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The Iberian lynx – rescue of an iconic species

lynxconnect

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The long and winding road from Andújar – a personal introduction

In the year 2002, an international seminar took place in Andújar in southern Spain to discuss how to save the Iberian lynx *Lynx pardinus* from extinction. There was no consensus over conservation concepts then, and the cooperation between scientists and conservationists, but also between the different political and administrative units was limited. A following series of consultative visits and meetings with various key institutions and experts has allowed to shape a strategy based on the benchmarks of the IUCN Red List categories. The first phase included establishing an ex situ population to prevent total extinction, the second was to expand the population in the Sierra Morena through translocation and release of captive-bred lynx that allowed to down-list the species to Endangered in 2015, and the third to start reintroduction projects beyond the Sierra Morena, what allowed now to down-list the Iberian lynx to Vulnerable.

This is a rather personal introduction to this Special Issue of Cat News on the Iberian lynx, but considering how important the Iberian lynx was in the early years of our co-chairmanship of the IUCN SSC Cat Specialist Group and for the development of our understanding of strategic planning in species conservation, such an approach seems to be justified. It gives us also the opportunity to honour some friends who are no longer involved in this Special Issue, but have played a key role in the struggle for and over the best way to save this species from extinction.

Meaningful conservation is best informed by facts and scientific insight – and the IUCN Species Survival Commission SSC lives up to this theorem –, but we all know that decisions are more often the result of gut feeling than brain power. In so far, it was fortunate for the Iberian lynx that the Spanish cuisine treated our guts so well in all these years.

The Special Issue is published to remember the long way from the first – and very depressing – international meeting on the conservation of the Iberian lynx in Andújar in 2002 up to this moment, when we celebrate the second down-listing of this charismatic felid within less than ten years. This makes the Iberian lynx rescue the most successful cat conservation project, possibly one of the most successful projects for saving a mammal species from extinction. Many of the strategic approaches applied for the conservation of the Iberian lynx were already available as concepts 25 years ago; but to our knowledge, they were never applied as consistently and comprehensively as for the rescue of the Iberian lynx. This was possible because of the incredible dedication of many scientists and conservationists, the lasting commitment from the authorities in charge, and the long-term financial support from the European Union and other donors (see e.g. López et al. 2024a, Perez de Ayala et al. 2024, Serra et al. 2024 ; Chapters 4, 9 and 5 of this Special Issue respectively). However, what now retrospectively may look like a thoughtful plan was indeed the result of many hefty and controversial disputes and lasting disagreements.

In summer 1982, a master student from Switzerland had a poster on the reintroduction of the Eurasian lynx in the Alps at the 2nd International Theriological Congress in Helsinki. Next to him was another young man with a poster on the Iberian lynx in southern Spain. They were both a bit wary and not all that comfortable with English, but they had an intensive discussion on lynx ecology in French, and they found that the two kinds of lynx were so different that they should clearly not be considered the same species. This was then still debated. In the first version of the IUCN Red List, the Iberian lynx was listed as *Felis lynx pardina* and considered "very rare and believed to be decreasing in number". The Swiss and the Spanish decided there in Helsinki that "radio telemetry" – a mystical word back then – would be the way to study these elusive cats.

In 1986, we visited southern Spain, especially lynx ranges in the Sierra Morena (Fig. 1), and then Miguel Delibes and his research group in Sevilla. His research group had now equipped several lynx with radio collars, and we saw our first Iberian lynx – for two seconds when it crossed one of the fire strips in the dense shrub vegetation in the Doñana Biological Reserve within the National Park. The continuous research of Miguel Delibes and his team provided not only insight into the ecology and life history of the Iberian lynx, but also formed an important base for repeated and improved assessments (Rodríguez 2024; Chapter 3 of this Special Issue).

In 2002 the IUCN SSC Cat Specialist Group had to list *Lynx pardinus* – as the first cat species ever – as Critically Endangered (Cat Specialist Group 2002). The bad news was released during a meeting with governmental, scientific, and private conservation organisations in Andújar (Figs 2, 3). During the meeting, our colleagues referred repeatedly to the "Spanish lynx", and we insisted that it should be called the "Iberian lynx". The very dedicated delegate of the environmental department of the region, however thought it should be called the "Andalusian lynx". She was right in so far that only two population nuclei had survived, one in the Sierra Morena of Andújar and one in the Doñana National Park.

In the early 1990s, Rodriguez and Delibes (1992) estimated the Iberian lynx to number some 1,100 individuals in 48 patches. The first robust camera trapping survey across the entire assumed range revealed that only two of these nuclei were still extant, with 53

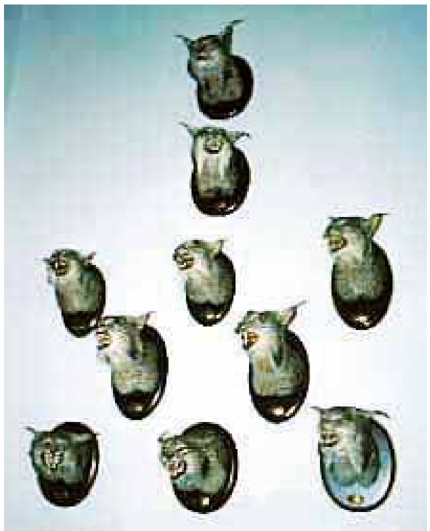

Fig. 1. Iberian lynx trophies of a private collection photographed in 1987. Although the lynx has been granted legal protection since the 1960s, illegal hunting and accidental killing in traps set for other predators or rabbits continued to be a major cause of mortality until the conservation campaign improved public awareness in the late 1990s.

lynx in Andújar-Cardeña and 41 in Doñana (see also Rodríguez 2024; Chapter 3 of this Special Issue).

The Department of the Environment of Andalucía had launched an action programme, but the mood during the first Andújar meeting was depressed, and the mistrust between the key actors was deep. The lack of any consensus with regard to the way forward risked to block further activities. The interest of the media was enormous, and all activities, leave alone mistakes made were publicly debated and condemned. In this situation, Eladio Fernandez Galiano, then Secretary of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), suggested to establish a task force, made up by the Large Carnivore Initiative for Europe (today an IUCN SSC Specialist Group), the Cat Specialist Group, and the Bern Convention Secretariat, to facilitate the development of a common understanding and help developing a conservation strategy. In the following two years, we visited Spain every three to six month to meet with key players such as Miguel Aymerich and Borja Heredia from the MIMAM (Spanish Ministry of the Environment in Madrid), Miguel Angel Simón Mata, Rafael Cadenas de Llano, and Javier Madrid Rojo from the Junta de Andalucía in Sevilla, with the scientists around Miguel Delibes, and with many colleagues from conservation NGOs such as WWF/Adena or the Fundacíon Biodiversidad to discuss strategic questions around the saving of the lynx. Besides the frequent bilateral and multilateral meetings, larger seminars were organised to discuss progresses and challenges and review the conservation strategy, e.g. 2004 in Cordoba, 2008 in Huelva, and 2010 again in Cordoba (López et al. 2024a; Chapter 4 of this Special Issue).

There was consensus from the start on the importance to halt any further decline of the two remnant populations and their close surveillance (Rodríguez 2024; Chapter 3 of this Special Issue), including genetic monitoring (Godoy et al. 2024; Chapter 6 of this Special Issue). The general goal that the Iberian lynx must be rescued was also agreed, but the proposed interventions to reach this goal were controversially debated both on the tactical and strategic level. Key elements were threat reduction (e.g. prevention of illegal killings and road mortalities) and the increase of the rabbit *Oryctolagus cuniculus* density, which is the staple food of Iberian lynx, but strongly affected by disease (see also Garrote et al. 2024a, Pérez de Ayala et al. 2024; Chapters 7 and 9 of this Special Issue, respectively). Working on rabbits was challenging, as a considerable part of the lynx area in the Sierra Morena was private land used for extensive ungulate hunting.

The strategic key question was the level of interventions needed for the rescue of the Iberian lynx. Would protection and active conservation (e.g. fostering local rabbit density) of the two remnant populations alone allow saving the species, or would reintroduction projects be required? Considering the isolation of the Doñana population, which is surrounded by intensive agricultural lands, and the unsecure future of the Andújar population under the constant threat of disease outbreaks in the rabbits, we recommended to safeguard *Lynx pardinus* in captivity and to re-establish, as soon as ever possible, additional lynx population nuclei. This required a spatial strategy for the reintroduction and the build-up of an ex situ programme that could serve as a source population.

