Status and habitat changes in the endangered Spanish Imperial Eagle *Aquila adalberti* population during 1974–2004: implications for its recovery

LUISE MARIANO GONZÁLEZ, JAVIER ORIA, ROBERTO SÁNCHEZ, ANTONI MARGALIDA, ANTONIO ARANDA, LUIS PRADA, JAVIER CALDERA and JOSÉ IGNACIO MOLINA

Summary

The distribution and abundance of Spanish Imperial Eagle *Aquila adalberti* populations between 1974 and 2004 were determined using information from national censuses. Its breeding area occupies the south-western quadrant of the Iberian Peninsula (Spain and Portugal) and is composed of 13 nuclei and 5 subpopulations. Since 1974, population levels in all nuclei, except the one in Doñana, have expanded. The non-breeding dispersion area, according to sightings of juvenile and immature individuals in quadrants of 10 x 10 km, coincided with that of the breeding area. Bibliographical information showed that halfway through the 19th century the Spanish Imperial Eagle was considered abundant, at least locally; and most cited breeding areas were in relatively human-occupied plains. Towards the end of the 19th century the population became scarce; remaining so for most of the 20th century, with remote mountain ranges being the most cited breeding habitats. The comparison between the data from the first census, in 1974, that located 38 territorial pairs, and the 2004 census that located 198 pairs, shows that: 1) percentages of pairs in plains have increased, while those in mountains have decreased; 2) the trophic quality of the habitat, based on rabbit abundance, has decreased, and 3) numbers of nests in both protected areas and on private ground have increased significantly. The type of land ownership did not seem to affect breeding performance. Populations have increased more outside protected areas than within, despite the availability of potential habitat. In the past century, legal protection and attitude changes towards this eagle seem to have been influential in preventing its extinction. At present, habitat management seems also to be an important factor in its continuing recovery.

Introduction

Birds of prey generally, and large eagles in particular, have been extensively hunted to protect domestic animals and small game species (Newton 1979, Holmes *et al.* 2003, Whitfield *et al.* 2004), especially during the last 150 years in Europe where numerous populations have disappeared (Bijleveld 1974). Compared to other raptors, large eagles are even more vulnerable to human persecution due to their large size, their proximity to humans, their use of obvious perches and nests which facilitates their capture with traps, and their frequent habit of feeding on carrion, so they can be easily poisoned (Newton, 1979).

The Spanish Imperial Eagle *Aquila adalberti* is one of the rarest and most endangered birds in the world (BirdLife International 2004), whose present population of nearly 200 breeding pairs is
found only in the Iberian Peninsula (González and Oria 2004). In past centuries, the species occupied the Iberian Peninsula and the north of Morocco (González et al. 1989a). During this period, human persecution and reduction of its main prey, the Rabbit *Oryctolagus cuniculus* were the main causes of decline of the Spanish Imperial Eagle (Valverde 1967, Garzón 1972, 1974). In 1989 the wild Rabbit was affected by viral haemorrhagic disease (RHD) that reduced rabbit populations to between one-half and two-thirds of their original size in few years (Blanco and Villafuerte, 1993, Villafuerte et al. 1995). This had a negative effect on Spanish raptors that prey extensively on rabbits (Fernández 1993, Martínez and Calvo 2001) and caused great concern for the recovery of Spanish Imperial Eagle populations (González 1996).

However, in recent years the species has been recovering thanks to the contributions made by important conservation projects and the implementation of a national strategy for the conservation of this species and of recovery plans in the Autonomous Communities (González and Oria 2004). Despite the fact that its historical abundance had not been studied, it has been suggested that the Spanish Imperial Eagle has always been a scarce species and that therefore it was inappropriate to propose conservation goals aimed at making the population abundant (Ferrer and Negro 2004). For endangered species, like the majority of large eagles, knowledge of former and present abundance and of factors that may limit population recoveries can be important in proposing realistic and effective conservation measures (Caughley and Gunn 1996).

According to the literature, the Spanish Imperial Eagle inhabited woodlands, plains and marshes (Valverde 1960, González et al. 1990, Bisson et al. 2002). However, several studies of threatened species have shown that their present habitat may not coincide with the one they frequented when they were abundant and unthreatened (e.g. Newton et al. 1996, Black 1995). This may modify the view of their ‘optimal’ or ‘typical’ habitat, and thus conservation strategies should consider expansion into more historical habitats. There are no studies of the preferred habitat of the Spanish Imperial Eagle in past centuries when it was abundant. This knowledge is important for proper conservation programmes, since it would indicate which areas, in regards to habitat, could be recolonized by the species in its recovery process, leading to better management plans.

