap 10.1. Topographic variables were estimated using a 25-m resolution digital elevation model (http://www.eea.europa.eu/dataand-maps/data/eu-dem). For each buffer, we computed the means and standard deviations of elevation and slope of raster grid cells, and we estimated an index of ruggedness using the Vector Ruggedness Measure Tool (Sappington, Longshore, & Thompson, 2007). This index measures terrain ruggedness as the variation in three-dimensional orientation of grid cells within a neighborhood, effectively capturing variability in slope and aspect into a single measure (Sappington et al., 2007). The density of paved roads was estimated using the Open Street Map (www.openstreetmap.org/copyright), and it was taken as a broad indicator of potential human disturbance. Distribution power lines were also taken as an indicator of potential disturbance because they are a source of mortality in Bonelli's eagles (Real, Grande, Mañosa, & Sánchez-Zapata, 2001; Rollan, Real, Bosch, Tintó, & Hernández-Matías, 2010), and their density was estimated from electric network maps. Land cover was estimated using Portugal's 2007 Land Cover Map with land cover classes aggregated in five main categories judged a priori to be the most relevant for Bonelli's eagles nesting habitat selection (see Table 1 for details). We have used relatively broad habitat land cover classes, because they have changed less over time than more detailed categories (ICNF, 2013), thereby reducing errors potentially associated with considering only a land cover map from 2007 to analyze habitat selection from territories established between 1990 and 2014. We also estimated the density of waterlines, because Bonelli's eagles frequently nest along streams and gullies (Palma et al., 2013). Finally, we considered the distance to the nearest nest of a different breeding territory, to account for the possibility of individuals avoiding sites because of their proximity to those occupied by neighboring breeding pairs.

2.5 | Data analysis

Prior to statistical analysis, skewed variables were transformed to approach normality and to reduce the influence of extreme values using the angular and logarithmic transformations (Table 1). All variables were standardized to zero mean and unit variance, to enhance comparability of effect sizes (e.g., Schielzeth, 2010). Principal component analyses (PCA) of ecological variables were used to investigate multicollinearity and to describe dominant environmental gradients (Legendre & Legendre, 1998). Varimax normalized rotations were applied to the set of principal components with eigenvalues >1, to obtain

TABLE 1 Variables used to analyze the environmental correlates of nesting site selection by the Bonelli's eagle in southern Portugal

Variable (unit)	Code	Description (transformation)
Topography		
Elevation (m)	ELMEN ELSTD	Elevation above sea level (DEM 25 m)—mean and standard deviation (log10)
Slope (°)	SLMEN SLSTD	Slope—mean and standard deviation (log10)
Ruggedness Index	VRMEN VRSTD	Terrain ruggedness measured as the variation in three-dimensional orientation of grid cells within a neighborhood—mean and standard deviation (log10)
Human disturbance		
Paved road network (m/m2)	DEPR	Density of paved roads (Asin [√x])
Power line (m/m2)	DEPL	Density of High/Very High Tension (>60 kv) and Medium Tension (<60 Kv) power lines (Asin [√x])
Land cover		
Artificial areas (%)	EXAR	Proportion of artificial areas (urban areas, industrial, commercial and industrial units, mine, dump and construction sites, artificial nonagricultural vegetated areas) (Asin [√x])
Agricultural areas (%)	EXAG	Proportion of heterogeneous agricultural areas, permanent pastures and crops, arable land and rice fields (Asin[√x])
Forests (%)	EXFO	Proportion of forests (broad leaved forests, coniferous forests, mixed forests) (Asin [√x])
Open forests (%)	EXOF	Proportion of open forests, shrubs, herbaceous vegetation, and open spaces with little or no vegetation (Asin [√x])
Water bodies (%)	EXWA	Proportion of water bodies (e.g., reservoirs, lagoons) and wetlands (Asin [√x])
Waterline (m/m^2)	DEWL	Density of waterlines (Asin [√x])
Intraspecific relationship		
Distance to nest (m)	DIBN	Distance to the nearest Bonelli's eagle nest (log10)

simpler and more interpretable gradients (Legendre & Legendre, 1998). Varimax rotated axes were then used in subsequent analysis, because they provide a reduced set of synthetic variables, which are orthogonal to each other and thus are not affected by multicollinearity. A separate PCA and varimax rotation was carried out for variables estimated in 250-, 500-, and 1000-m buffers, because we were interested in modeling habitat selection in relation to scale-specific factors. We excluded the distance to the nearest nest from PCAs, because we were interested in estimating its unique effect and because preliminary analysis showed that it was uncorrelated with other variables.