Already in 1992, the El Acebuche Breeding Centre had been established in the Doñana National Park, but breeding of Iberian lynx started only after an agreement between the Ministry of Environment MIMAM and the Department of Environment of the Junta de Andalucía was signed in 2003, and Astrid Vargas was hired as director of the conservation breeding programme (Programa de Conservación ex-situ del Lince Ibérico). In spite of the fact that it faced many challenges and some serious crisis in the early years (see various articles in Vargas et al. 2009), the conservation breeding programme became a central part of the rescue programme. This was not at least possible thanks to the great support the programme received from the international scientific community[1]. From the first ungainly trials at Acebuche in the 1990s, the programme has evolved into the largest and most successful conservation breeding programme for a threatened cat (Serra et al. 2024; Chapter 5 of this Special Issue).

The spatial strategy developed for the recovery and reintroduction needed to meet several preconditions: From a biological point of view, any newly founded population should be far enough from the remnant nuclei to minimise the risk to be affected by a rabbit disease outbreak in these populations, but still close enough and connected through habitat corridors to permit dispersing subadult lynx to reach a neighbouring population. From a political point of view, it was important to make the "Andalusian lynx" as soon as possible the "Iberian lynx" again. The first releases in the frame of the first EU LIFE project took place in the Sierra Morena in Andalucía, allowing the best balance between distance and connectivity. But subsequent releases intended to include other regions of Spain and in Portugal. Finally, practical considerations required selecting reintroduction sites with sufficient rabbit densities and support from the local communities and

Fig. 2. Ernest faces at the first international seminar on the conservation of the Iberian lynx in Andújar in 2002. From the left: Miguel Delibes de Castro (CSIC), Javier Nicolás Guzmán (national coordinator lynx surveys), Pedro Sarmento (ICN Portugal), Miguel Aymerich (DGCINA-MIMAM), Margarida Lobes Fernandes (ICN Portugal), Eladio Fernandez Galiano (Council of Europe).

[1] One of the key scientists to help solving veterinary problems in the Iberian lynx conservation breeding was Hans Lutz (1946–2024), professor emeritus at the Zurich University. Hans passed away on 12 March 2024 and shall here be remembered for his work on feline diseases and his invaluable support of the Cat Specialist Group in health questions of cats.

private land owners. The first two reintroduction sites were Guadalmellato and Guarrizas, in the "not too close" vicinity of the remnant Andújar population, where the first lynx were released in 2009 (Simón et al. 2012; López et al. 2024a; Chapter 4 of this Special Issue).

Population goals and time frame were estimated literally according to the "Reverse the Red" principle: What would it take to down-list from Critically Endangered to Endangered (≥250 mature individuals) and then to Vulnerable (≥1,000 mature individuals)? Based on an assumed density and reproduction rate, and the expected number of lynx to be made available from the ex situ source population, the area and time span needed to reach these goals were estimated (López et al. 2024a; Chapter 4 of this Special Issue). Indeed, both goals were reached earlier than expected. *Lynx pardinus* was down-listed to Endangered in 2015 (Rodríguez & Calzada 2015) and to Vulnerable in 2023 (Rodríguez 2024a; Rodríguez 2024b; Chapter 3 of this Special Issue). In 2024, the population has reached the benchmark of 2000 individuals.

The rescue of the Iberian lynx had, beyond all conservation lessons learnt, also a considerable political dimension. The fate of this medium-sized felid triggered an enormous media interest on the Iberian Peninsula, but also across Europe and world-wide. Important decision makers in conservation in Sevilla, Madrid and Lisbon, but also in Strasbourg, Brussels and Gland agreed that such a charismatic flagship species cannot go extinct in Western Europe at the beginning of the 21st century. Of course, the political support was never unanimous. In Andalucía, where the dedication of the conservation authority was steadfast, illegal strawberry fields were nevertheless tolerated to encroach more and more into the lynx habitats west of Doñana National Park, and Portugal had let the Iberian lynx go extinct in the late 1990s and had to be "invited" by the European Commission to reintroduce the cat as a green compensation for a hydropower project co-financed by the EU. But all in all, the support from the media, the public, and the politicians was large, enabling also the considerable financial support needed. In an early stage of the strategic planning, we once came up with a rough estimation of the costs to down-list the Iberian lynx from Critically Endangered to Endangered, based on the area to be resettled and the average costs then estimated per km²: 100 million Euro. Participants in that meeting were shocked. Only

Fig. 3. Panellists at the Andújar seminar (cont.). From left: Urs Breitenmoser (IUCN), Miguel Angel Simón Mata (Junta de Andalucía), Borja Heredia Armada (DGCONA-MIMAM), Eladio Fernandez Galiano (Council of Europe), Jesús Cobo Anula (Adena/WWF).

Miguel Aymerich from the MIMAM said: "So what – this is only about 10 km of our new high-speed train." Assumedly, most citizen would agree that saving a species from extinction is worth 10 km of a railroad track.

The total costs for saving the Iberian lynx have never been evaluated. However, the EU LIFE NATURE projects coordinated by the Junta de Andalucía (but not restricted to Andalucía) sum up to some 90 million Euro for the years 2002–2025, of which about 50% was contributed by the European Union (F. J. Salcedo, pers. comm). There were related LIFE projects, smaller conservation projects implemented by NGOs, and costs for the conservation breeding centres that are not included in this sum. Saving a carnivore species that requires an enormous area for a viable population in Western Europe is not cheap. But on the other hand, all this funding created jobs, perspectives and hope in Spain and Portugal, and this during a period of economic hardship after the turn of the century, when the unemployment rate

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo T. Céron).

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo M. P. Lara).

among young people in Andalucía reached up to 40%.

The Iberian lynx conservation project in Andalucía and indeed across the Iberian Peninsula, had an enormous echo and this public interest has facilitated many enabling factors. It nowadays seems common sense to implement conservation measures not against, but with the integration of local stakeholders and the people. But 25 years ago, this was not standard in southern Spain. However, the charisma of the Iberian lynx and its precarious destiny has touched the people from the young student to the large landowner. This has led to a societal pact in Andalucía and opened the door for agreements with the landowners and other conservation activities, which had not yet been possible when we visited Sierra Morena and Doñana for the first time in 1986. This Special Issue of Cat News was produced to celebrate the down-listing of *Lynx pardinus* to Vulnerable. The articles of this issue review the road from Andújar, which was winding indeed, but all in all not that long. Only twenty years ago, we were fearing that the Iberian lynx would go extinct, and now we are planning to remove it from the threatened categories in the IUCN Red List for good (Garrote et al. 2024b; Chapter 10 of this Special Issue). One novel instrument to do this is the Green Status of Species assessment, that has been performed for the Iberian lynx for the first time (Grace & Carlton 2024; Chapter 8 of this Special Issue). The Iberian lynx is a vulnerable species per se. With a rather restricted original distribution range (López et al. 2024a; Chapter 2 of this Special Issue) and an even more restricted potential recovery area (Grace & Carlton 2024; Chapter 8 of this Special Issue), it will remain a species that we need to observe and conserve. But its significance for the ecosystems of the Iberian Peninsula is undisputed, and its role as flagship species for conservation has been demonstrated in the past 25 years.

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Historical distribution of the Iberian lynx

During the Pleistocene and Holocene, the geographical range of *Lynx pardinus* included the Iberian Peninsula, southern France and possibly the Italian Peninsula. In historic times, the Iberian lynx distribution was restricted to the dry-summer-climate areas of the Iberian Peninsula. The distribution range between the 16th and the 20th centuries inferred from historiography was mainly restricted to the south-western quadrant of the Iberian Peninsula with isolated nuclei elsewhere. The Central Range, Montes de Toledo and eastern Sierra Morena were the larger populations. Both historiography studies and genomic analyses coincide determining a dramatic population bottleneck during the 17th century, probably linked to an increased human pressure. A population increase followed from the 18th to the 19th centuries, as a consequence of a lower anthropogenic persecution due to a rural exodus. At the turn of the 20th century, the species was almost absent in northern and eastern Iberia, but was still abundant in the southwestern quadrant. The depletion continued, and, during the second half of the century, two additional threats hit the Iberian lynx population: the "Extinction Councils" and the decrease of rabbit populations due to diseases. Despite being legally protected since the 60s, the depletion continued and many population nuclei vanished during the 1970s and the 1980s. Only eastern Sierra Morena and Doñana display records after 1993. By 2000, a survey based on photo-trapping and molecular analysis of scats found that only ca. 95 individuals remained alive in two secluded areas of southern Spain: Andújar-Cardeña in eastern Sierra Morena and Doñana. The species was found to be extinct in Portugal.