The aims of this study were: 1) to analyse changes in the abundance of the Spanish Imperial Eagle from the 19th century to 1970 and its temporal variations; 2) to evaluate changes both in habitat preference and in distribution from 1974 to 2004, and 3) to consider these results in relation to its recent population recovery.

**Methods**

**The species**

The Spanish Imperial Eagle is a sedentary, territorial and monogamous species with a maximum lifespan of 31 years (authors’ data). The majority of breeding birds inhabit plains and mountain ranges with patches of Mediterranean forest and ‘dehesa’, a kind of open forest of *Quercus rotundifolia* and *Q. suber* of anthropogenic origin (González et al. 1990). Clutch size varies from one to four eggs and eagles can raise up to four chicks when rabbits are abundant (Margalida et al. 2007). In addition to rabbits, its diet mainly includes wildfowl (*Anas* spp., *Anser anser*) and Wood Pigeons *Columba palumbus* (Delibes 1978, González 1991, authors’ data). It nests in tall trees which stand out in the landscape and occasionally nests on electricity pylons (González 1991). The average home range obtained using radio telemetry from five territorial breeding adult eagles, monitored over almost a year in 1996 in Madrid (central Spain), was nearly 5,000 ha. But in areas with high rabbit densities (> 1 rabbit ha⁻¹) the average area was smaller (1,987 ha) and with low rabbit densities (< 1 rabbit ha⁻¹) was larger (6,612 ha) (authors’data).

**Data collection**

The first quantified population estimates of the Spanish Imperial Eagle throughout its entire distribution were carried out at the beginning of the 1970s (Garzón 1972, 1974). Hence, prior to
the 1970s, estimates of the eagle’s abundance have to be based on subjective opinions and published comments (first records date from the 19th century). The abundance of the species from 1974 to 2004 was studied using six censuses covering the whole distribution range and carried out in the following years: 1971–1974 (Garzón 1972, 1974), 1981–1986 (González et al. 1987), 1989 (González 1991), 1994 (González 1996), 1999 (González and Oria 2004) and 2004 (present data). Survey effort varied from year to year: the number of people directly involved in each census was three in 1974, 10 in 1986, 11 in 1989, 14 in 1994, 16 in 1999, and 18 in 2004. The area covered in all censuses was limited to Spain and some areas on the border with Portugal and was similar except during the first census (1974), when Sierra Morena, in the Andalucía region, was not covered adequately.

The distribution range of the species was established in the 1974–2004 censuses at three levels. 1) The area of presence, defined as the area contained within the shortest continuous limits that included all locations in which the species had been observed. It was established using sightings and captures of individuals in this period and referred to in publications (i.e. Calderón et al. 1988, Blanco and Pacheco 2003, Thévenot et al. 2003, Kayser et al. 2003, Martí and del Moral 2003) and from our own information. 2) The non-breeding dispersion area, defined as the area with records of individuals of non-breeding age (< 2 years old) (González 1991, Forsman 1999). It was established using 10 x 10 km UTM quadrants based on sightings from the literature, personal information, recoveries from the Migration Office (Ministry of Environment) and from the tracking of 68 individuals fitted with transmitters as nestlings (57 with VHF and 11 with satellite) between 1990 and 2003, in Madrid, Castilla y León, Castilla-La Mancha and Extremadura. In addition, information from the Andalucía region was obtained from published reports of the Doñana National Park (Ministry of Environment) and public reports and miscellaneous publications of this Autonomous Community. This area has also been named as the juvenile dispersion area. 3) The occupied breeding area or the breeding nucleus, defined as the foraging areas of breeding pairs located during the censuses. It was established using 10 x 10 km UTM quadrants, in accordance with the methodology of the Atlas of Breeding Birds of Spain (Martí and del Moral 2003). A breeding nucleus was defined as quadrants with presence of breeding pairs and their eight adjacent quadrants. Two occupied quadrants are in the same nucleus if they are in contact or share non-occupied quadrants; and they are in different nuclei when there are at least two non-occupied quadrants between them. This criterion is based on the fact that a quadrant can contain up to five territorial pairs and their foraging areas can extend out of this quadrant to the non-occupied adjacent quadrants, in particular when the nests are near or on the border of the quadrant. Also the area of two unoccupied quadrants was larger than the average size of the range of an individual (5,000 ha) and larger than the average distance between nests (González 1991). The nuclei were brought together by their geographical proximity (< 20 km between them) in groups of nuclei called subpopulations. The area occupied by breeding pairs was calculated by multiplying the number of breeding pairs of each nucleus by 1,987 ha in the case of breeding pairs situated in quadrants with rabbit density considered abundant (see later) and by 6,612 ha in case of breeding pairs situated in quadrants with rabbit density considered scarce.

