
The Near Extinction of Two Large European Predators: Super Specialists Pay a Price

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Abstract: *Despite recovery plans, the Spanish Imperial Eagle (Aquila adalberti) and the Iberian lynx (Lynx pardinus) are in danger of extinction. These two flagship species tend to occur in pristine Mediterranean forests, and both prey preferentially on the rabbit (Oryctologus cuniculus). Spanish lynxes and eagles have sister species in continental Europe, the Eurasian lynx (Lynx europaeus) and the Eastern Imperial Eagle (A. heliaca), respectively. Recent genetic evidence indicates that these two pairs of species started to diverge from their ancestor species slightly less than 1 million years ago, when the longest-lasting Pleistocene glaciations covered Europe. We hypothesize that the Iberian lynx and the Spanish Imperial Eagle emerged as separate species in the Pleistocene refugia of southern Spain, where they hunted yet another locally evolved species, the rabbit, on which they have become dependent for survival. Two large predators that emerged at the same time may go extinct simultaneously because of their inability to shift to alternative prey. Many other relict species, including numerous species from oceanic islands, have naturally small populations because of evolutionary constraints and are permanently threatened with extinction. Recovery plans aimed at putting these species out of danger are unrealistic, as their populations are and have been chronically scarce. We suggest that what these species need are maintenance plans designed to buffer population declines due to either stochastic or human-induced events. A metaphor for this would be "emergency care units" for conservation.*

La Cuasi Extinción de Dos Grandes Depredadores Europeos Mayores: los Súper Especialistas Pagan el Precio

Resumen: *A pesar de planes de recuperación, el Águila Imperial Española (Aquila adalberti) y el lince Ibérico (Lynx pardinus) se encuentran en peligro de extinción. Estas dos especies bandera tienden a ocurrir en bosques mediterráneos prístinos y preferentemente depredan al conejo (Oryctologus cuniculus). Los linceos y águilas españoles tienen especies hermanas en Europa continental, el linco Euroasiático (Lynx europaeus) y el águila Imperial Oriental (A. heliaca), respectivamente. Evidencia genética reciente indica que estos dos pares de especies comenzaron a divergir de su especie ancestral hace poco menos de 1 millón de años, cuando las glaciaciones más prolongadas del Pleistoceno cubrían Europa. Nuestra hipótesis es que el linco ibérico y el águila imperial española emergieron como especies separadas en refugios pleistocenos del sur de España, donde cazaban a otra especie que evolucionó localmente, el conejo, de la que se han vuelto dependientes para sobrevivir. Dos depredadores grandes que emergieron al mismo tiempo pueden extinguirse simultáneamente debido a su incapacidad de cambiar a presas alternativas. Muchas otras especies relicto, incluyendo numerosas especies de islas oceánicas, tienen poblaciones naturalmente pequeñas debido a restricciones evolutivas y están permanentemente amenazadas de extinción. Los planes de recuperación enfocados en poner a estas especies fuera de riesgo, son calistas, ya que las poblaciones son y han sido crónicamente escasas. Sugerimos que lo que necesitan estas especies son planes de conservación diseñados para amortiguar declives poblacionales debidos a eventos estocásticos o inducidos por humanos. Una metáfora para esto sería "unidades de cuidado de emergencia" para la conservación.*

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Introduction

Two flagship species for conservation in Europe, the Spanish Imperial Eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*), are on the brink of extinction (Delibes et al. 2000; Ferrer 2001), despite sustained management efforts in the last two decades. The Spanish Imperial Eagle is one of the most endangered birds of prey in the world (Collar & Andrew 1988), with <400 individuals left (Ferrer 2001). The Iberian lynx (*Lynx pardinus*), the largest wild cat in southern Europe, is one of the world's most endangered felids (Nowell & Jackson 1996), now numbering <500 individuals (Delibes et al. 2000).