According to DNA analyses, the Iberian lynx diverged around 1.53–1.68 million years ago (Johnson et al. 2004), in the lowland glacial refuges of southwestern Europe (Abascal et al. 2016, Jianzuo et al. 2022). Its origin likely occurred in the Iberian Peninsula following the intense glacial stages MIS 66–64, subsequent to the isolation of local populations of the Issoire lynx *Lynx issiodorensis*. Consequently, the speciation of the Iberian lynx is related to the faunal turnover that occurred between the Middle and Late Villafranchian, considered to be one of the major changes in the European macromammal fauna (Boscaini et al. 2015). In its evolution, the species adapted its body size to the consumption of the native wild rabbit *Oryctolagus cuniculus*, probably the most abundant prey species in the area (Naff & Craig 2012, Boscaini et al. 2016, Petrescu-Mag et al. 2019).

The Iberian lynx population experienced limited gene flow with related lynx species during interglacial periods (Abascal et al. 2016), including a proven interspecies admixture with the Eurasian lynx *Lynx lynx* during the Holocene (Lucena-Pérez et al. 2024). Paleontological records show that the Iberian lynx was distributed throughout southwestern Europe during the late Pleistocene, including the Iberian and the Italian peninsulas (Mecozzi et al. 2021). In the Holocene, its distribution has been restricted to the Iberian Peninsula and southern France, whereas in historic times it has been restricted just to the Iberian Peninsula (Villalpando-Moreno 2020). Genomic analyses showed three main bottlenecks since its divergence: the first one 47,000 years ago, the second one 315 years ago and the last one during the 20th century (Abascal et al. 2016). The first one could be attributed to changes in climate and environment due to the Würm glaciation. The second one was probably due to direct human alteration of the ecosystems in a period that was marked by a distinct demographic shift, featuring rapid human population growth across Europe. This led to the increased persecution and displacement of large carnivores, as well as widespread deforestation and the expansion of agricultural land use (Ellis et al. 2010). The third one was also attributed to direct human actions (i.e. changes in habitat and land uses, anthropogenic mortality and human-carried rabbit diseases (Abascal et al. 2016, Villalpando-Moreno 2020), which almost led to the extinction of the species only twenty years ago.

Here, we use paleontological data, historiography and contemporary data to review the Iberian lynx distribution during the Pleistocene and Holocene, and the last 500 years. To investigate the period between 16th and 19th centuries, we used information on historic reports, taxidermic remains, genome studies and complementary published information. Regarding the 20th century, we use published data to re-construct the story of the almost extirpation of the population. Special attention was paid to the difference in the methodologies of the published population estimations, since some methods, such as polls, tend to overestimate actual populations while others, such as looking at hunting trophies, trend to underestimate them. Given that the Eurasian lynx was also living in Northern Iberian Peninsula during the study period (Jiménez-Clavero 2018), some historic data are difficult to assign to either of the two species.

The areas of Iberian lynx occurrence during the last 500 years can be grouped in 14 populations: 1) Central Range (composed of Sierra de Gata-Malcata, Sierra de Gredos and Sierra de Guadarrama), 2) Montes de Toledo (composed of many small chains of hills in the north of the Southern Plateau), 3) E Sierra Morena (composed of Guadalmellato, Andújar-Cardeña, Guarrizas, Campo de Calatrava, Campo de Montiel and Sierra de Alcudia), 4) Central Sierra Morena (composed of Sierra Norte and Hornachuelos), 5) W Sierra Morena (composed of Sierra de Aracena, Contiendas-Contendas and Moura-Barrancos), 6) Far-E Sierra Morena (including Sierra de Alcaraz), 7) Baetic Mountains (composed by Sierras Subbéticas and Sierras Béticas), 8) Doñana (composed by Guadalquivir delta lowlands and Aljarafe), 9) Algarve (composed of Serra de Monchique, Serra do Caldeirão and Alcoutim), 10) Vale do Sado, 11) Sierra de San Pedro, 12) Guadiana Valley, 13) Sierra de Santo Domingo and 14) Muntanyes de Benifassà.

Distribution range of the Iberian lynx during the Pleistocene and Holocene

Since its appearance and throughout the Early Pleistocene, the Iberian lynx was restricted to the Iberian Peninsula (Fig. 1A). The oldest occurrence of *Lynx pardinus* has been reported in the Early Pleistocene cave of Avenc Marcel (Barcelona, Spain). The only available fossil from this site is a cranial fragment dated to approximately 1.6 million years ago (Boscaini et al. 2015), placing this

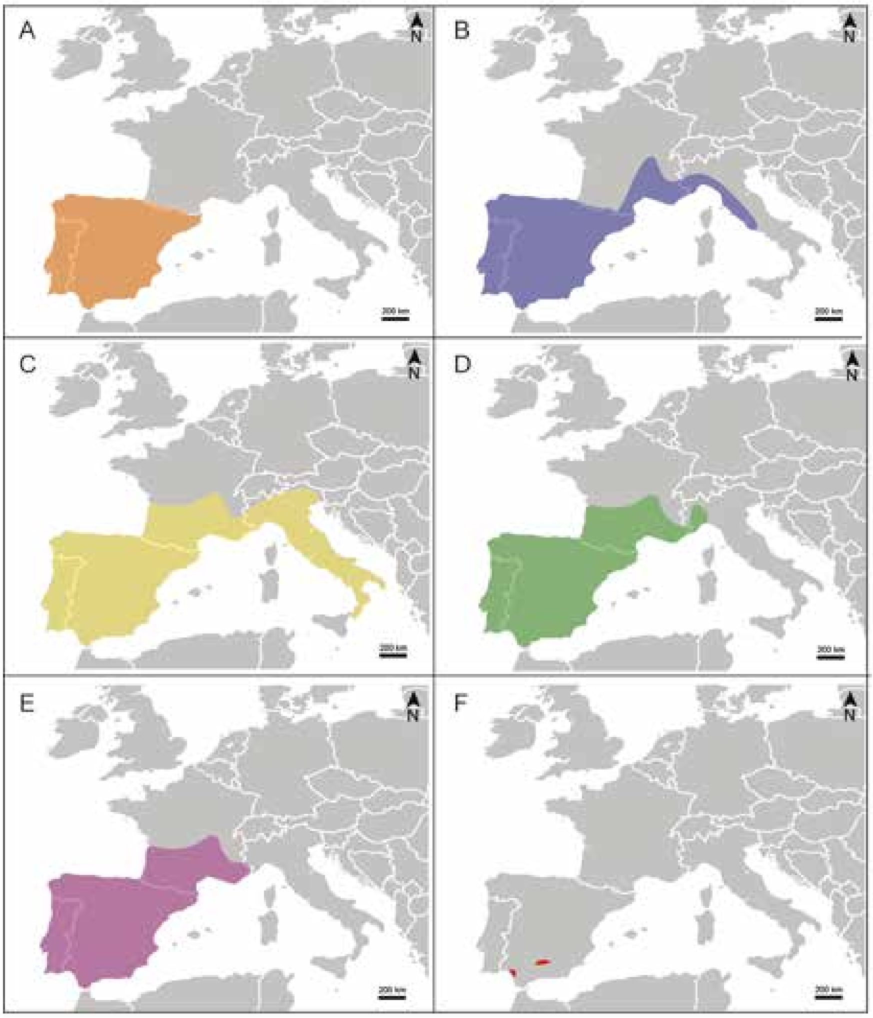

Fig. 1. Evolution of the geographical distribution of the Iberian lynx during the Pleistocene and Holocene. A) Distribution range during the late Early Pleistocene. B) Distribution range during the Middle Pleistocene. C) Distribution range around 40,000 years ago (Late Pleistocene). D) Distribution range around 18,500 years ago (latest Pleistocene). E) Distribution range around 4,000 years ago (Holocene). F) Distribution range in 2002.

specimen chronologically near the purported origin of the species (see Johnson et al. 2004). Subsequently, around 1.1 to 0.8 million years ago, fossil specimens attributed to the Iberian lynx have been found from the south to the north of the Iberian Peninsula, including the late Early Pleistocene sites of Quibas (south-eastern Spain), Vallparadís (north-eastern Spain), Cueva Victoria (south-eastern Spain), and Gran Dolina (northern Spain; Montoya et al. 1999, Madurell-Malapeira et al. 2012, Boscaini et al. 2016).

The Iberian lynx, currently restricted to the Iberian Peninsula, had a broader geographical distribution during the Middle-Late Pleistocene and Holocene, exceeding the limits of the Pyrenees (Tura-Poch et al. 2023). By the onset of the Middle Pleistocene, *Lynx pardinus* dispersed into southern France and Italy (Fig. 1B). Its distribution reached its maximum extent during the Late Pleistocene, approximately 40,000 years ago, when the primitive Iberian lynx spread to the southern latitudes of the Italian Peninsula (Ingarano site, Mecozzi et al. 2021; Figure 1C). The Iberian lynx was still present in northern Italy (Arene Candide site) by the latest Pleistocene, around 18,500 years ago (Rodríquez-Varela et al. 2015; Fig. 1D).