Nesting habitats of eagles located during the censuses were classified according to the topography, elevation and surrounding landscape into a) wetlands: marshland close to sea level (0–200 m asl) with a predominantly flat topography; b) plains: landscape at 200–700 m, with plateau topography, peneplain or hills with low slopes; c) sierra: foothills at mid-altitudes (700–1,000 m) with abrupt topography; and d) mountain: high altitude (> 1,000 m) and predominantly medium to high mountain topography.

Given the importance of Rabbits in the eagle’s diet and the distribution overlap of both species (González et al. 1990, Delibes-Mateos et al. 2007), eagle habitat quality was measured using Rabbit abundance as an indicator of habitat quality during the study period. This was determined according to a study of Rabbit abundance and distribution in Spain at a 1:100,000 scale in the period before and after the spread of the RHD disease in the distribution area of the Spanish
Imperial Eagle (Blanco and Villafuerte 1993, Villafuerte et al. 1995). We considered areas with densities of $>1$ rabbit ha$^{-1}$ (range 1–7.8) to be high quality habitat, and those with densities $<1$ rabbit ha$^{-1}$ (range 0–0.9) (Blanco and Villafuerte 1993) to be a low quality habitat.

Human management of the breeding habitat was categorised according to whether located nests were situated within a natural or Specially Protected Area for birds (SPA) officially declared by the Autonomous Communities and under provisions of the EC Birds Directive, or whether they were located on private or on public land. The breeding parameters studied were: hatching success (number of chicks hatched in relation to the number of egg-laying territories) and breeding success (number of fledglings in relation to the number of egg-laying territories).

The normality of the variables was checked using Kolmogorov-Smirnov tests, and non-parametric statistics were applied to non-normal data (Sokal and Rohlf 1981).

**Results**

**Distribution area**

During the study period the Spanish Imperial Eagle occupied most of the south-western quadrant of the Iberian Peninsula (Figure 1). No sightings were registered in the north-western corner of the Peninsula (the Cantabrian region and Galicia) and on the east coast of Spain. The farthest sightings were recorded in the south of France (Kayser et al. 2003, Duchateau 2007) and Libya (Calderón et al. 1988) and towards the south in Mauritania (A. Araújo pers. comm.) and Senegal where a young individual equipped with a satellite radio transmitter as a nestling arrived in its first autumn.

The breeding area in 2004 was composed of 13 breeding nuclei (Figure 2a). These nuclei were grouped into five aggregations or subpopulations according to their geographical location, proximity and habitat type: Northern (Guadarrama, Gredos and Tiétar Valley); Central (Montes de Toledo, Sierra de Guadalupe, Sierra de Almadén and Valley of Guadiana); Western (Sierra de San Pedro, Sierra de Coria and Monfragüé-Trujillo); Southern (Sierras in the south of Badajoz, Eastern Sierra Morena, Sierra Morena of Córdoba and Sierra Morena of Córdoba-Sevilla); and Doñana (Guadalquivir marshlands and Coto de Doñana nucleus). In 1974 there were 17 breeding nuclei (Figure 2b). Compared to the breeding area in 2004, every nucleus, except Doñana, has increased its area.

The non-breeding dispersion area was similar to the breeding area (Figure 3), except in two areas, one situated in El Andévalo (Huelva) and another in the south of Cádiz (Ferrer and Harte 1997). Most of the sightings (more than 10 in each quadrant) were recorded in the following four areas: 1) west and south of Madrid-north of Toledo; 2) foothills of the Sierra de Guadarrama and basin of the Tajo river in Toledo; 3) Campo de Montiel and Calatrava, and 4) Tierra de Barros in the south of Badajoz. Other areas with a smaller number of sightings were located in the Tajuña basin (Madrid-Guadalajara), the Guadalmez valley (Ciudad Real, Córdoba), Zorita-Logrosan and Trujillo-Magasca (Cáceres) and Doñana (Huelva-Sevilla).

