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LETTER

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CHANGES FROM CLIFF- TO TREE-NESTING IN RAPTORS: A RESPONSE TO LOWER HUMAN PERSECUTION?

ALEJANDRO MARTÍNEZ-ABRAÍN

*Universidade da Coruña, Evolutionary Biology Group (GIBE), Facultad de Ciencias, Campus da Zapateira s/n,
15008 A Coruña, Spain*

JUAN JIMÉNEZ

*Generalitat Valenciana, Servicio de Vida Silvestre, Ciutat Administrativa 9 d'Octubre, Torre 1, C/ Democracia, 77,
46018 Valencia, Spain*

MIGUEL FERRER¹

Applied Ecology Group, Estación Biológica de Doñana, CSIC. C/Américo Vespucio 26, 41092 Isla de la Cartuja, Sevilla, Spain

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Human persecution of top predators has been historically very intense worldwide. In many countries, top predators have been or are still persecuted because they are considered competitors for resources, especially within subsistence economies (Bildstein 2008, Madden et al. 2019). As a result, many large mammalian predators have adapted their behavior to avoid humans, in extreme examples becoming nocturnal (Gaynor et al. 2018). In southern Europe, centuries- or millennia-old and intense historical persecution of large predators can be traced from the time of the Roman Empire to the present (Jennison 1937). However, the level of persecution has decreased substantially during the last few decades. This shift has been mainly driven by diverse socio-economic changes and the associated new human attitudes toward wildlife (Martínez-Abraín et al. 2008, 2009, Mayhew et al. 2016, Martínez-Abraín and Oro 2018), in combination with awareness campaigns and conservation laws. In addition, fewer humans live near wild lands and wildlife in Spain than in the past years. Human population density in Spain is 92 inhabitants/km²; well below the European mean (177 inhabitants/km²). Most Spaniards live now in large cities (51%), a result of a rural exodus that started in the 1950s–1960s and is still ongoing. Currently, a large part of the Spanish territory (53%) has densities lower than the threshold used by the European Union to classify a territory as sparsely populated or depopulated (11.5 inhabitants/km²).

This centuries- or millennia-old persecution of top predators most likely has shaped many aspects of the present ecology of large predators both via selection and cultural processes (Martínez-Abraín et al. 2019). One of the animal traits most susceptible to negative influence by historical human persecution is habitat selection and, in particular, nesting habitat selection. For example, Fernández (1993) found that Golden Eagles (*Aquila chrysaetos*) not only choose cliffs for nesting—due to human disturbance—but also that they choose the most inaccessible cliffs that are located farthest from tracks, roads, and villages. Osprey (*Pandion haliaetus*) populations from northern Europe (less intensively persecuted during the last century) nest on trees, whereas Mediterranean populations (most intensively persecuted in the recent past) nest on island cliffs (Ferrer and Morandini 2018, Martínez-Abraín 2018, Monti et al. 2018). A similar situation exists with the Booted Eagle (*Aquila pennata*): on the island of Mallorca (Spain), the eagles currently nest on cliffs after a long period of intense human persecution, but in the Iberian Peninsula, they are tree-nesters (Viada and de Pablo 2009). In a systematic review, Martínez-Abraín et al. (2010) found that large raptors nesting in trees exhibited greater displacement distances from roads (using roads as a proxy of human presence) than large raptors nesting on cliffs. Similar examples of negative demographic consequences for obligate tree nesters under strong human persecution include the Great Spotted Eagle (*Aquila clanga*) that was extirpated from Finland during the first half of the 20th century, whereas other large facultative tree-nesting species, such as the Golden Eagle, persisted (Pohja-Mykrä et al. 2012); however, evidence was equivocal, as several obligate tree nesters were affected much less or not at all (Pohja-Mykrä et al. 2012). Likewise, the White-tailed

¹ Email address: mferrer@ebd.csic.es

Table 1. Number of breeding pairs over time in Spain of two facultative tree/cliff nesters (left columns) and two obligate tree nesters (right columns). The numbers of Golden Eagle pairs for 1984, 1990, and 2008 are minimum values of the range estimates.