The factors influencing nest site selection were analyzed at each spatial scale by comparing nest site and random locations within territories, using conditional logistic regression (Duchesne, Fortin, & Courbin, 2010; Hosmer & Lemeshow, 2000). This analysis followed a match-control design framework, using a binomial variable coding the nest (1) vs. three random points (0), thereby creating a group "stratum" (e.g., Hosmer & Lemeshow, 2000). Model selection was based on the information theoretical approach of Burnham and Anderson (2002) using the Akaike Information Criterion (AICc) and the corresponding Akaike weights (w_i). Candidate models were built based on all possible subsets of the ecological gradients obtained in the vPCA, including the null (i.e., without explanatory variables) and the full (i.e., with all explanatory variables) models. Models were ranked according to their Akaike weights (w_i), and the average parameters and their unconditional standard errors (*SE*) were estimated based on the 95% confidence set of models (Burnham & Anderson, 2002). The relative importance of each variable (ecological gradient) was judged based on the sum of Akaike weights of models where the variable was included (w_+), and on the magnitude of the average model coefficient. Model fit was assessed with the pseudo R-squared of Tjur (2009), and model discrimination ability was assessed with the area under the remote operating characteristic curve (AUC; Fielding & Bell, 1997). These analyses were performed using the packages mclogit (Elff, 2013), MuMIn (Barton, 2013), and modEva (Barbosa, Brown, Jiménez-Valverde, & Real, 2014) for R 3.3.2 software (R Development Core Team 2016).

The analysis of trends in nesting habitats was based on quantile regression, following the rationale outlined in Cade and Noon (2003). This approach was used because we were interested in assessing changes over time in the mean (median) habitat conditions used by breeding pairs, but also in whether variability in nesting habitats increased over time due for instance to a few pairs settling in unusual habitats. In quantile regression, the latter hypothesis may be tested by examining temporal rates of change in quantiles near the maximum (e.g., 95% quantile) or the minimum (e.g., 5%), response. Increases in variability of habitat conditions may be inferred when the absolute value of the slopes estimated for extreme quantiles is significantly larger than that estimated for the median response. The analyses focused on the relations between nesting habitat characteristics described using the PCA axis and the first year of territory occupation. Also, we estimated relations between the prediction errors of the habitat model and the year of territory establishment, assuming that changes in behavior would lead to temporal changes in the median or in the variability of the prediction errors, or both. Model prediction errors were computed for nest sites as one minus the model predicted probability that a site was a nest site. Analysis was carried out at the level of breeding territories by averaging variables across all nest sites within each territory. Separate analyses were made for the three spatial extents used in this study (i.e., 250, 500, and 1,000 m). We estimated the temporal trend of the response variables using ordinary least squares, and we then estimated trends in the quantiles from 5% to 95% at 5% intervals. For each coefficient of the quantile regression, we computed the 90% confidence intervals based on inverting a quantile rankscore test (Cade & Noon, 2003). We also compare the slopes of the regression coefficients of the 5% and 95% quantiles with those of the median, using an ANOVA function for quantile regression fits based on the Wilcoxon score (Koenker et al., 2016). In trend analysis, all territories estimated to be present before the beginning of the study in 1991 were assigned to 1990 as the year of establishment. These analyses were performed using the package quantreg (Koenker et al., 2016), and results were visualized using ggplot2 (Wickham & Chang, 2016), for R 3.3.2 software (R Development Core Team 2016).

3 | RESULTS

3.1 | Bonelli's eagle nests and nesting population

We estimated the approximate boundaries of 84 Bonelli's eagle territories from 197 nests (mean number of nests per territory [±*SD*, range] = 2.3 ± 1.4, 1–8) detected during the study period (Figure 2). The eagle population in southern Portugal before 1991 was estimated at 25 territories (29.8% of the total studied). For the territories established after 1990 ($n = 59$), the mean (±*SD*) estimated year of establishment was 2004 ± 5.7 years (1992–2012). From all the nests recorded, only 11 (5.6%) were on cliffs, whereas the others ($n = 186$) were in *Eucalyptus globulus* (36.5%), *Pinus pinaster* (18.8%), *E. camaldulensis* (15.2%), *Quercus suber* (14.7%), *Pinus radiata* (7.1%), *Pinus pinea* (1.5%), and *Populus nigra* (0.5%). There was a significant tendency (chi-squared = 4.80, $p = .030$) for the initial territories (<1991) having a higher proportion of nests on cliffs (4.1%) than more recent territories (1.6%). There were also significant differences between periods in the species of nest tree used (chi-squared = 31.4, $p < .001$), mainly due to a higher use of *E. camaldulensis* (24.6% vs. 2.8%) and a lower use of *Q. suber* (7.0% vs. 29.2%) in the second period.