**Abundance**

The first references on Spanish Imperial Eagle abundance that we found date from the 1850s when Graells (1852), writes that in the areas of Madrid, Segovia and Avila, the Imperial Eagle is “less common than the Golden Eagle”. During the same period, Machado (1854) considers it “common” in the mountains of Andalusia, and Brehm (1857) states that it is “more abundant than the Golden Eagle” in the centre and south of Spain.

In the following decade López-Seoane (1861) considers it “more frequent in western Andalusia” and Lilford (1865), comments “eagles of many species abound in Andalusia, one of the most common being the Imperial (Aquila heliaca)... The Imperial Eagle appears to be rare in the east of Spain...”
Figure 1. Area of presence of Spanish Imperial Eagle between 1974 and 2004 incorporating all records, breeding and non-breeding. The area in grey represents the area containing 90% of all records and the black points mark the locations outside this area of sightings from the literature and the authors’ own information.

Figure 2. Breeding nuclei of the Spanish Imperial Eagle in 1974 (a) and in 2004 (b). The nuclei in white contain < 2 territories, in light grey 3–10, in dark grey 11–20, and in black > 21 territories. In a) the letters B and D mark the nucleus of the Sierra de Guadarrama, C the Monte del Pardo; E the east of Madrid and Gredos, F the Valley of the river Tietar, H the Sierra de Guadalupe, I Monfragüe; J the Sierra de Coria, K and L the Sierra de San Pedro, M the Montes de Toledo, N the Sierra de Almadén, O, P and Q the Eastern Sierra Morena, R the Sierra Morena of Seville-Cordoba and S the Doñana Reserve and the Guadalquivir Marshlands. In b) the letter B mark the nucleus of Sierra de Guadarrama, M the Montes de Toledo, H the Sierra de Guadalupe, I the Monfragüe-Trujillo, J the Sierra de Coria, L the Sierra de San Pedro, N the Sierra de Almadén, X the valley of the River Guadiana, U the Sierras of the South of Badajoz, P the Eastern Sierra Morena, W the Central Sierra Morena of Córdoba, R the Sierra Morena of Seville-Cordoba, and S the Doñana Reserve and the Guadalquivir Marshlands.
Describing the year 1869, Irby (1895) writes: “In wooded districts in the west of Andalusia this eagle is universally distributed, being most abundant in the reserves towards Seville and about Cordova, not infrequently occurring near Gibraltar.”

Saunders (1871) finds it only in Sevilla where he says “…it is tolerably abundant…” and Dresser (1873), points out: “Lord Lilford informs me that this eagle is very common in the plains of Andalusia…It is essentially a bird of the plains; I have never met with it nor heard of its occurrence in the mountains…Major Irby informs me that it is common in the vicinity of Gibraltar, though by no means so numerous as near Cordoba and Seville…Mr. Howard Saunders writes that the habitat of this species appears to be restricted to the wooded plains watered by the principal rivers of Southern and Central Spain. It frequents the whole of the wooded and flat portion of the valley of the Guadalquivir, and the tributaries of that river…”

Chapman (1888) points out: “…The Spanish Imperial Eagle (Aquila adalberti) is now a comparatively scarce bird in this region; twenty years ago it bred here quite commonly, but I only observed a single adult during the two expeditions I made to the Doñana Reserve last winter.” He commented that “there are still a few pairs of this superb Eagle in the district, though their numbers are sadly thinned by the greed of collectors since 1872”. However, Rudolph de Habsburgo (1889), who observed and collected immature individuals in El Pardo and Doñana, wrote “…It must, however, be very rare in Spain, for during my numerous expeditions into the interior of the country I did not see one of these birds.”

Finally in the last decade of the 19th century, Chapman and Buck (1893), wrote “Several pairs live in the majority of the rugged provinces of the Centre and South, even if in Andalusia its number has greatly diminished since our first sighting in 1872…the plains, are their favourite places…..we have had numerous opportunities to observe their habits…in the wooded plains of Andalusia and Extremadura…The Imperial Eagle is a bird exclusively from the plains and it is not found in the mountains….” Also in those days, Irby (1895) mentioned “…I find now, in
1894, that their numbers are much reduced...” and “Verner writes me that this Eagle was not uncommon in the Cork-woods about twenty years ago, but they have now, from persecution, retired to the more unfrequented parts of the country...” Verner (1909) wrote “...broadly speaking in southern Spain... the White-shouldered eagle frequents the low-lying ground and is usually seen circling over the plains and marshes or beating along the low scrub-covered hills adjacent to them...being essentially a bird of the plains...”