The contraction process of the Iberian lynx began at the end of the Late Pleistocene and continued throughout the Holocene. During the Holocene, the geographical range of *Lynx pardinus* declined until it became again restricted to the Iberian Peninsula, which likely acted as a refugium for the species (Mecozzi et al. 2021). In Italy, there are no Holocene records of the Iberian lynx, whereas in southern France, the species persisted until the beginning of the Iron Age (Vigne & Pascal 2003). For instance, the presence of this feline has been confirmed in Grotte Cabias (Gard, France) through molecular analyses, dating to approximately 4,000 years before present (Rodríguez-Varela et al. 2015; Fig. 1E). The most recent remains of this species beyond the Pyrenees have been found in archaeological sites located in the western margins of the Languedoc plains (Guilaine et al. 1986, Gascó et al. 1996). From then on, the distribution range of the Iberian lynx dramatically contracted, with the species being reduced to isolated populations in the southern Iberian Peninsula by the beginning of the 21st century (Fig. 1F).

At the end of the Pleistocene, the Iberian lynx may have contracted its range following the extinction of the European rabbit, alongside interspecific resource and habitat competition with the Eurasian lynx, which entered Europe during the Late Pleistocene (Mecozzi et al. 2021 and references therein). However, the presence of this species in France in historical times suggests that a shift in prey availability provoked a replacement of the Iberian by the Eurasian lynx in the region.

16th-17th centuries: bottleneck

Between 1500 and 1600, the main source for ecological information in Spain is *Relaciones Topográficas* of the Spanish king Philip II, statistic works mainly covering the Kingdom of Castille (Ortega-Rubio 1918). Here, Iberian lynx is referred to as *gato cerval, lobo cerbal,* or *gato montés*. It is quoted in Castille-La Mancha (Cabezarados, Chillón, Daimiel, Rostro, Cañada del Moral, Malagón, Puertollano and El Viso del Marqués in Ciudad Real; Velada Calera y Chozas, El Casar de Talavera, Cardiel de los Montes, Espinoso, Garvin, Menasalbas. Navalmoral, Los Navalmorales, Navahermosa, Saelices, Villanueva del Horcajo, Yébenes and El Viso de San Juan in Toledo; Alpera and Ballesteros de Calatrava in Albacete; Auñón, Bustares, Gacueña, Palmaces, Trillo, Uceda, Yebra and Yélamos de Yuso in Guadalajara; El Provencio in Cuenca), Madrid (Colmenar Viejo, Estremera and Perales), Extremadura (Castilblanco, Fresnedoso, Herrera del Duque, Santa Cruz de la Sierra, Villanueva de los Infantes, Belvís de la Jara, Berrocalejo, Brea, Corralrubio, Garrovillas, Granadilla de Cáceres, Guijo de Granada, Villar del Pedroso and El Bronco) and Andalusia (Beas and Orcera). Villegas & García (1976) and Gutierrez-Alba (2007) reported Iberian lynxes at Beas de Segura, Benatae, Hornos, Orcera, Segura de la Sierra and Chiclana de Segura. All these data can give a map of the situation between 1500 and 1600 (Fig. 2).

The 17th century is a stage where data about Iberian lynx become very scarce. It is absent in most significant works, such as *Origen y Dignidad de la Caça*, (Mateos-Ballesteros, 1634) and *Arte de la Ballestería y Montería* (Martínez de Espinar, 1644). Only a few lynx references exist from Central Range, Montes de Toledo, Doñana, E Sierra Morena and some isolated spots in the north (perhaps some confused with Eurasian lynx) in Galicia/El Bierzo, the Pyrenees and Alcubierre/Los Monegros (Clavero & Delibes 2013, Piñeiro-Maceiras 2013, Jiménez et al. 2018, Villalpando-Moreno 2020).

Available data suggest that a progressive depletion of Iberian lynx population took place between 1500 and 1625, up to the point of a near-extinction. Moreover, genomic studies have demonstrated the effect of such a bottleneck on the Iberian lynx genome (Abascal et al. 2016). This decrease suffered in the 17th century can be related to 1) an increase of human population and farming activities, 2) climate crisis and 3) human pressure due to fur trade. Interestingly, the Iberian lynx suffered an important direct persecution because of the value of its fur, and a huge number of portrait where kings and aristocracy are wearing lynx fur clothes are preserved (Villalpando-Moreno 2020). Complementary, a climate crisis (the Little Ice Age) led to a crisis among farmers. Peasants made pressure on all "vermins" and hunting as economic activity increased. Meanwhile, crossbows were replaced by firearms. The increased pression could have fragmented Iberian lynx populations, driving small populations to extinction. As a result, Iberian lynx populations became critically endangered from 1620 to 1700.

18th–19th centuries: temporary recovery

References in the early 18th century are scarce, and main quotes begin around 1760. After that, reference rate increases until 1850. There is a large dataset of historical records from 19th century, when 254 references in the wider *Lynx pardinus* distribution range are documented. Data from Galicia, the Pre-Pyrenees, Central Range, Iberian Range, Sierra Morena, Montes de Toledo, Extremadura, La Mancha, Andalusia and Portugal (Algarve, Estremadura, Montesinho and Malcata; Villalpando-Moreno 2020; Fig. 3). The main reason likely underlying the apparent increase of the Iberian lynx population from late 18th to mid 19th centuries was the high occurrence of wars. Between Spanish Succession War (1705) and 1850, wars happened throughout the whole territory (Spanish Independence war, Revolutionary Period and Carlist wars). The field becomes a dangerous place, and farmer activities decreased during war stages. Thus, Iberian lynx population increased. As judged by the frequency of references, the Iberian lynx population reached its maximum in the first half of the 19th century. The species was distributed throughout the SW quadrant of the Iberian Peninsula and some areas in the E and N Spain. The divergence between Doñana and the rest of the historical population was estimated at the beginning of the 19th century (Casas-Marcé 2017), showing that a new contraction of the populations began in this century. Depletion apparently increased during the second half. From 1850 on, the Industrial Revolution took place in Spain and Portugal. Railways spread through the territory. Mining of coal and ore, iron and steel industry and farming changed in all territories in the north. Southern region around Huelva, Almería y Murcia were huge mining centres. Villages became towns and towns became cities. Human population grew and deforestation increased as never before. Public lands were sold by Desamortizaciones, so a huge number of scrubland and forest became agricultural land. In this period, persecution of Iberian lynx increases again (Villalpando-Moreno 2020). Around 300 fur per year were collected in Sierra de Guadarrama (Central Range) and around 500 fur per year for the whole of Spain at the end of the 19th century (Brehm 1880).

20th Century: the last bottleneck

The Iberian lynx population continued to suffer an unceasing depletion during the 20th century, mainly provoked by an extremely

Fig. 2. Iberian lynx quotes recorded in 16th and 17th centuries.

Fig. 3. Lynx quotes recorded in Spain during 18th and 19th centuries. Records in Northern Cantabric Mountains and Pyrenees (white dots) might refer to Eurasian lynx.

high human pressure (i.e. direct persecution, habitat transformation and emerge of rabbit diseases; Guzmán et al. 2004). As a result, a dramatic genetic erosion was proven to occur along the century, representing the last and largest bottleneck suffered by the species (Casas-Marcé et al. 2017). Regression and fragmentation provoked genetic drift at some extent in all the population nuclei, which was not related to nuclei extirpation (Casas-Marcé et al. 2017).

At the early 20th century, Cabrera (1912) stated that the Iberian lynx was virtually extinct in northern and eastern Iberian Peninsula, while it was still abundant in the southwestern quadrant. At this stage, populations living in this quadrant were thought to be quite continuous. The Iberian lynx continued to be hunted for fur trade during the first decades of the 20th century. The Central Range population (specially Sierra de Guadarrama) is known to have suffered an intensive depletion due to fur trade before 1940, what resulted in a very fragmented nucleus and the extirpation of some nuclei (Rodríguez & Delibes 1990). There is a lack of data during the 30s, probably due to the political situation and the Spanish Civil War.