Iberian lynxes and imperial eagles are only found in the Mediterranean forests and scrublands of southwestern Spain. In sharp contrast, their nearest relatives in continental Eurasia, of which the Iberian species were considered local races until recently, occur in a variety of habitats—including steppes for the eagle and boreal forests for the lynx—and across vast distribution ranges, and their populations are relatively healthy (Fig. 1). There are over 40,000 Eurasian lynx (*L. lynx*) and over 5000 Eastern Imperial Eagles (*A. heliaca*) in existence. Eurasian lynx populations are even expanding in some countries, where hunting quotas are allowed for this species (Breitenmoser et al. 2000). The Eastern Imperial Eagle has also recently increased its numbers in the western part of its range after being protected by law (Horvath et al. 2001).

The critical conservation status of Iberian lynxes and imperial eagles has been attributed to human persecution and habitat loss (Collar & Andrew 1988; Nowell & Jackson 1996). Raptors and mammalian carnivores were persecuted in Spain, and rewards were offered by the government for their eradication from the 1950s until the early 1970s, when protective laws were passed for all raptors and some carnivores, including the lynx. Today a significant proportion of lynx and imperial eagle populations are within nature reserves, and they have benefited from multimillion dollar Life Projects cofinanced by the European Union and the Spanish government. These projects aimed to boost population sizes, but they did not succeed. These two species have lost a significant portion of their historical distribution ranges in just one century, which, to begin with, were the smallest among the species in their respective genera. These facts, along with the comparatively better situation of Eurasian lynxes and Eastern Imperial Eagles, led us to explore whether the conditions in which these species evolved could be a constraint depressing their persistence time, a possibility that has not been taken into account.

Predatorial Sister Species

The two imperial eagle species existing in the world present similar adult plumage patterns, differing only in

the small feathers covering the edge of the wing. However, the markings of juveniles are noticeably different (Ferrer 2001). The species have similar diets (with a preference for medium-sized ground mammals), and the main aspects of their breeding biology are also similar (e.g., nests in trees, clutch sizes of two to four eggs). The Eurasian and Iberian lynxes differ in the dotting patterns of their fur, and the former is larger, but they share numerous physical characteristics. Both occurred in central Europe during the Pleistocene (Kurten 1968, 1978), but they may never have had significantly overlapping geographic ranges (Breitenmoser et al. 2000). Now, the distribution areas of both pairs of sister species are separated by a large expanse of land in Central Europe (Fig. 1), an area covered by temperate forests before humanization took place (Moreau 1955). The ranges of the eastern species are, however, orders of magnitude larger than those of their Iberian counterparts.

Dating the Origin of Spanish Eagles and Lynxes by Molecular Means

Molecular evidence supports the full-species status of the Spanish Imperial Eagle in relation to the Eastern Imperial Eagle (Seibold et al. 1995). The same study, based on the sequencing of 1026 base pairs of the mitochondrial cytochrome *b* gene, permits the dating of the split of the two species. They differ in 1.7–1.8% of their nucleotide sequences. Assuming a mutation rate of 2.0% per million years for avian mitochondrial genes (Shields & Helmy-Bychowski 1988), a separation between the lineages of the Spanish Imperial Eagle and the Eastern Imperial Eagle may have occurred 850,000–900,000 years ago.

The analysis of three mitochondrial gene fragments (ATP-8 and two control region segments) of the species in the lynx genus and related felid species has confirmed the separate taxonomic status of the Iberian lynx (Beltrán et al. 1996). Eurasian, Canadian, and Iberian lynxes may have diverged into monophyletic lineages around 835,000–1,130,000 years ago (W. E. Johnson, J. A. Godoy, F. Palomares, M. Delibes, M. Fernandes, E. Revilla, and S. J. O'Brien, unpublished data).

Pleistocene Glaciations

Considering the coincidental dates for the origin of both imperial eagles and Iberian lynxes as separate species, was there a special event in the area at the time? The relationship between two oxygen isotopes found in marine sediments (i.e., the marine isotope stage 24) indicates that a cold period was found in strata 980,000 years old (Mix et al. 1995). It was the starting point of the first glacial period of the last million years in the Quaternary, and it lasted over 100,000 years (Tallis 1990; Raymo 1998).