In the 20th century, the first author to mention it is Noble (1902), who considered it as “rare in Doñana.” Baldwin-Young (1906) said that in the Doñana area not one individual had been seen. Dresser (1910) noted: “Formerly it nested commonly in the cork-woods in the south of Spain, but it has become much less common...it inhabits the wooded plains...”. In the same period, Cabrera (1916) wrote “I have never seen the species in the Guadarrama.”

Later in the 1920s, Medinaceli (1921), cited it as an “uncommon” species and emphasized that it was only present in three locations: El Monte del Pardo, Doñana, and Guadarrama. Witherby (1928), pointed out that in his travels he did not see any and that “in central Spain it is very scarce”, citing only El Pardo and Gredos; and the Vizconde de la Armería (1929) said that in Spain “it is infrequent” and that “it is very rare to see an adult individual.” Later, Gil Lletget (1945) only cited it in El Pardo and in the 1950s Valverde (1958) considered it as a species in danger of extinction and only cited it as present in El Pardo, Doñana and Guadarrama. Subsequently, this author included the Tajo Valley (Monfragüe) to these enclaves (Valverde 1959, 1960). In the sixties it was considered as very scarce (Bernis 1966) and its population was estimated at no more than 50 pairs in Spain (F. Bernis in Bijleveld 1974) with presence in the same locations (Valverde 1967).

In 1970 its population was estimated at 30 pairs (Simon and Geroudet, 1970); and between 1971 and 1974 the first census was carried out covering most of its distribution area (Garzón 1972, 1974), locating 38 occupied territories (Table 1). Of these, 21 territories were in the four previously mentioned locations and the rest in the three breeding areas which had not been located until then: Sierra de San Pedro, Sierra Morena and Montes de Toledo. In subsequent surveys its population increased, reaching 198 breeding pairs in 2004 (Table 1). Parallel to the population increase, the area of habitat occupied by territorial pairs increased from 60,913 ha in 1974 to 800,408 ha in 2004 (Table 2); with Guadarrama, Eastern Sierra Morena and Sierra de San Pedro nuclei having the largest surface area in 2004.

Habitat changes and breeding parameters

The number of nests located in the different types of habitat (Figure 4) varied across the census ($\chi^2_{15} = 41.66, P < 0.001$). The proportion of nests in plains increased from 1974 to 2004, whilst in the mountains and marshlands it decreased, and in the sierras it remained stable. On the other hand, the proportion of nests located in habitats of high trophic quality has declined significantly ($\chi^2_{5} = 163.4, P < 0.001$), from 100% in 1974 to 47% in 2004 (Figure 5).

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<td>14</td>
<td>15</td>
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<td>42</td>
<td>51</td>
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</tr>
<tr>
<td>SOUTHERN</td>
<td>5</td>
<td>7</td>
<td>22</td>
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</tr>
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<td>9</td>
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<td><strong>Total</strong></td>
<td><strong>38</strong></td>
<td><strong>92</strong></td>
<td><strong>120</strong></td>
<td><strong>140</strong></td>
<td><strong>132</strong></td>
<td><strong>198</strong></td>
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The proportion of nests in protected areas increased slightly from 1974 to 2004 although the differences were not significant ($\chi^2 = 5.58$, $P = 0.35$, Figure 6) while the percentage of territories in SPAs decreased by 80% ($n = 112$) in 1994 and 89.9% ($n = 116$) in 1996 to 68.9% ($n = 131$) in 2004. The number of nests on private land increased by 55.5% in 1974 to 77.9% in 2004 (Figure 7); while those on public land decreased in the same period by 45.5% to 22.1%; the differences being statistically significant ($\chi^2 = 13.85$, $P = 0.017$).