Between 1944 and 1968, the Spanish Government implemented the "Extinction Councils", aimed to drive carnivores to the extinction across the Spanish territory. The government paid for every carnivore killed in the country, and more than 5,000 carnivores are known to be killed under this programme (Corbelle & Boquete 2008). Between 1954 and 1961, the government paid for 152 Iberian lynxes: 107 in the province of Toledo, 19 in Córdoba, 18 in Salamanca, five in Ciudad Real, two in Granada and one in Cáceres. In Portugal, a similar intervention was implemented during the period spanning the 1950s and the early 1960s; official reports revealed the killing of more than 100 Iberian lynx specimens. The exceptionally high numbers of Iberian lynx eliminated, coupled with the evident regression of the population, led to increased awareness regarding the imminent risk of extinction of this feline (Roque de Pinho 1959). A review of the legally-hunted lynx in Spain between 1935 and 1960 revealed 10 population nuclei of Iberian lynx (Valverde 1963), including Doñana, four in Sierra Morena (Sierra Norte, Hornachuelos, Andújar-Cardeña and Guarrizas), Montes de Toledo, Sierra de San Pedro, Sierra de Gata, Sierra de Santo Domingo and Muntanyes de Benifassà. Under this scenario, the depletion of most Iberian lynx populations went on during the 40s and 50s, and the last verified records of Iberian lynx in Sierra de Santo Domingo, Sierra de San Pedro, Vale do Sado, Baetic Mountains and Sierra de Guadarrama (in the Central Range) were recorded in these decades (Gil-Sánchez & McCain 2011, Casas-Marcé et al. 2017; Fig. 4). Isolation of the different nuclei is patent after 1950, with Doñana and far-E Sierra Morena holding very low population sizes during the second half of the century (Casas-Marcé et al. 2017). Only Montes de Toledo and E Sierra Morena were relatively large (over 750 individuals) by 1950 and declined abruptly in the second half of the century (Casas-Marcé et al. 2017). In the early 60s, the Iberian lynx was recognised as the most endangered carnivore in the Iberian Peninsula, mainly due to the extermination provoked by routinely use of leghold traps for killing rabbits (Valverde 1963). The Iberian lynx protection was enacted in 1967 in Portugal and in 1969 in Spain. The last verified Iberian lynx record of Sierra de Gredos (in the Central Range) occurred in 1968 (Gil-Sánchez & McCain 2011).

In the 70s, Delibes (1979) described six major remnant nuclei throughout Iberia based on scat detection and literature review: Doñana, Eastern Sierra Morena, western Sierra Morena, Montes de Toledo and nearby hills, Sierra de Gata-Malcata, and Algarve. The main threats for the species at that time were 1) human persecution, 2) habitat destruction (due to afforestation with pines and eucalyptus) and 3) myxomatosis affecting rabbit populations (Delibes 1979, Palma 1996). Despite being protected, Delibes (1979) reported 80 individuals trapped in Montes de Toledo and 20 in Sierra Morena only in 1974-1975. The use of legholds to kill rabbits continued to be widespread in the 70s and 80s (Simón et al. 2013). The depletion in these decades continued (Fig. 5); the last verified Iberian lynx record in W Sierra Morena was documented in 1972 (Casas-Marcé et al. 2017). By 1978, the Iberian lynx was recognised as the most endangered carnivore in Europe (Mallinson 1978).

In the 80s, studies on lynx distribution relied on questionnaires distributed to hunters and other key groups (Palma et al. 1999). Following this methodology, Rodríguez & Delibes (1992) and Castro & Palma (1996) described more than 50 nuclei throughout Iberia that could be grouped in nine major occurrences:

Fig. 4. Iberian lynx distribution in 1945–1960 as inferred by Valverde (1963; black polygons; the two northernmost polygons might correspond to Eurasian lynx) and complementary references (open dots; Roque de Pinho 1959, Corbelle & Boquete 2008, Gil-Sánchez & McCain 2011, Casas-Marcé et al. 2017).

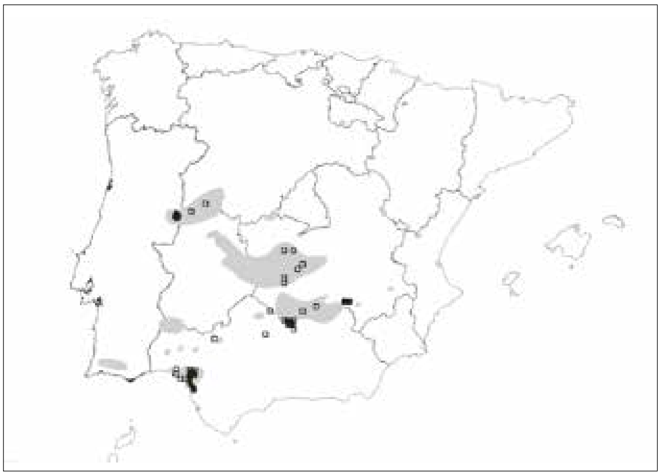

Fig. 5. Iberian lynx distribution in the 1970's according to Delibes (1979; grey polygons) and Gil-Sánchez & MacCain (2011; open squares). Black polygons represent the Iberian lynx distribution inferred by verified records in 1986-1999 (Castro 1994, Sánchez & McCain 2011, Casas-Marcé et al. 2017).

Doñana, W Sierra Morena, Central Sierra Morena, E Sierra Morena, Baetic Mountains, Montes de Toledo and nearby hills, Sierra de San Pedro, Central Range, and Algarve. These studies estimated a population size of 1185 individuals (1135 in Spain and 50 in Portugal). Gil-Sánchez & McCain (2011), however, found a more restricted distribution range (Doñana, E Sierra Morena and Montes de Toledo) for the 1980s using verified data (hunting trophies and scientific collections). This discordance matched the proven over-estimation of the first method over the second one (Garrote & Pérez de Ayala 2015); the real situation was probably in-between. The main recognised threats for the species during the 1980s were 1) lack of prey due to viral diseases of rabbits, 2) anthropogenisation of the environment (including road kills and predator control), 3) fragmentation, and 4) habitat destruction (due to both urbanisation and pine and eucalyptus plantations; Rodríguez & Delibes 1990). The last verified Iberian lynx record in Montes de Toledo and the Far-E Sierra Morena were recorded in 1985 and 1989, respectively (Casas-Marcé et al. 2017; Fig. 5). Unhappily, the Montes de Toledo population, which was the largest and more diverse Iberian lynx population in the entire Iberian Peninsula, became thus abruptly extinct, probably in the middle 1980s. The last record of Central Range was recorded in Serra da Malcata (Portugal) in 1993 (Castro 1994). Apart from this record, verified data of the presence of the Iberian lynx during the 1990s came only from Doñana and eastern Sierra Morena (Gil-Sánchez & McCain 2011).

Fig. 6. Iberian lynx distribution in 2002 obtained by photo-trapping and molecular analysis (Guzmán et al. 2005).

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo A. M. Morillas).

Situation in the early 21st century

Between 2000 and 2003, a new comprehensive status survey using photo-trapping and molecular analysis of scats was conducted in the Iberian Peninsula (Guzmán et al. 2004, Sarmento 2009). In Spain, 188 10x10 UTM squares were sampled, corresponding to more than 10,000 kms of line transect and 4,100 man-hours. In Portugal, 133 10x10 UTM squares were sampled, corresponding to 4,252 km of line transect and 1,975 man-hours. The surveys showed that only two isolated Iberian lynx nuclei survived at that time: Doñana and Andújar-Cardeña (in E Sierra Morena). Both nuclei totalled ca. 95 Iberian lynxes (Guzmán et al. 2005; Fig. 6). The remnant genetic diversity was extremely low, the Iberian lynx being the cat species with the lowest genetic diversity of the world (Casas-Marcé et al. 2017). Under this critical scenario, the IUCN catalogued the Iberian lynx as Critically Endangered, and it was recognised the most endangered felid on earth (IUCN 2003). This was the starting singe to the implementation of the subsequent conservation measures.

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Trends in geographic range and population size of the Iberian lynx as reflected in IUCN Red List assessments

The Iberian lynx *Lynx pardinus* has experienced notable changes in distribution and numbers during the past 70 years. Parallel strong variation in extinction risk was adequately reflected in the 11 IUCN Red List assessments RLAs published since 1966, from Endangered (1986–1996), through Critically Endangered (2002–2008) and Endangered (2015), to Vulnerable (2024). The use of original data sources, the access to raw data, and the transparency of the narrative supporting the assigned threat category increased over time. Access to original data allowed recalculation of parameters following RLA standards, yielding sometimes quite different results. A detailed rationale supporting the threat category assigned is presented as a supplement to the 2024 RLA.

An increasing number of species undergo marked changes in abundance and range shifts largely attributed to human activity (Daskalova et al. 2020). Many affected species may not receive proper conservation attention, or may not respond to conservation measures, triggering population declines. These population changes are thought to be timely and adequately reflected in the categories of the IUCN Red List of threatened species (Mace et al. 2008). Indeed, both the impact of drivers of global change and conservation success are often measured in terms of the proportion of species changing its Red List category (Macdonald 2019).