3.2 | Nesting habitat selection

At each spatial scale, the principal component analysis with varimax rotation extracted four dominant environmental gradients that accounted for 68%–74% of total variance in the data and that were largely consistent across scales (Table 2). The dominant gradient (PC1; 36%–38% of variance) was largely related to terrain ruggedness, reflecting a joint increase in mean and standard deviation of slope, standard deviation of elevation and index of ruggedness, and a decline in agricultural land cover. The second gradient was related to human infrastructures (PC2; 12%–17%), showing a joint increase in cover by artificial areas, and in paved roads and powerline densities. The third gradient (PC3; 11%) contrasted areas at higher elevation with lowland areas with more waterlines and waterbodies. Finally, the fourth gradient was mostly related to the increase in forest cover (PC4; 8%–9%), showing a contrast between open and closed woodland at the two smaller spatial scales.

The model selection and averaging procedure yielded conditional logistic regression models that were very similar at the three spatial scales considered, consistently showing that within territory boundaries the Bonelli's eagle nests were located in areas with higher terrain ruggedness and lower agricultural cover (PC1), and less human infrastructures (PC2) than random sites (Tables 3 and S2). Also, nests were farther than random points from the nearest nest of a neighbor territory. Support for the negative effect of elevation (PC3) and the positive effect of forest cover (PC4) was moderate at the 1,000-m scale (Akaike weights > 0.8), but it was weak at lower scales. The T-Jur coefficients showed that the models at the three spatial scales had a reasonable fit to the data (0.635–0.655), while the AUCs indicated high model discrimination ability (0.946–0.955).

3.3 | Temporal trends

Considering the variables most related to nesting site selection (Table 3), there was a very marked tendency for mean and median terrain ruggedness (PC1) to decline in relation to the estimated year of territory occupation at all spatial scales (Table 4). A similar trend was found for most quantiles at all spatial scales, with no significant differences among slopes (ANOVA, $p > .05$), thus suggesting that variability in ruggedness among territories did not change over time (Figures 3 and S1–S5). In contrast, there was no trend in the mean amount of human infrastructures around nests (PC2) in relation to the year of territory establishment, although the median significantly declined at the 250-m scale (Table 4, Figures 3 and S1–S5). There was also some evidence for increasing variability in more recent territories, as underlined by the contrast between the negative slopes estimated for the lower quantiles (5% and 25%) and the positive slope for the upper quantile (95%), particularly at the 1,000-m scale. It should be noted, however, that variation among slopes was not significant (ANOVA, $p > .05$) and that the response for the 95% quantile appeared driven

TABLE 2 Scores of habitat variables used to characterize nesting habitats of the Bonelli's eagle in southern Portugal, on the axis (PC#) extracted through a principal component analysis (PCAs) with varimax rotation. Separate PCAs were performed for variables extracted at three spatial scales. We provide the proportion of variance accounted for by each axis extracted in each PCA

	250 m				500 m				1,000 m			
Variables	**PC1**	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**
Mean slope	0.95				0.96				0.96			
Standard deviation of slope	0.95				0.96				0.97			
Ruggedness	0.94				0.94				0.95			
Standard deviation of ruggedness	0.90				0.91				0.92			
Standard deviation of elevation	0.90				0.91				0.90			
Agricultural areas	−0.75				−0.75				−0,79			
Open forests				−0.81	0.55			−0.77	0.59			
Paved road density		0.81				0.84				0.90		
Artificial areas		0.74				0.74				0.84		
Power line density		0.60				0.78				0.83		
Mean elevation			0.73				0.74				0.71	
Waterline density			−0.54				−0.51				−0.56	
Water bodies			−0.81				−0.83				−0.85	
Forests				0.76				0.77				0.78
% Explained variance	36	12	11	9	37	14	11	9	38	17	11	8

by a few recent territories with an unusually high amount of human infrastructures around nests (Figures 3, S1 and S2). Regarding the distance to the nearest nest of a neighbor territory, there were no significant trends in the mean or in any quantile, although there were a few recent territories where nests were unusually distant from their nearest neighbors (Table 4, Figures 3 and S1–S5). Considering the less influential variables, there was a tendency for the mean and median (except at 250-m scale) elevation (PC3), and the median (only at the 1,000-m scale) of forest cover (PC4), declining in more recent territories, with no significant differences (ANOVA, $p > .05$) among the slopes of different quantiles. There was also no evidence for model prediction error varying in relation to the year of territory establishment (Table 4). It is noteworthy, however, that the highest prediction errors were found in a few recent territories (Figures 3, S1 and S2).