<table>
<thead>
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<th>Subpopulation</th>
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<td></td>
<td>SGU</td>
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<td></td>
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</tr>
<tr>
<td></td>
<td>SA</td>
<td>1,987</td>
<td>6,612</td>
</tr>
<tr>
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<td>VGM</td>
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<td>138,862</td>
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<td>1,987</td>
<td>6,612</td>
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<tr>
<td></td>
<td>SAL</td>
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<td></td>
<td>SGR</td>
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</tr>
<tr>
<td>Subtotal</td>
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<td>800,408</td>
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<td>TOTAL</td>
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Figure 4. Evolution of the number of breeding territories of the Spanish Imperial Eagle in the censuses according to the type of habitat. In squares mountains, in black sierras, in grey plains and in white marshlands.
Throughout the study period, the hatching and breeding success of nests situated in protected and non-protected areas did not vary significantly (Kruskal-Wallis \( H_3 = 0.31, P = 0.29 \) and \( H_5 = 3.48, P = 0.32 \), respectively for hatching success and Kruskal-Wallis \( H_5 = 7.46, P = 0.19 \) and \( H_5 = 9.68, P = 0.09 \), respectively for breeding success, Figure 8). However, the hatching success of nests situated in non-protected areas shows a certain tendency (marginally significant) to be greater than in the protected areas (1.49 ± 1.70 vs 1.06 ± 0.20, Mann-Whitney U-test, \( z = -1.92, P = 0.055 \)) but not the breeding success (0.91 ± 0.16 vs 1.27 ± 0.09, Mann-Whitney U-test \( z = -1.49, P = 0.14 \)).

During the study period, hatching and breeding success did not vary significantly between the territories situated on public land (Kruskal-Wallis \( H_4 = 2.06, P = 0.73 \) and \( H_4 = 2.19, P = 0.70 \), respectively), and private land (Kruskal-Wallis \( H_5 = 5.07, P = 0.41 \) and \( H_5 = 9.64, P = 0.09 \), respectively). Hatching success was not significantly different between the nests situated on public and private land (1.44 ± 0.07 vs 1.45 ± 0.08, Mann-Whitney U-test \( z = -0.37, P = 0.71 \)).

Figure 5. Percentage of breeding territories of the Spanish Imperial Eagle in the censuses according to the trophic quality. In black, high quality; in white, low quality.

Figure 6. Changes in the number of breeding territories of the Spanish Imperial Eagle according to the legal protection of the habitat. In black, non-protected areas; in white protected areas.
Discussion

Spanish Imperial Eagle abundance can only be analyzed from 1974 onwards, since there are no previous estimates. Observations from 19th century naturalists indicate that the Spanish Imperial Eagle was an abundant species during the first half of the century. Such records are supported by the extensive distribution area where it was found, including most of Portugal and the north of Morocco, countries where it is now rare (Blanco and Pacheco 2003, Thévenot et al. 2003). A general impression of its abundance can be gathered from the collection between 1869 and 1893 of 37 clutches of eggs and 44 individuals (González et al. 1989a) in the Guadalquivir marshlands. The highest recorded densities in recent times here, 16 occupied territories, were recorded in the 1980s (Ferrer and Donázar 1996). Our results have demonstrated that during the first half of the 19th century, the Spanish Imperial Eagle was widely distributed, possibly continuously, at least throughout the south-west quadrant of the Iberian Peninsula. Support for this can be found in genetic studies that show no evidence of genetic structuring in historical Spanish Imperial Eagle populations (Martínez-Cruz et al. 2007).

Greatest population decline, and subsequent fragmentation, must have taken place at the end of the 19th century. Throughout most of the 20th century and until the early 1970s, its breeding area was severely fragmented, reduced to four isolated zones: El Monte del Pardo (Madrid) and the Valsaín-La Granja royal forests (Guadarrama nucleus), Monfragüe ( Cáceres) and the Guadalquivir Marshlands. In other areas it was very scarce. The genetic structure and low levels of mitochondrial DNA present in the population are interpreted to be a consequence of this population decline (Martínez-Cruz et al. 2004).

In recent years, the breeding population of the Spanish Imperial Eagle has experienced a gradual and steady increase, from 38 pairs located in 1974 to 198 in 2004. Yet some of this increase could be a result of variation in survey effort: during the first two surveys, 1974 and 1986, the number of surveyors was low, while the Andalucía region was not fully surveyed until the last census. This could explain the notable increase from 25 pairs in Andalucía in 2001 to 45 pairs in 2002. Therefore, at least in that region, part of the apparent population increase must be related to better survey efforts. The increase in the area occupied by territorial pairs in 2004 with respect to 1974 could have been higher. In this sense, the home range of the eagles (the estimator
used to obtain this area) could have been smaller in 1974 (a pre-RHD disease period when rabbits were more abundant) than in 2004 (a post-RHD disease period) and thus over-estimate the extent of the occupied area.