GOLDEN EAGLE		BONELLI'S EAGLE		SPANISH IMPERIAL EAGLE		CINEREOUS VULTURE	
YEAR	PAIRS	YEAR	PAIRS	YEAR	PAIRS	YEAR	PAIRS
1984	998	1987	620	1981	104	1989	774
1990	1190	1990	680	1990	140	1993	1027
2008	1553	2000	710	2000	240	2006	1854
		2005	733	2013	407	2014	2068
		2018	710	2017	520		

Eagle (*Haliaeetus albicilla*) was extirpated from Scotland, where it bred only as a tree-nester, whereas the Golden Eagle, a facultative tree nester, persists to the present (Evans et al. 2012).

All these examples suggest that nesting on trees makes raptors more vulnerable to human disturbance than nesting on cliffs. Facultative tree/cliff nesting by raptors likely evolved as an adaptation to increase plasticity in relation to habitat availability along with intra- and inter-specific competition for nesting space. Several suggestions can be made about why some raptor species seem to be much more plastic than others, including the habitat of origin for the species (Ferrer 2019, Martínez-Abraín and Jiménez 2019). Alternatively, from a conservation perspective, the ability to nest on trees or cliffs might have been helpful for avoiding historic human persecution simply by allowing increased options for nest sites that minimized the potential for conflict.

If obligate tree-nesters (i.e., species never recorded breeding on cliffs) are more sensitive to human persecution than facultative tree-nesters (i.e., species that breed on both substrates), we might predict that the population recovery of obligate tree-nesters in recent decades should have been proportionally stronger than that of facultative tree/cliff nesting species. This would have resulted because obligate tree-nesters suffered stronger declines in the past due to their lack of capacity to shift from trees to cliffs when affected by direct persecution. We might also predict that the proportion of nests of facultative species placed on trees versus cliffs would have increased during the last few decades as direct persecution of raptors by modern urban people in Europe declined.

To test the role of nesting substrate on changes to population size, we collected information on abundance over time (1980 to present) for four large raptor species in Spain: two facultative tree-nesters, Golden Eagle and Bonelli's Eagle (*Aquila fasciata*) and two obligate tree-nesters, Spanish Imperial Eagle (*Aquila adalberti*) and Cinereous Vulture (*Aegypius monachus*; Martínez-Abraín and Jiménez 2019). We also analyzed the proportion of nests on trees versus cliffs for the two facultative species, Golden Eagle and Bonelli's Eagle. All these species are

large, long-lived species with high annual survival probabilities, low fecundities, and delayed sexual maturity.

We obtained population size data for an entire southern European country (Spain) from available national censuses and diverse specialized bibliographies (Equipo de Estudio del Águila Real y el Águila Perdicera 1987, Arroyo et al. 1990, 1995, Gonzalez 1990, Ferrer 2001, Real 2004, De la Puente et al. 2007, Del Moral 2006, 2009, 2019, SEO/BirdLife (in press), Sánchez 1998 and references therein, Spanish Imperial Eagle Working group, proyecto monachus.grefa.org/el-buitre-negro/). Both groups of species (facultative and obligate tree-nesters) have increased since the 1980s; however, the magnitude of the increase varied for the species in each group (Table 1). The population growth rates, or lambdas ($\lambda = N_{t+1} / N_t$), for facultative tree-nesters (Golden and Bonelli's Eagles) were 1.2 and 1.1 respectively, indicating mean decadal increases of 20% and 10% respectively. Lambdas for obligate tree nesters (Spanish Imperial Eagle and Cinereous Vulture), however, were 1.5 and 1.4, indicating mean decadal increases of 50% and 40% respectively. The higher lambda for obligate tree nesting raptors during our target time period is likely because their populations were much lower in the 1980s, potentially as a result of human persecution, leading to a more marked population increase. The more plastic behavior of facultative nesters could have helped them better tolerate past human persecution.

Although population growth rate increased more for obligate tree-nesting raptors than for facultative tree-nesting raptors, there are other potential explanations beyond the influence of persecution. For example, funds for conservation may also explain differences in population growth rates among groups, with some species benefiting from more total funds spent for targeted conservation actions. However, one obligate (Spanish Imperial Eagle) and one facultative (Bonelli's Eagle) species were supported by European Union funds and, although both increased, the Spanish Imperial Eagle increased at a higher rate. Similarly, Golden Eagles and Cinereous Vultures did not benefit from significant EU funds and also increased at different rates. Hence, we do not think the amount of

Figure 1. Percentages of Bonelli's and Golden Eagle pairs breeding on trees (Sierra Morena area, Andalusia, Spain), during the period 2001–2014. There is a trend for increased proportion of nests on trees vs. cliffs in both species.

investment in conservation can explain the differences in recovery rates between the two raptor groups.