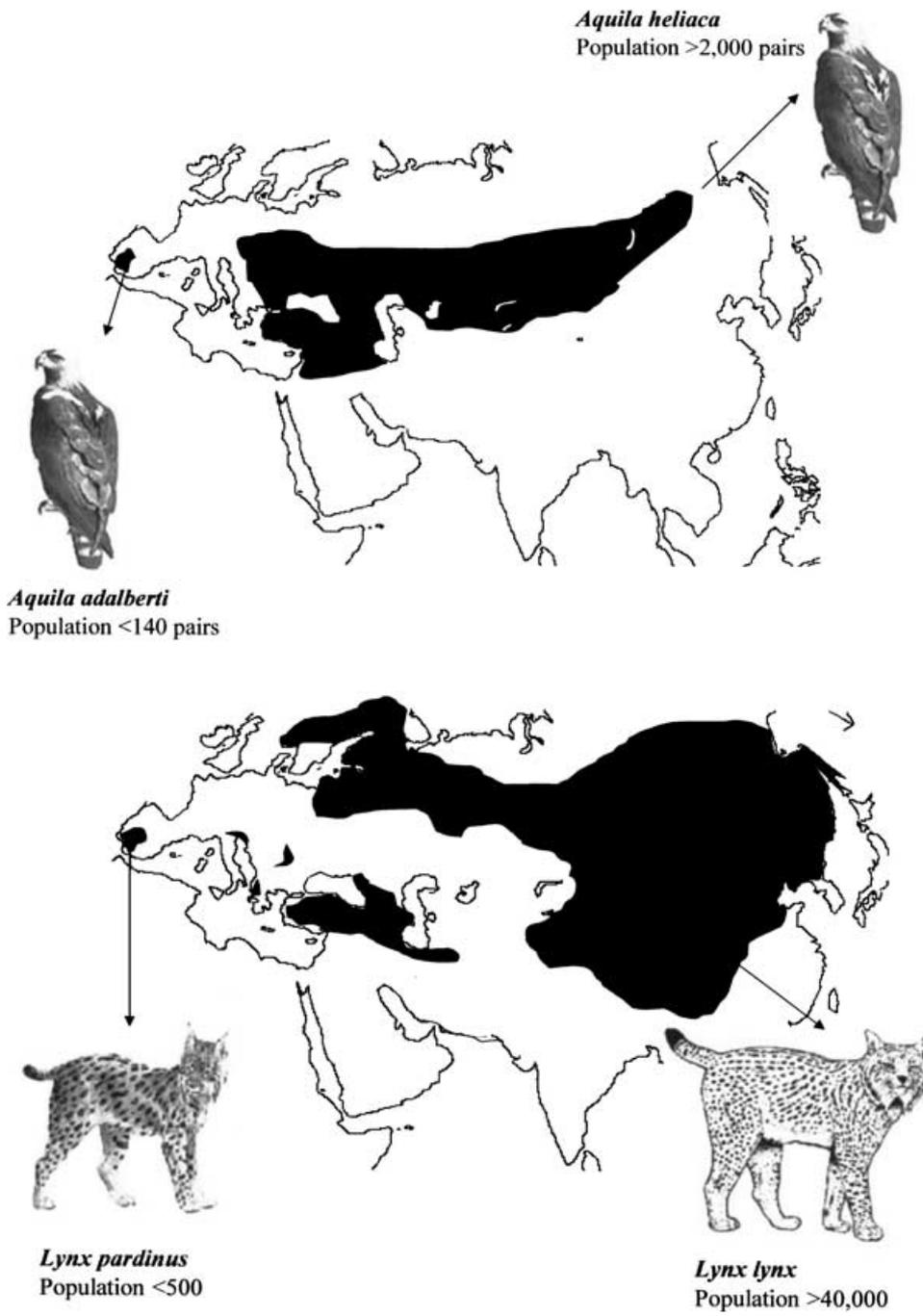


Figure 1. Current world distribution and population sizes of imperial eagles (*Aquila heliaca* and *A. adalberti*) and lynxes (*Lynx pardinus* and *L. lynx*).

Although the position of ice margins and vegetation in general in Eurasia are not known accurately for that time because of the absence of terrestrial records, we have an idea for the last glacial maximum that occurred approximately 18,000 years ago. According to pollen records, the Iberian Peninsula had very little closed woody vegetation during that last recorded glaciation. The predominant landscape was arid, semi-desert steppe, similar to that of the Pamirs of today's southern Russia, with sparse vegetation cover and scattered trees (Moreau 1955) equivalent to current habitat for the Eastern Imperial Eagle.