The reduction in the percentage of high quality territories in the last three censuses could be related to the drastic rabbit population decrease in Spain provoked by RHD. This reduction negatively affected the population breeding parameters of this eagle (González et al. 2006a, Margalida et al. 2007). The fact that the new territories established after 1989 appear mainly in low quality habitats on the periphery of the breeding nuclei, could also explain the increase in the number of low quality territories.

In the 19th century, Spanish Imperial Eagles, like all raptors, were considered to be vermin and intensively hunted, with financial rewards being offered for killing them (Lilford 1866). Towards the end of the 19th century, the species declined and became scarce. In fact, the number of

Figure 8. Hatching success (a) and breeding success (b) of the Spanish Imperial Eagle in protected areas and in non-protected areas.
clutches and skins collected was notably reduced in comparison with previous years (González et al. 1989). The change from abundant to scarce occurred at the end of the 19th century. Along with this change came increased efficiency at shooting eagles. At the end of the 19th century, the muzzle-loader type shotgun was replaced by the breech-loader, which could be loaded more quickly and easily, even while mounted, and had greater firing rate, distance and precision (Bijleveld 1974). At the same time, hunting small game became fashionable in Spain and elimination of predators by any method, including the use of poison, became standard (Chapman and Buck 1893, 1910, Verner 1909). Additionally, the demand for Spanish Imperial Eagle specimens by museums and scientific institutions increased, due to the fact that it had recently been described and there were still doubts about its taxonomic identity (Saunders 1871, Chapman 1884, Calderón 1892). Paradoxically, the first Spanish legal regulations which offered the eagle a certain level of protection came from this period (Madrid Gazette, 26/10/1896), which prohibited shooting falcons, eagles and Bearded Vultures Gypaetus barbatus.

Nevertheless, during the 20th century, persecution of the Spanish Imperial Eagle continued with officially established incentives (Hunting Law of 1902 and Royal Order of 1915). In 1953 a Law Decree created an official organization dedicated to this task, the Committee for the Extinction of Harmful Animals. This institution from 1954 to 1962 the death of at least 1,206 “Large Eagles” and 3,602 “Eagles”, the general name under which the Aquila eagles would be found (SNPFYC 1962). Also, at this time a Rabbit epizootic (myxomatosis) decimated the populations of its prey species and probably further compromised the survival of the Spanish Imperial Eagle (Valverde 1967, Garzón 1972). At this time, hunting raptors with owls was introduced in Spain (España-Paya 1965), a practice which became common and which was considered one of the most frequent causes of mortality in the Spanish large eagles (Rodríguez de la Fuente 1964, F. Bernis in Bijleveld 1974). In the 1950s and 1960s, the species survived mainly on a few private properties, where it was respected and where its conservation was promoted (Trigo de Yarto 1962, Valverde 1960, 1967, Garzón 1972). At the end of the 1960s, F. Rodríguez de la Fuente published articles to raise awareness of raptors (see Pou 1995), which led to a change in society’s attitude. This resulted in the Spanish Imperial Eagle being declared a game species in 1966, initially conferring a partial degree of protection (Ministerial Order 26/4/1966) and subsequently a fully protected species in 1973 (Law Decree 2573/1973). The discovery of more breeding territories in the 1970s could be a consequence of changing attitudes and an improvement in its protection.

It is interesting to note that the positive population trend of the Spanish Imperial Eagle after the 1970s was similar to that recorded for other raptor species in Spain in the same regions, such as the Cinereous Vulture Aegypius monachus and the Eurasian Griffon Vulture Gyps fulvus (Donázar and Fernández 1990, Martí and del Moral 2003). The efficient implementation of the prohibition on the use of poison to eradicate terrestrial carnivores (mostly Red Fox Vulpes vulpes and Grey Wolf Canis lupus), until then a common practice (Rodríguez de la Fuente 1964, Garzón 1972), first in official hunting grounds in 1983 and, since 1989 on all land, contributed to raptor populations’ recovery. In addition, other management practices such as supplementary feeding (González et al. 2006a) and nest-vigilance to establish buffer zones (González et al. 2006b) have probably contributed to this recovery during the last 15 years.