The recent assessment of extinction risk in the Iberian lynx illustrates how the ups and downs in distribution and abundance result from the balance between the strength of agents of extinction and the effectiveness of conservation action. Here, I expand on the rationale supporting the threat category assigned to the Iberian lynx in the last RLA (Rodríguez 2024). First, I summarise trends in lynx geographic range and population size during the past seven decades. Then, I detail the application of the IUCN Red List criteria, and show how access, evaluation and re-analysis of raw data can improve the quality of assessments. Next, I examine temporal trends in reporting source data in published RLAs for this species. I end by briefly recalling the value of RLAs for lynx conservation.

Trends in geographic range and population size

For most of the last four centuries, the Iberian lynx had a relatively stable distribution in the southwestern quarter of the Iberian Peninsula (Rodríguez & Delibes 1990, Clavero & Delibes 2013). A population decline started around 1950 when the size of the area of occupancy AOO was estimated as 40,600 km² on a 10-km grid (Rodríguez & Delibes 2002). The decline accelerated during the 1970s, and by 1985 the AOO had contracted by 45% to 22,300 km². High-resolution measurements yielded a figure of just 14,636 km² with an AOO strongly fragmented into 48 breeding areas and nine genetically isolated populations (Rodríguez & Delibes 1992). Between 1985 and 2001, the AOO declined by a further 90% to 2,400 km² on a 10-km grid (Guzmán et al. 2004). Lynx occurred in just two isolated breeding areas. Fine-scale measurements revealed that AOO was not larger than 300 km² (Rodríguez & Calzada 2017). Prompt conservation management halted this trend and the Iberian lynx expanded soon. During a phase of population consolidation, AOO tripled between 2001 and 2012 up to 1,040 km² with a geographic range made of four discrete breeding areas (Simón 2013). During the following phase of reintroduction, AOO tripled again between 2012 and 2022 up to 3,320 km², and lynx expanded over 50 discrete breeding areas (Rodríguez 2024).

Estimates of Iberian lynx numbers are available for a shorter period. The first figures date from 1988 when population size was estimated to be around 700 mature individuals (or 350 breeding females; Rodríguez & Delibes 1992). Between 1985 and 2002, population size declined by 93% to 52 mature individuals (Simón et al. 2012a). During the recovery phase, population size tripled up to 156 mature individuals in 2012 (Simón 2013), and grew again by a factor of four to 648 mature individuals between 2012 and 2022 (Rodríguez 2024).

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Data treatment

All relevant data were published in websites and the scientific literature, complying with the requirement for Red List data to be available. However, some unpublished data were accessed to calculate dispersal distances,

Iberian lynx from El Acebuche breeding centre (Photo A. Sliwa).

Fig. 1. Camera trapping was the main tool to determine the occurrence and location of breeding females. The identity of adult females was determined by coat spot patterns, often known since they were juveniles. This allows relating the location of current and natal territories for resident individuals. Detection of cubs in pictures is one of the goals of camera traps, and one important tool to count the number of breeding females and to estimate territory boundaries. Image provided by Leonardo Fernández, courtesy of Consejería de Sostenibilidad, Medio Ambiente y Economía Azul, Junta de Andalucía.

demographic parameters, and AOO. Original data were collected by 14 teams from five different governmental agencies or private entities. Data were disseminated and had to be prepared, revised and compiled between February 2022 and October 2023 with the help of 15 contributors.

Camera trapping was the basic tool to map the home ranges of resident individuals, to confirm reproduction, and to detect as many individuals as possible. Annual estimates of population size were given in terms of minimum number of territorial females, cubs, and individuals detected (Life+ Iberlince 2017, Life Lynxconnect 2023). Territorial females were defined on the basis of actual reproduction (Fig. 1) and/or exclusive access to space with regard to other adult females. This fits the IUCN definition of mature individual because adult females need to hold a territory for breeding. Population data were accepted without correction because the minimum number of mature females was deemed realistic and also a slightly conservative estimate. The number of mature individuals was twice the number of territorial females because monogamy and intra-sexual territoriality is the most common pattern of social organisation (Ferreras et al. 1997, 2023), and adult sex-ratio closely approaches 1:1.

Raw distribution maps represented areas where lynx presence was detected or suspected by any method, including sites where resident lynxes do not occur (Life+ Iberlince 2017, Life Lynxconnect 2023). To avoid overestimation of AOO, the boundaries of female territories that actually reproduced each year were plotted on a 2-km grid. Cells were considered occupied only if they overlapped the territories of females that bred at least three times during the past five years. Using this approach, AOO was 51% of the published distribution map for 2022 (Life Lynxconnect 2023).

Calculations were made during a period of 18 years (2005–2022), equivalent to three Iberian lynx generations. Generation length (6 years) was empirically derived using option 1 among those suggested by IUCN Standards and Petitions Committee (2019: 29). Population size in 2005 and 2022 was 84 and 648 mature individuals, respectively.

Criterion A. Population size reduction

Subcriterion A1 requires a "population reduction observed, estimated, inferred, or suspected in the past where the causes of the reduction are clearly reversible AND understood AND have ceased". No decline was observed in area of occupancy, extent of occurrence, or the overall availability of suitable habitat. Current levels of non-natural mortality might have kept the growth of specific subpopulations low, but did not seem to limit the general expansion of the species. Introduced taxa, hybridisation, pollutants and competition were not identified as factors affecting lynx population trends. The effect of pathogens and parasites contributed to lynx mortality but did not preclude positive growth rates in most subpopulations. No population reduction was observed, and subcriterion A1 was not met.

Subcriterion A3 states a "population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years)". Extrapolating population trends during the last 18 years into the future did not yield a projected population reduction. Based on the known performance of the ex-situ conservation programme, the selection of re-introduction areas, the outcome of reintroduction attempts, the productivity, recruitment, and dispersal distances of lynx in the wild, the rate of natural recolonisation, and the ongoing and projected reintroduction attempts, a population reduction could not be inferred or suspected, at least in the near future. Thus, subcriterion A3 was not met. Subcriterions A2 and A4 were not applicable, and under Criterion A, the taxon qualifies for the Least Concern category.

Criterion B. Size of geographic range

Subcriterion B1 refers to the extent of occurrence EOO which was 85,152 km² in 2022. EOO was four times larger than the threshold value for the Vulnerable threat category (<20,000 km²) and subcriterion B1 was not met.

Subcriterion B2 deals with area of occupancy, which was 3,320 km² in 2022. AOO was 67% larger than the threshold value for the Vulnerable threat category (<2,000 km²) and subcriterion B2 was not met. Under Criterion B, the taxon qualifies for the Least Concern category.

Criterion C. Small population size and decline
Population size in 2022 was smaller than the threshold value for the Endangered threat category (≤ 2,500 mature individuals), but the conditions established by either subcriterion C1 or subcriterion C2 should concur for assigning the Iberian lynx to this category.

Subcriterion C1 requires "an observed, estimated or projected continuing decline" which did not occur.

Subcriterion C2 reads "an observed, estimated, projected or inferred continuing decline AND at least one of the following three conditions:

(a) (i) Number of mature individuals in each subpopulation [under a threshold value]

(a) (ii) % of mature individuals in one subpopulation [in a given range]

(b) Extreme fluctuations in the number of mature individuals

No decline was observed or could be estimated, projected or inferred for the near future, and subcriterion C2 was not met. Regarding the additional conditions, the number of mature individuals per subpopulation fell in the range 50–322. The distribution of mature individuals among populations did not meet the condition C2a(i) for the Endangered category because one subpopulation (Sierra Morena, 322 mature individuals) exceeded the threshold of ≤ 250 mature individuals. However, condition C2a(i) was met for the Vulnerable category because all subpopulations had ≤ 1,000 mature individuals. The number of mature individuals was well distributed among subpopulations as the largest subpopulation only contained 50% of total. Condition C2a(ii) was not met, nor was condition C2b because extreme fluctuations in the number of mature individuals was not observed. In summary, under Criterion C, the taxon qualifies for the Least Concern category.

Criterion D. Very small or restricted population
Subcriterion D1 considers the number of mature individuals. As the number of mature individuals was lower than the threshold value for the Vulnerable threat category (1,000), subcriterion D1 was met for the Vulnerable threat category.

Subcriterion D2 requires a "restricted area of occupancy or number of locations, with a plausible future threat that could drive the taxon to CR or EX in a very short time". The threshold AOO in this criterion should be interpreted as an indicator of the risk of the species becoming extinct due to a threat acting quickly and impacting strongly on a small geographic range. When using subcriterion D2 there must be a substantial possibility of threatening events actually occurring.