4 | DISCUSSION

Our results suggest that during the 25-year expansion of Bonelli's eagles in southern Portugal, the nesting habitat characteristics and selection patterns remained very similar to those of the initial population nucleus, albeit with some changes over time. In terms of nest substrate, the tree nesting behavior typical of the initial nucleus was not only retained but even amplified over time, although with some variation in the trees most used. In terms of habitats, nests were consistently located in areas with relatively high terrain ruggedness, low cover by both agricultural land and human infrastructures, and away from conspecific nests in neighboring territories. The main temporal change was a decline in terrain ruggedness around nests in more recent territories, although they were still located within the most rugged areas available within each territory. Mean cover by human infrastructures was little affected by territory age, although variability appeared to be somewhat higher in more recent territories, particularly due to the presence of a few territories with unusually high infrastructure cover around nests. Also, a few recent territories appeared to have an unusual pattern of nesting site selection, as suggested by particularly high model prediction errors. Overall, these results suggest that an initial uncommon behavior, tree nesting, may have triggered the ability of this Bonelli's eagle population to colonize vast areas without suitable cliffs for nesting. However, during the subsequent population

TABLE 3 Average models describing the estimated effects of explanatory variables on the nesting area selection of tree nesting Bonelli's eagle at three spatial scales: 250, 500, and 1,000 m. For each case, multimodel averaging was based on the 95% confidence set of models. For each variable, we show the standardized regression coefficient (β), the unconditional standard errors (*SE*), the 95% confidence interval of coefficient estimate (CI), and the selection probability (w+). Coefficient estimates whose 95% CI exclude zero are in bold

Variables	β	*SE*	CI	ω+
Buffer: 250 m				
Terrain ruggedness (PC1)	**2.199**	**0.640**	**0.944, 3.455**	**1.000**
Human infrastructures (PC2)	**−3.845**	**1.555**	**−6.893, −0.797**	**1.000**
Elevation (PC3)	−0.707	0.533	−1.752, 0.337	0.490
Forests (PC4)	0.529	0.533	−0.516, 1.575	0.380
Distance to nest	**4.626**	**1.157**	**2.357, 6.895**	**1.000**
Buffer: 500 m				
Terrain ruggedness (PC1)	**1.782**	**0.599**	**0.606, 2.957**	**1.000**
Human infrastructures (PC2)	**−1,495**	**0.629**	**−2.728, −0.261**	**1.000**
Elevation (PC3)	−0.891	0.458	−1.789, 0.006	0.670
Forests (PC4)	0.607	0.454	−0.283, 1.49	0.490
Distance to nest	**4.336**	**1.088**	**2.203, 6.469**	**1.000**
Buffer: 1,000 m				
Terrain ruggedness (PC1)	**2.550**	**0.965**	**0.659, 4.442**	**1.000**
Human infrastructures (PC2)	−1.833	0.956	−3.709, 0.041	1.000
Elevation (PC3)	−1.143	0.592	−2.304, 0.017	0.800
Forests (PC4)	1.153	0.600	−0.023, 2.330	0.890
Distance to nest	**5.240**	**1.480**	**2.338, 8.142**	**1.000**

expansion, the selection of habitats appeared to be dominantly conservative rather than innovative, although rare unusual behaviors may have started to emerge in recent years.

The interpretation of our results requires due consideration of study design and data analysis approaches, which differed to some extent from other studies on Bonelli's eagle habitat selection. First, our study was conducted at relatively detailed spatial scales, with variables measured at most within 1 km from nests, whereas several other studies considered larger buffers (e.g., Carrete, Sánchez-Zapata, Martínez, Sánchez, & Calvo, 2002; Di Vittorio, Sara, & López-López, 2012; Gil Sánchez, Molino Garrido, & Valenzuela Serrano, 1996) or evaluated species presence/absence using 10 × 10 km squares (e.g., Carrascal & Seoane, 2008; Di Vittorio et al., 2012; Muñoz, Márquez, & Real, 2013; Real et al., 2016). This is important because different aspects of Bonelli's eagle habitat selection may become apparent at different spatial scales (López-López, García-Ripollés, Aguilar, García-López, & Verdejo, 2006; Muñoz & Real, 2013; Real et al., 2016), with studies at smaller scales such as ours probably showing the requirements associated with nest sites, and studies at larger spatial scales probably revealing a combination of nesting and foraging habitat requirements. Second, our analysis was based on conditional logistic regression, matching nesting site conditions with those available within territories, whereas all other studies used unmatched comparisons between sites with and without Bonelli's eagles. This may affect results, because conditional regression identifies what is selected considering local availability, and so it is able to reveal selection patterns that might be difficult to discern otherwise (e.g., Carvalho et al., 2016; Duchesne et al., 2010). Finally, our study introduced a temporal dimension to habitat selection patterns that had never been considered before. Although we could not incorporate actual temporal changes in habitat composition due to lack of detailed data, we believe that our approach based on comparisons of current conditions in relation to the year of territory establishment provided a first approximation to how nesting habitat characteristics and selection patterns changed over time. We believe this assumption is reasonable, because the main variables used to characterize Bonelli's eagle habitats have either remained unchanged (e.g., elevation, ruggedness), or they likely varied little over time. In particular, the area occupied by the broad land cover categories used in our study has remained largely stable within Bonelli's eagle territories, as for instance the growth in urban areas and associated infrastructures has been mostly concentrated in a narrow fringe along the coast (Freire, Santos, & Tenedório, 2009), while cover by agriculture and forest areas has remained essentially constant in rural areas of southern Portugal (Godinho et al., 2016; ICNF, 2013). Estimates of the year of territory establishment were associated with some uncertainties, which may have introduced noise in the data but we believe this is unlikely to have biased trends in selection patterns relative to territory age.