To assess variation in the proportions of tree versus cliff nesters in facultative species (i.e., Golden and Bonelli's Eagles), we selected a large and well-monitored region in southern Spain (Sierra Morena, Andalusia) where both substrate types are widely available. According to some authors (Arroyo et al. 1990, 1995, Del Moral 2006, 2009), these cliffs cannot be considered to be saturated with nests and so availability is not a limiting factor. The Andalusian Environmental Administration provided data on the proportion of tree/cliff nests for Golden Eagle (2006 vs. 2014) and Bonelli's Eagle (2001 vs. 2013).

For both species, the proportion of tree vs. cliff nests used has increased over time (Fig. 1). In Andalusia, 38 pairs of Golden Eagles nested on trees in Sierra Morena in 2006 (45.2% of the total population), whereas 52 pairs were tree nesters in 2014 (61.7% of the total population; a 40% increase in 8 yr, Fisher exact test $P = 0.0244$). Likewise, six pairs of Bonelli's Eagles (12.5% of the total population) nested on trees in Sierra Morena in 2001 whereas 12 pairs

nested on trees in 2013 (25.8% of the population, a 100% increase in 12 yr; Fisher exact test $P = 0.0634$). To our knowledge, no nests of Spanish Imperial Eagles or Cinereous Vultures were found on cliffs in Spain.

Because large, tree-nesting raptors may be more susceptible to human persecution, the increase in the percentage of nests built on trees in Spain during the last few decades might be explained by the reduction in direct human persecution (Martínez-Abraín et al. 2013). But other factors may also have influenced the documented increase in the use of trees for nesting. For example, intra- or interspecific competition may have acted as a proximate trigger of cliff abandonment, perhaps in parallel with population recovery of many species across the associated communities. In fact, many large species are now recovering from past persecution, which in turn can cause negative effects to smaller species. For example, common Griffon Vultures (*Gyps fulvus*; minimum of 30,946 pairs in 2018 in Spain; Del Moral and Molina 2019) have been reported stealing nest material from

Bonelli's Eagles (Jiménez 2019), which could force eagle pairs to abandon cliff nests.

Alternatively, it is possible that the increasing number of tree nests reflects pairs relegated to suboptimal habitat due to increasing population density and limited numbers of breeding sites available. It would be interesting to determine whether the productivity of the new tree-breeding pairs is lower than the productivity of cliff-breeders. If true, this could lend support to the proposed explanation. According to the habitat heterogeneity hypothesis (HHH), as density rises, an increasing proportion of individuals are relegated to lower quality habitats, leading to declines in mean population fecundity (Ferrer and Donazar 1996). However, considering that the availability of cliff nest sites is still high (see above), this potential explanation does not seem very plausible.

Another alternative explanation for the increasing percentage of tree-nesters in facultative tree/cliff nesting species would be changes in distribution and abundance of prey. A change in the distribution of high density areas of prey away from potential cliff-nesting sites together with a general increase in prey populations could be the reason for an increase in tree nesters. However, due to several infectious diseases during recent decades, the density of wild rabbits (*Oryctolagus cuniculus*; the main prey for raptors in Spain) is far lower than in the past, suggesting that changes in density or distribution of prey are not the main factors driving these changes (Ferrer and Negro 2004).

More detailed study of the role played by direct human impacts on nest site substrate selection could help inform future policymaking, and guide conservation activities for facultative cliff/tree nesting raptors worldwide. Reintroduction or population supplementation programs could benefit from this new perspective through consideration of identified behavioral patterns. For example, selection of nesting substrate by raptors could be part of the traits linked to the shy-bold behavioral complex (Bell 2007, Réale et al. 2007). Changes in fear of humans, aggressiveness, and exploratory behavior have been identified in urban birds as a response to changes in human density, with a higher frequency of bold behaviors in areas having higher human density (Riyahi et al. 2015, 2017). Additionally, an increase in the intensity of nest defensive behavior over the years in relation to human presence has been documented in both large and small raptors (Ferrer et al. 1990, 2007, Arroyo et al. 2017). This increase suggests that bold defensive behavior, including striking humans, could have been positively reinforced when adults did not lose their offspring after a hypothetical human attack. The use of bold young from tree-nesting populations in hacking programs, implemented in areas with high but harmless human presence, could introduce behavioral plasticity into populations of shy individuals, likely leading to improved success (Réale et al. 2007, Martínez-Abraín 2018).

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