Rabbit diseases have triggered lynx declines at least three times during the past 70 years. A new enzootic disease affecting most rabbit populations could be a plausible threat, able to provoke a lynx decline again. However, it is unlikely that such scenario will bring about a sudden collapse of Iberian lynx populations. This is because, in the absence of concurrent threats, adult lynx can bear low prey density and might survive and even breed occasionally. A delayed, resilient response of this kind might give some time for conservation action. On the other hand, mature individuals are distributed into distant subpopulations, up to 400 km apart, reducing the risk that spatial autocorrelation in the intensity of any threat will affect all subpopulations simultaneously and with the same strength. Therefore, subcriterion D2 was not met but, under Criterion D, the Iberian lynx qualifies for the Vulnerable D1 threat category.

Criterion E. Quantitative Analysis
The probability of extinction in the wild was calculated using a complex population model of Iberian lynx distribution and dynamics (Fordham et al. 2013). The model was parametrised with data derived during phases of lynx population decline, and probably overestimates extinction risk in current conditions. The probability of extinction within three and five generations was estimated to be about 1% and <4%, respectively. The probability of extinction within 100 years was also estimated to be <4%. These values did not meet the thresholds for any category, and under Criterion E, the taxon qualifies for the Least Concern category.

Data supporting threat category assignment in former RLAs
As shown above, applying a conservative definition of lynx residency based on regular breeding yielded estimates of AOO significantly lower than those of published distribution maps. This is not to say that the latter are inaccurate, as the way they were elaborated obeys the legitimate interest of conservation agencies to show the outcome of management. This raises the question of how access to original sources and subsequent data curation might have affected Iberian lynx RLAs. Published sources available for assessors are known but it is not possible to infer whether original data were actually accessed in previous assessments. We can, however, ask how transparent previous RLAs were regarding

Table 1. Explicit report of available knowledge used to support Iberian lynx RLAs before and after adopting current standards in 2001..

RLA year	Range size	Range trends	Population size	Population trend	Ecology	Threats	Threat category	Source
1966	Yes	Yes			Partial	Partial	1b*	Simon 1996
1986	No	No			No	No	EN	IUCN Conservation Monitoring Centre Cambridge UK 1986
1988	No	No			No	No	EN	IUCN Conservation Monitoring Centre Cambridge UK 1988
1990	No	No	No	No	No	No	EN	World Conservation Monitoring Centre Cambridge UK 1990
1994	No	No	No	No	No	No	EN	Groombridge 1993
1996	No	No	No	No	No	No	EN C1	IUCN 1996
2002	Partial	No	Yes	Yes	Partial	Yes	CR C2a(i)	IUCN SSC Cat Specialist Group 2002
2006	Partial	Partial	Yes	Yes	Partial	Yes	CR C2a(i)	Large Carnivore Initiative for Europe/IUCN SSC Cat Specialist Group 2006
2008	Yes	Partial	Yes	Yes	Partial	Yes	CR C2a(i)	von Arx & Breitenmoser-Würsten 2008
2015	Yes	Yes	Yes	Yes	Yes	Yes	EN D	Rodríguez & Calzada 2015
2024	Yes	Yes	Yes	Yes	Yes	Yes	VU	Rodríguez 2024

* Meaning of threat category in 1966: Very rare and believed to be decreasing in numbers. Subspecies. Giving cause to some anxiety.

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo T. Pérez).

data sources and whether the option for a critical look or the possibility of a reanalysis was considered. The threat category of the Iberian lynx in each of the 11 RLAs published so far is shown in Table 1, which also illustrates the general trends in the degree of detail provided to justify the assigned threat category. Several phases can be distinguished:

1. 1966 release. Very little information on the Iberian lynx was available at the time. However, in just one-page assessment, the first RLA published was crystal clear about data sources. Uncertainties affecting the threat category were reported.
2. 1986–1994. This was a long period of opacity. In the four RLAs published, no information other than the countries where the species occurred was given.
3. 1996. As a novelty, the criterion justifying the assignment was added to the threat category, but no further data or rationale was provided.
4. 2002–2024. RLAs included text and data explaining why a given threat category was assigned. The new system of categories and criteria approved by the IUCN in 1994 rescued transparency as a cornerstone of RLAs (Mace et al. 2008). However, the inclusion of explicit information in the Iberian lynx RLAs was a slow, gradual process since 2002. Most basic ecological knowledge on the species was generated between 1980 and 2010 (Ferreras et al. 2023). Interestingly, this rich body of information was seldom used, as secondary sources and grey literature dominated the references cited in RLAs until 2008. Succinct explanations evolved into longer narratives, and a growing proportion of existing knowledge on distribution, population, ecology and threats was incorporated to the RLAs during the period. This indicates that an independent scrutiny of original data was not considered until 2015 (Rodríguez & Calzada 2017). Overall, Table 1 shows that the assigned threat categories reflected timely and accurately the steep decline and the no less rapid recovery of the Iberian lynx.

Concluding remarks

Abundant data from research and monitoring allowed an improvement in the quality of the Iberian lynx RLAs over time. Early assessments suspected declines and assigned extinction risk categories based on scarce and fragmentary information whereas, in the current assessment, all criteria could be evaluated on the basis of excellent data and detailed local knowledge of major threats. IUCN RLAs have been shown to significantly contribute to boosting scientific knowledge, raising social awareness, ensuring conservation action, and attracting funds for sustaining all these activities (Betts et al. 2020). For the Iberian lynx, early worries triggered a wealth of ecological research (Ferreras et al. 2010, 2023). Scientific knowledge confirmed the species vulnerability and paved the way to both substantial funding (Palomares et al. 2011) and a precise design of conservation management (Simón et al. 2012a) which produced fruitful results in just one decade (Simón et al. 2012b). IUCN down-listing was an explicit goal of these conservation programmes (López et al. 2024), and management undoubtedly contributed to achieve it. Closing a virtuous cycle, the attention received by the species thanks to listing also yielded the unusually fine data that has supported well-documented RLAs.

Exposed to the many drivers of global change, between 22% and 36% of mammal species are or may be threatened worldwide, and are not experiencing a reduced extinction risk over time even if population declines might be alleviated by conservation measures (Hoffmann et al. 2011, Macdonald 2019). The genuine improvement in the conservation status of the Iberian lynx illustrates how the combination of social awareness, scientific knowledge, long-term monitoring, determined conservation action, adequate funding, and a fortunate timing in the general improvement of ecological conditions (i.e. recovery of prey abundance) may quickly bring a mammal species away from the brink of extinction. Under the pressing anthropogenic environmental change this successful story has not reached an end. Continuous monitoring of lynx range and numbers should go on and inform both management and conservation policy. Meanwhile the Iberian lynx story may hopefully inspire the course of action for other species under a delicate conservation situation.

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Iberian lynx conservation programme in the last 22 years

Given that the Iberian lynx *Lynx pardinus* was recognised as the world's most endangered cat species, a conservation programme (including both in situ and ex situ conservation measures) was implemented as of 2002. In situ conservation measures have mainly been implemented through four EU-funded LIFE-Nature projects. In the first stage, the goal was to prevent the imminent extinction of the species in the refuge areas, and measures to increase the carrying capacity by increasing rabbit density were implemented. Habitat improvement for rabbits (those favouring ecotones between meadows and bushes), wild rabbit restocking in large enclosures and supplementary feeding were performed. Moreover, measures to reduce poaching (including awareness, agreements with key sectors and surveillance), road kills (mainly through the construction of secure passes, fencing the risk road sections, awareness and signalling) and infectious diseases (sanitary control and genetic management.) were implemented. These two programmes together allowed the Iberian lynx population to grow from 94 individuals in 2002 to 310 individuals in 2011. Meanwhile, an ex situ conservation programme was created since 2003 to conserve the remaining genetic stock and provide individuals for reintroductions. After 2006, programs for genetic management and reintroduction were added to the conservation programme of the Iberian lynx. The genetic management programme mainly issued the negative effects caused by inbreeding in the Doñana population, such as fertility problems and a high impact of infectious diseases. The reintroduction programme allowed a much faster population growth than all previous measures. This programme included 1) the selection of best areas for reintroduction, 2) the preparation of the area for releases, 3) the selection of the best individuals to be released and 4) the post-release monitoring. Overall, 441 Iberian lynxes have been released in 8 reintroduction areas throughout Spain and Portugal. All reintroduction areas experimented a fast population growth until carrying capacity was reached. By 2023, a minimum number of 2,021 Iberian lynx were recorded, and releases of two new reintroduction areas began in 2024. To sum up, the result of the reintroductions allowed a faster population growth leading to a significant success of the Iberian lynx conservation programme.