Reasons for the association of Bonelli's eagle nesting sites to the most rugged areas within territories may be related to the presence of suitable nesting trees and to less human disturbance (Palma et al., 2013; Real et al., 2016). For instance, large eucalypts are among the most used nest trees and they are most often found along waterlines at the bottom of valleys (Palma et al., 2013), which may be one of the factors attracting the eagles to rougher terrain. Also, rugged areas are probably less affected by forest management operations such as understory clearing for fire prevention (Real et al., 2016; Santana, Porto, Reino, & Beja, 2011) and they may be less often crossed by people. Whatever the reasons for the observed pattern, it is noteworthy that breeding habitat selection of tree nesting Bonelli's eagles in Cyprus was also affected by local topography and the availability of suitable nesting trees away from disturbance (Kassinis, 2010). Cliff nesting Bonelli's eagles also seem to prefer areas with high terrain ruggedness, which seems to reflect the availability of suitable cliffs for nesting (Di Vittorio et al., 2012; Gil Sánchez et al., 1996; López-López et al., 2006; Real et al., 2016). Overall, therefore, the preference for nesting

TABLE 4 Trends in habitats conditions around Bonelli's eagle nesting sites (250-, 500-, and 1,000-m buffers) in relation to the year of territory establishment. Trends were estimated with both ordinary least squares regression (Mean) and quantile regression (Quantiles), considering the habitat gradients extracted from a principal component analysis (PC#), the distances to the nearest nest from a neighboring territory, and the prediction error of the habitat model. In each case, we provide the slope of the relation, and its 90% confidence interval. Coefficients with confidence interval excluding zero are in bold