An interesting result of our study is that parallel to its recovery, the percentage of breeding territories on plains has also increased. It is noteworthy that halfway through the 19th century, when the eagle was still abundant, it preferred habitats in relatively human-occupied areas, such as wooded plains and river valleys. However, when the eagles began to become scarce, their presence in much less populated habitats such as the sierras and in high mountain areas was observed. For example, in La Granja (Segovia), a high mountain area in the Sierra del Guadarrama, Castellarnau (1877), an experienced local naturalist, specifically noted its absence at this time. However, years later, in the period in which it was rare in the Peninsula, the eagle was mentioned for the first time in this Sierra (Verner 1909) and in 1914 the first known clutch was collected there (Witherby 1928). In the Sierra de Gredos, another high mountain area where
the species was unknown before the 20th century, the species was also recorded for the first time in 1925 (Witherby 1928). The fact that this eagle visited the plains more often when its population was abundant and not persecuted, suggests that it prefers this habitat, coinciding with habitat preferences of its sister species, the Eastern Imperial Eagle *Aquila heliaca*, in similar conditions of abundance and protection (Katzner et al. 2003). Human persecution possibly eliminated the populations of eagles living in the plains and in response to this persecution the eagles that survived occupied less developed habitats, e.g. mountains, where they remained during the 20th century. This suggests that a relationship exists between human persecution and the type of habitat occupied at any given moment. That is why studies on the selection of habitats by endangered species (e.g. González et al. 1992, Bisson et al. 2002), should consider these situations when interpreting the results. The case of the Spanish Imperial Eagle is a good example of how an endangered species’ contemporary distribution or ‘habitat use’ should not be taken as ‘optimal’ or ‘typical’ habitat. In addition, it is important to emphasize the importance that the variability in habitat preference shown by the Spanish Imperial Eagle has had in overcoming the process of population decline. For this reason, all of the habitats occupied by the species, including those where fewer pairs occur, must be considered important for the species.

Another interesting result of our study is that in the last 30 years, the population of Spanish Imperial Eagles has grown more outside protected areas than inside them, despite there being habitat available in the protected areas, and greater growth has occurred on private land than on public land. Thus, habitat management seems also to have been important for its recovery, together with legal protection. On private land, habitat management is mainly directed at favouring game species, potential prey-items for eagles, such as Rabbits, Red-legged Partridges *Alectoris rufa* and Wood Pigeons (Vinuélula and Villafuerte 2004). In fact, this is the case in the majority of non-breeding dispersal areas, where most are situated on non-protected and private land. It must also be emphasized that in recent years, a lot of these private lands have made management agreements with NGOs (covering 18.9% of eagle territories found in 2004), and habitat management there has focused on meeting eagles’ requirements (González and San Miguel 2004). Promoting this type of management is therefore very important for the survival of non-breeding individuals (Penteriani et al. 2005), and also for those breeding individuals that use these areas as secondary communal hunting zones (unpubl. data).

In conclusion, we think that the increase in the Spanish Imperial Eagle population will continue naturally into the future, since there is historical habitat available (woodland plains and fluvial valleys) which the species readily occupied when unthreatened and abundant. Also, the factor which seems to have been most influential in the positive evolution of their population has been the improvement in human attitudes towards the species, reflected first in private initiatives and later in legislation.

Habitat management has also been a determining factor in its growing population and will continue in the future as there are many potential habitats available. However, it must be taken into account that the breeding parameters of eagle subpopulations could be negatively affected as their habitats become saturated, as appears to be happening now (Ferrer and Donázar 1996, authors’ unpubl. data). It is therefore recommended that conservation measures include: 1) undertaking or maintaining the present management of habitats favoured by the species and 2) extending this type of management to potential habitats and breeding areas.

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Luis Mariano González

Javier Oria
Boscaje S.L, c/ San Agustín 22, E-40001, Segovia, Spain.

Roberto Sánchez
TRAGSA, c/ Velázquez 36, Madrid, Spain.

Antoni Margalida*
Bearded Vulture Study and Protection Group, Apdo. 43. E-25520 El Pont de Suert, Lleida, Spain.

Antonio Aranda
Junta de Castilla-La Mancha, c/ Pintor Matías Moreno, 4, 45071 Toledo, Spain.

Luis Prada
Consejería de Medio Ambiente, c/ Princesa 3, Madrid 28008, Spain.

Javier Caldera
Junta de Extremadura, Apdo. Correos 7, 10181, Sierra de Fuentes, Cáceres, Spain.

José Ignacio Molina
Junta de Castilla y León, c/ Rigoberto Cortejoso 14, 47071 Valladolid, Spain.

* Author for correspondence; e-mail: margalida@inf.entorno.es

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