Fossil records of small and medium-sized land mammals (mammals now typical in central Eurasian steppes) can be found in Spanish Pleistocene deposits around 980,000 years old (Altuna 1972; Cuenca-Bescos et al. 2001). Among them are several species that are the ancestors of the current typical prey for *A. heliaca*, such as hamsters (*Allocricetus* spp.), dormice (*Pliomys* spp.), and *L. lynx*, including mountain hares (*Lepus timidus*) (Huthammer & Aaris-Sørensen 1998). These fossil records suggest large-scale movements on the part of several species from the steppes in central Eurasia to southwestern Europe.

It is reasonable to assume that specialized predators (i.e., eagles and lynxes) followed their basic prey. Fossil records of small and medium-sized steppe mammals can be found in few strata in the Iberian Peninsula, however, suggesting that they lived in this area for only a short period.

The Iberian Peninsula, as with Italy and Greece, the two other southern peninsulas of Europe, was a major faunal refugium in the ice ages of the Pleistocene. These refugia resulted in the evolution of numerous genetically distinct taxa and greatly contributed to the current biodiversity of the Palearctic (Hewitt 1999).

Wild Rabbit as Ideal Prey for Eagles and Lynxes

The earliest known specimen of *Oryctolagus*, the wild rabbit, was found in 5-million-year-old strata (Rogers et al. 1994) in Salobreña, Spain. *Oryctolagus laynensis*, a direct ancestor of today's rabbits, inhabited the Iberian Peninsula 2.5 million years ago (Rogers et al. 1994). At present, there is a high polymorphism of mitochondrial DNA in southern Spain, decreasing toward the north, suggesting a southern Spanish origin for this rabbit (Biju-Duval et al. 1991). At the beginning of the mid-Pleistocene, therefore, when the ancestor of lynxes and eagles, predators specialized on medium-sized steppe mammals, arrived in the Iberian Peninsula, the wild rabbit was already living there.

European wild rabbits, weighing 0.7–3 kg (mammal body masses hereafter from Schilling et al. 1983), today represent more than 88% of the diet of both the Spanish Imperial Eagle and the Iberian lynx (Delibes et al. 2000; Ferrer 2001). Seventy-eight percent of the prey of the Eastern Imperial Eagle are land mammals smaller than the rabbit, such as lemmings (*Lemmus lemmus*, 15–130 g), hamsters (*Cricetus cricetus*, 150–400 g), and susliks (*Citellus citellus*, 200–300 g) (Del Hoyo et al. 1994). The Spanish Imperial Eagle is marginally larger than the Eastern Imperial Eagle (mean tail length in mm: *A. adalberti* male, 287 g; female, 303 g; *A. heliaca* male, 274 g; female, 290 g) (Hiraldo et al. 1976). However, the Iberian lynx (8–15 kg) (Delibes et al. 2000) is smaller than the Eurasian lynx (12–35 kg) (Breitenmoser 2000), which mainly hunts hares (1.7–5.8 kg) and roe deer (*Capreolus capreolus*, 15–35 kg), animals much larger than the Eurasian wild rabbit.

During the interglacial periods, Central Europe was covered by temperate forests (Moreau 1955; Tallis 1990) mainly inhabited by tree-dwelling squirrels (*Sciurus* spp.), as remaining forest fragments are today (Gurnell 1987). Lacking both adequate hunting habitat and prey elsewhere, lynxes and imperial eagles seem to have stayed in the Iberian Peninsula, making a living on the wild rabbit. Concurrently, their Asian counterparts, the ancestors of today's Eurasian lynx and the Eastern Imperial Eagle, returned from their refugia—presumably located below the

range limits of the permanent ice cover during glaciations (e.g., in Eastern Africa and the Indian subcontinent)—to their former breeding grounds in Eastern Europe and Asian steppes, but they were deterred by the temperate forests of central Europe. It is therefore possible that western and eastern lynx and eagle populations have not regained contact after their initial separation about 1 million years ago.