		Quantiles				
Buffer	**Mean**	**5%**	**25%**	**50%**	**75%**	**95%**
Terrain ruggedness (PC1)						
250 m	**−0.044 (−0.062, −0.026)**	−0.047 (−0.087, 0.002)	**−0.061 (−0.082, −0.017)**	**−0.056 (−0.065, −0.035)**	**−0.023 (−0.051, −0.021)**	**−0.046 (−0.061, −0.009)**
500 m	**−0.047 (−0.064, −0.030)**	−0.053 (−0.073, 0.002)	**−0.064 (−0.081, −0.026)**	**−0.052 (−0.068, −0.035)**	**−0.033 (−0.058, −0.02)**	−0.031 (−0.062, 0.008)
1,000 m	**−0.046 (−0.063, −0.029)**	**−0.053 (−0.079, −0.006)**	**−0.062 (−0.079, −0.03)**	**−0.052 (−0.066, −0.025)**	**−0.044 (−0.059, −0.024)**	−0.025 (−0.059, 5.4 × 10^{-5})
Human infrastructures (PC2)						
250 m	−0.004 (−0.010, 0.002)	**−0.009 (−0.013, −0.005)**	**−0.010 (−0.017, −0.005)**	**−0.005 (−0.009, −2.3 × 10^{-4})**	−0.003 (−0.007, 0.002)	0.012 (−0.013, 0.024)
500 m	−0.002 (−0.013, 0.009)	**−0.009 (−0.011, −0.005)**	**−0.007 (−0.012, −0.004)**	−0.006 (−0.017, 3.3 × 10^{-5})	−0.001 (−0.021, 0.010)	0.060 (−0.048, 0.087)
1,000 m	0.005 (−0.005, 0.015)	0.004 (−0.008, 0.005)	−0.003 (−0.011, 0.003)	−0.004 (−0.010, 0.005)	0.002 (−0.006, 0.021)	**0.016 (0.011, 0.084)**
Elevation (PC3)						
250 m	**−0.024 (−0.044, −0.004)**	−0.010 (−0.048, 0.014)	−0.037 (−0.060, 0.001)	−0.034 (−0.047, 0.011)	−0.021 (−0.04, 0.004)	−0.007 (−0.039, 0.035)
500 m	**−0.020 (−0.037, −0.002)**	−0.006 (−0.038, 0.031)	−0.023 (−0.047, 0.010)	**−0.032 (−0.040, −0.009)**	**−0.011 (−0.040, −0.003)**	−0.010 (−0.073, 0.029)
1,000 m	**−0.023 (−0.042, −0.005)**	−0.004 (−0.024, 0.047)	**−0.028 (−0.057, −0.004)**	**−0.030 (−0.047, −0.006)**	**−0.018 (−0.032, −0.008)**	−0.039 (−0.066, 0.019)
Forests (PC4)						
250 m	−0.010 (−0.012, 0.032)	−0.013 (−0.026, 0.007)	−0.019 (−0.040, 0.004)	−0.023 (−0.056, 0.019)	−0.008 (−0.029, 0.01)	0.023 (−0.095, 0.088)
500 m	−0.019 (−0.042, 0.004)	−0.015 (−0.039, 0.002)	−0.046 (−0.056, 0.003)	−0.012 (−0.059, 0.003)	−0.005 (−0.039, 0.018)	0.016 (−0.107, 0.059)
1,000 m	−0.022 (−0.046, 0.002)	−0.020 (−0.046, 0.005)	**−0.040 (−0.067, −0.027)**	−0.04 (−0.056, 0.015)	−0.002 (−0.041, 0.028)	−0.016 (−0.060, 0.052)
Distance to nest						
Distance	47.5 (−120.9, 215.9)	−1.4 (−30.7, 55.9)	20.1 (−75.5, 64.3)	46.1 (−114.7, 89.3)	0.0 (−98.4, 119.8)	588.4 (−986.2, 2110.1)
Model prediction error						
250 m	0.001 (−0.001, 0.003)	0.0 (−1.4 × 10^{-8}, 1.2 × 10^{-8})	8.0 × 10^{-7} (−3.0 × 10^{-7}, 4.8 × 10^{-6})	4.8 × 10^{-6} (−1.0 × 10^{-4}, 5.4 × 10^{-5})	4.8 × 10^{-5} (−9.9 × 10^{-4}, 1.2 × 10^{-3})	0.008 (−0.004, 0.030)

(Continues)

TABLE 4 (Continued)

		Quantiles				
Buffer	**Mean**	**5%**	**25%**	**50%**	**75%**	**95%**
500 m	0.002 (−0.001, 0.005)	-7.6×10^{-8} (-1.1×10^{-4}, 9.5×10^{-8})	-7.1×10^{-6} (-1.0×10^{-5}, 1.3×10^{-5})	1.3×10^{-4} (-5.4×10^{-5}, 5.3×10^{-4})	7.2×10^{-4} (−0.003, 0.004)	0.010 (−0.021, 0.042)
1,000 m	0.003 (−0.0001, 0.007)	0.0 (-2.5×10^{-8}, 6.9×10^{-9})	5.4×10^{-7} (-7.3×10^{-7}, 3.7×10^{-6})	9.1×10^{-5} (-3.0×10^{-5}, 3.1×10^{-4})	1.2×10^{-3} (4.8×10^{-4}, 2.1×10^{-3})	0.030 (−0.026, 0.051)