The Common Fate of Spanish Lynxes and Eagles

Rabbits, now found over most of Western Europe (Schilling et al. 1983), were until at least 10,000 years ago confined to the Iberian Peninsula and southern France (Rogers et al. 1994). Being top predators, lynxes and imperial eagles possibly would not have reached large population densities there (Colinvaux 1978). Their extreme dietary adaptations made them prisoners of the rabbit in its formerly small distribution area. It has been argued that both lynxes and eagles are on the verge of extinction due to human pressures of overhunting and habitat destruction and fragmentation. But relict species living in isolated and small areas are naturally extinction-prone (Pimm et al. 1993). Therefore, the expected persistence time of chronically small populations, such as those of both Spanish lynxes and eagles, is short in any case (see, for example, the extinction-prone species concept described by Primack [2002]), and the maintenance of current populations in their precarious states is an enormous challenge that will demand continuous action from wildlife managers. Even if the highest densities in all potential habitats were reached for both species, their populations would still be relatively small and subject to genetic and demographic hazards.

Refugial genomes are well known in Europe, but most of the models of postglacial colonization that have been studied so far have generated subspecific diversity with hybrid zones, enriching genetic variability overall for those species (Hewitt 1999). The model we describe produced somewhat different results because the relict predators of the Iberian Peninsula have become genuine species with low genetic variability (Negro & Hiraldo 1994; Beltrán 1996). Rabbit populations in Spain have crashed in the late 1950s due to two successive viral diseases—mixomatosis and hemorrhagic fever—accidentally introduced by humans (Villafuerte et al. 1994, 1995), but lynxes and eagles were already rare before this (Delibes et al. 2000; Ferrer 2001). If anything, the recent scarcity of rabbits demonstrates the inability of both eagles and lynxes to shift to alternative prey. These two species evolved over the same period, their populations were never abundant, and both may go extinct due to an ecological trap: their extreme and apparently irreversible “adaptation” to a rabbit prey base.

To delay extirpation of these species, a duty for conservation scientists and managers alike, we propose the joint management of the two species, an obvious step that has not been attempted. A coordinated plan focusing on rabbit populations and the preservation of Mediterranean scrub areas in the Iberian Peninsula is thus imperative.

Conclusions

Eagles and lynxes teach us a lesson that may apply to other relict species. Many, including numerous species from oceanic islands, have naturally small populations as a result of evolutionary constraints and are permanently threatened with extinction. Recovery plans aimed at getting those species off the endangered list are doomed to fail because their populations are and have been chronically scarce. The areas of the Iberian Peninsula providing habitat for a high rabbit density, around one-third of the peninsula (Villafuerte et al. 1998), are not large enough to accommodate healthy populations with negligible extinction risk of either lynxes or imperial eagles. The current rabbit range, even after successive viral diseases, is not very different from the former range, because environmental factors such as climatic conditions and soil structure are the main limits on rabbit distribution (Villafuerte et al. 1998). In addition, a failure to protect imperial eagles and lynxes may generate a negative perception of conservation efforts by the public, particularly if these efforts are compared with the success stories of large vertebrates in Spain, such as the Griffon Vulture (*Gyps fulvus*), which has tripled its population in two decades of protection and now numbers 17,500 breeding pairs (Tella 2001).

What relict species such as the Spanish Imperial Eagle and the Iberian lynx need are maintenance plans designed to buffer population declines due either to stochastic events or human causes. We need "emergency care units" that are prepared to save species from immediate extinction through a variety of management options. And we should be aware that these options may vary from one year to the next.

Potential management actions to be undertaken depend on the results of continuous monitoring of individuals and populations. This monitoring, aimed at providing early warnings of population decline (Balbontín et al. 2003, Ferrer et al. 2003), should include demographic, genetic, behavioral, nutritional, and epidemiological aspects. If food scarcity is a problem and likely to affect reproduction, a food supplementation scheme should be implemented. If a given subpopulation experiences a sudden decline due to disease, inbreeding depression, or natural catastrophes, it should be reinforced with healthy individuals translocated from other areas. The same procedure may be useful to restore skewness in the sex ratio or age structure of a population. For species suffering

from predation, at least during part of their life cycles, predators should be controlled or eliminated. Competition or any other interaction with other species should also be investigated. Depending on the type of interaction, some symbiotic or mutualistic species should be favored while competitors are locally depressed.

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