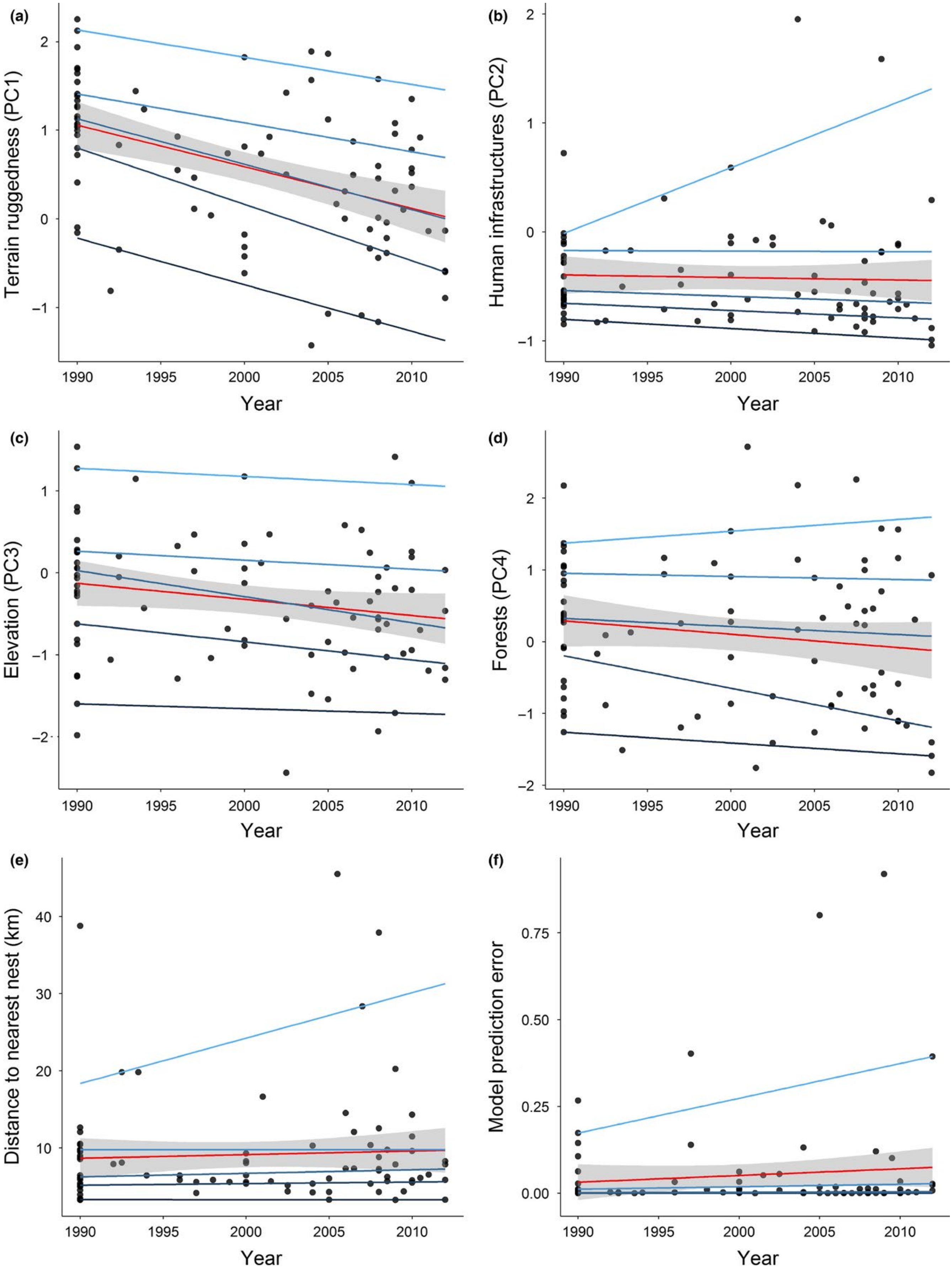
in rugged areas may be a conservative characteristic of Bonelli's eagles seemingly maintained across geographical regions and nest site typologies, and that may constrain range expansion into milder terrain.

Bonelli's eagle nests were also associated with areas with the lowest cover by built-up areas and the lowest densities of roads and powerlines. Comparable patterns have been reported elsewhere (Gil Sánchez et al., 1996; López-López et al., 2006; Real et al., 2016), although other studies did not find significant avoidance of human infrastructures close (<3 km) to occupied nests (Ontiveros 1999; Carrete et al., 2002). Interestingly, Ontiveros (1999) reported that occupied cliffs closer to roads were taller than those farther from roads, suggesting that tolerance to human disturbance may depend on the relative safety of nesting sites (Real et al., 2016; Rollan et al., 2010). Overall, we suggest that our observations regarding human infrastructures, together with the preference for particularly rough terrain, indicates that Bonelli's eagles avoid human disturbance at small distances (<1 km) from nesting sites. It should be noted, however, that our inferences based on conditional logistic regression imply that Bonelli's eagles select the least disturbed areas within their territories, although this may correspond to areas that may still have some human disturbance. Therefore, our results do not contradict the general view that Bonelli's eagles can tolerate a certain degree of human disturbance and that human infrastructures and other indicators of disturbance may be relatively unimportant to explain the species distribution at larger spatial scales (López-López et al., 2006; Carrascal & Seoane, 2008; Di Vittorio et al., 2012; Muñoz et al., 2013; but see Bosch et al., 2010; Muñoz & Real, 2013 and Real et al., 2016). In addition, it should be noted that a few recent territories had an unusually high cover by human infrastructures around nests, although this patterns was not statistically significant probably due to small sample sizes. The presence of these few pairs apparently more tolerant to human disturbance may imply that in the future the species may be able to expand into more anthropic areas, and this should be the subject of further research.

The trends in nesting habitats in relation to territory age observed in our study suggest that new Bonelli's eagle pairs chose habitats that are structurally comparable to those of the initial population nucleus. This may be a consequence of imprinting of young to natal habitat conditions, which may affect the kind of places the individuals select later in life (Davis & Stamps, 2004). Testing this idea, however, would imply detailed information on the natal and breeding habitats of a large number of marked individuals (e.g., Mannan, Mannan, Schmidt, Estes-Zumpf, & Boal, 2007), which was unavailable in our case. Nevertheless, there is evidence that the new pairs largely originated from the initial population nucleus, based on the assignment of individuals to the unique genetic profile of the population inhabiting southern Portugal (Mira et al., 2013; Palma et al., 2013), and by the tracking of individuals with conventional and genetic tags (L. Palma and R. Godinho, unpublished). Despite this general trend for conservative behavior, there was still some flexibility in the selection of the nesting area. This was supported to some extent by the decrease in terrain ruggedness in more recent territories, although nests were consistently located in the roughest areas available within territories. Also, there were a few recent territories where nesting site selection was different, as suggested by the higher cover by human infrastructures and the poor predictive ability of the habitat model to differentiate nesting from random sites. Therefore, an even longer time frame would probably be needed to understand whether innovative habitat selection patterns might eventually emerge, although this was not apparent during our 25-year study.

Taken together, our results suggest that Bonelli's eagles expanded in southern Portugal because the individuals produced by the original nucleus could find vacant nesting habitats of basically similar structure in various landscape types across the region (Beja & Palma, 2008; Palma et al., 2013), rather than through the occupation of novel habitats. Agricultural land abandonment and the depopulation of the countryside since the 1960s was probably responsible to at least some extent for this process, because it released large areas with low disturbance and that have been progressively occupied by uncultivated woodland and scrublands (Diogo & Koomen, 2012; Van Doorn & Bakker, 2007), thus becoming available for Bonelli's eagle colonization during the study period. Another main driver was probably the prevalence of tree nesting behavior, which allowed the colonization of cliffless landscapes that would be unavailable if strict cliff nesting behavior would be retained, as it is commonest in remaining Iberia (Hernández-Matías et al., 2013; Palma et al., 2013). This idea was supported by genetic studies and demographic modeling, which

FIGURE 3 Scatterplots showing trends in habitat conditions around Bonelli's eagle nests (500-m buffer) in relation to the time of territory establishment. Trends were estimated using ordinary least squares regression (red line, confidence intervals in gray) and quantile regression (light blue to dark blue lines), considering the habitat gradients extracted from a principal component analysis (PC1-4; a-d)), the distances to the nearest nest from a neighboring territory (e), and the prediction error of the habitat model (f). The quantiles represented are 5% (dark blue), 25%, 50%, 75%, and 95% (light blue)


(a)
Terrain ruggedness (PC1)
2
1
0
−1
1990
1995
2000
2005
2010
Year
(b)
Human infrastructures (PC2)
2
1
0
−1
1990
1995
2000
2005
2010
Year
(c)
Elevation (PC3)
1
0
−1
−2
1990
1995
2000
2005
2010
Year
(d)
Forests (PC4)
2
1
0
−1
−2
1990
1995
2000
2005
2010
Year
(e)
Distance to nearest nest (km)
40
30
20
10
1990
1995
2000
2005
2010
Year
(f)
Model prediction error
0.75
0.50
0.25
0.00
1990
1995
2000
2005
2010
Year

showed that the genetically isolated tree nesting population of southern Portugal was likely the main source of colonists throughout the expansion process (Hernández-Matías et al., 2013; Mira et al., 2013; L. Palma and R. Godinho Unpublished Data). Therefore, the conservation of populations with tree nesting behavior may be particularly relevant for the conservation of Bonelli's eagles at wider scales, as this behavioral trait may help the species respond better to ongoing climatic and land use changes (Hernández-Matías et al., 2013; Muñoz et al., 2013; Palma et al., 2013).

In general, our study shows the importance of understanding the contribution of habitat selection patterns to population expansion (Butcher et al., 2014; Veech et al., 2011). In particular, we showed that species can expand despite a relatively conservative nest site selection behavior, when changes in land use and human demographics provide new vacant areas open to colonization by the growing population (e.g., Balbontin, Negro, Sarasola, Ferrero, & Rivera, 2008; Cardador, Carrete, & Mañosa, 2011). We also found that the fast expansion of this particular eagle population was facilitated by a specific but relatively rare behavior in the Mediterranean region (tree nesting), which allowed the colonization of habitats that otherwise would be unavailable. The study thus adds to the increasing evidence suggesting that preserving behavioral diversity within populations may be essential for species persistence under anthropogenic environmental change (Caro & Sherman, 2012; Sutherland, 1998; Van Dyck, 2012).

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CONFLICT OF INTEREST

None declared.

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