At the turn of the 20th century, the conservation status of the Iberian lynx was quite uncertain. In 1998–2002, the first Iberian lynx conservation measures were implemented by the Spanish Ministry for the Environment, some Autonomous Communities and some NGOs. These preliminary actions prepared the ground and, above all, allowed the development of the first Iberian census that raised all the alarms (Guzmán et al. 2004, Sarmento et al. 2009). By 2002, only the isolated Andújar-Cardeña and Doñana Iberian lynx populations survived, totalling 94 individuals (Guzmán et al. 2004, Simón et al. 2012a). This pre-extinction scenario was the worst situation ever recorded, so that the IUCN catalogued the Iberian lynx as Critically Endangered (IUCN 2003). Unless urgent measures were taken, the species would probably become extinct in the short-term. As a consequence, a programme for the conservation of the Iberian lynx (ILCP) was implemented from 2002 on, including both in situ and ex situ conservation actions. Given that the whole population survived in Andalusia, the Andalusia Regional Ministry of Environment ARME was competent in its conservation. After 2002, the ARME, together with the European Union EU and different stakeholders (conservation NGOs, landowners and hunters and local populations), implemented four comprehensive LIFE projects (EU funded projects for environmental and nature conservation) in a row aimed to preserve the in situ Iberian lynx populations: Lince-Andalucía (2002–2006), Lince (2006–2011), Iberlince (2011–2019) and Lynxconnect (2020–2026). Complementary to these LIFE projects, the ARME, the Spanish agency *Organismo Autónomo de Parques Nacionales*, WWF, and CBD-habitat Foundation developed several conservation projects with their own or other funds. As of 2011, the ministry of environment of Portugal and the regional ministries of environment of Castilla-La Mancha, Extremadura, and Murcia joined the in situ LIFE programme. At the end of the ongoing LIFE project, 24-year geographic extensive conservation programme will be implemented. Moreover, the ARME, with the Spanish and the Portuguese ministries of Environment, implemented an ex situ conservation programme ESCP in 2003, aimed to both 1) maintain a genetic pool of the species and 2) produce individuals for potential future reintroductions (Vargas et al. 2008). Here we describe all the measures taken in the ICLP, as well as presenting its major results. The ICLP was born trying to address all the threats faced by the species, and included 1) enhancement of trophic resources, 2) reduction of mortality, 3) genetic management, 4) captive breeding program, 5) reintroductions and 6) favouring connectivity. The ICLP allowed reversing the decline of the Iberian lynx and recover former population nuclei (Simón et al. 2012a).

Material and methods

Enhancement of trophic resources

The Iberian lynx did not survive in the areas with higher trophic resources, but in two refuge areas were the levels of anthropogenic mortality were low. In fact, rabbit density in most of the occupied area in 2002 ranged between the thresholds allowing the occurrence and the reproduction of the Iberian lynx (Simón et al. 2012b). Hence, the first actions to be implemented were those focused on increasing rabbit densities in the occupied areas and surroundings in order to 1) increase lynx productivity, 2) increase lynx density and 3) favour the spreading of the nuclei through the colonisation of new territories. Given that almost the entire distribution area occurred within private property, collaboration agreements with the owners or beneficiaries of the land were necessary. With these agreements, habitat management for rabbits was implemented in private lands, where Iberian lynx monitoring was allowed. Moreover, agreements were the decisive tool to establish a relationship of trust with the stakeholders (land owners and hunters), through their involvement in the recovery process of the species.

1. Habitat management for rabbits: The Iberian lynx is not a habitat-specialist, but they select for breeding areas with a given wild rabbit density and some refuge (Garrote et al. 2017). Because1) wild rabbit density increases in ecotones between scrubland and pastureland (Lombardi et al. 2003) and 2) remnant lynxes were occupying scrubland areas with medium-low rabbit density, the first strategy in the conservation of the species was managing the habitat to increase ecotones between scrubland and pastureland. This habitat management included selected bush clearance, pruning and protection of rabbit warrens, creating small patches of cereal crops and creating additional watering points for rabbits. The final goal was to create a mosaic structure favouring the wild rabbit population, thus favouring the settlement and breeding of the Iberian lynx. In 2002–2024, habitat management for rabbits has been conducted in more than 100 km^2 throughout the working area and a collaboration agreement have been signed on an area of around 3,000 km^2.
2. Rabbit restocking: rabbit restocking from nearby agricultural lands was performed if rabbit densities were almost null at the beginning of a work in a given area. Restocking was made using soft or hard releases. Soft releases were made on 0.03 km^2 average (0.005–0.07 km^2) enclosures to prevent both the meso-carnivore predation and the rabbit dispersion. Artificial warrens were built in and around the encloser to encourage the establishment of released rabbits. In hard releases, rabbits were released in open areas where artificial warrens were previously built at a density of 100 per km^2. In the period 2002–2011 98 enclosures and 2,251 artificial warrens were built in Andujar - Cardeña and 104 enclosures and 1,530 artificial warrens in Doñana.
3. Supplementary feeding: In order to 1) increase lynx productivity and 2) avoid a high lynx predation in the first stages of the abovementioned actions, supplementary feeding with domestic rabbits was provided. Stations of supplementary feeding were spread throughout the home range of the target individuals. This strategy was used from 2002 to 2010, and more than 50 breeding females increased their productivity thanks to it. In Andújar - Cardeña supplementary feeding is currently applied on the territories of some breeding females where the abundance of wild rabbits has fallen below the threshold that would allow reproduction.

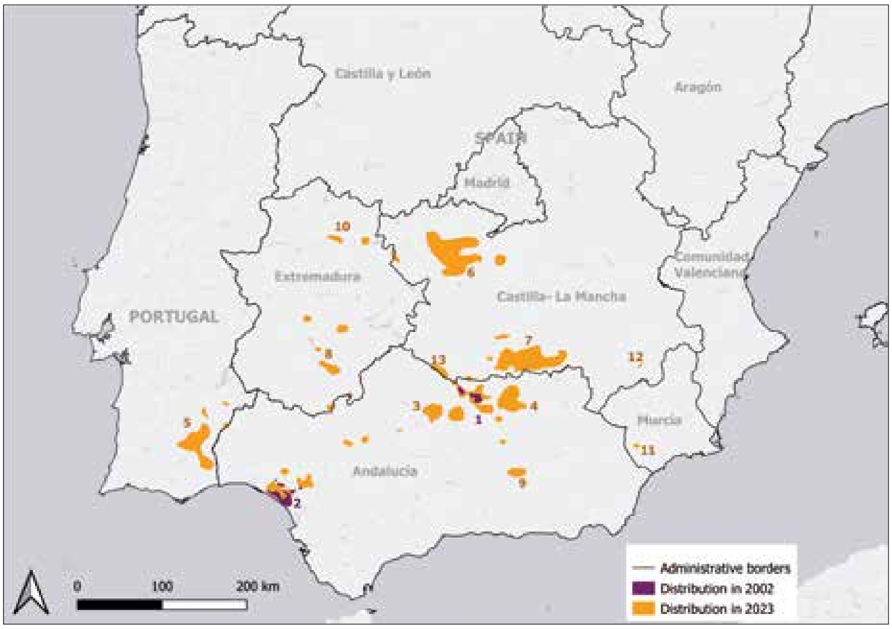

Fig. 1. Distribution range of the Iberian lynx in 2002 (purple area) and 2023 (orage area). Remnant populations:1) Andújar-Cardeña and 2) Doñana. Reintroduced populations: 3) Guadalmellato, 4) Guarrizas, 5) Vale do Guadiana, 6) Montes de Toledo, 7) Campo de Montiel, 8) Matachel, 9) Sierra Arana, 10) Valdecañas-Ibores, 11) Lorca and 12) Campos de Hellín. Naturally funded population: 13) Guadalmez Valley.

All the previous measures were included in a wider strategy of "Territory Recovery Units", consisting in the combination of different measures (in different proportion depending on the initial needing of the area) along a surface similar to that of a lynx home range (around 6 km^2) in order to allow an individual to settle (Simón et al. 2012b). In 2002–2011, around 40 new breeding female territories have been recovered through the "Territory Recovery Units". The Iberian lynx is an ally of hunters by controlling other medium predators and contributing to increase rabbit populations.

Reduction of mortality

By 2002, the two main recognised causes of non-natural mortality in the Iberian lynx were illegal persecution and road kills (Rodríguez & Delibes 2004). The ICLP tried to address both of them since the beginning.

1. Fight against illegal persecution: The ICLP tried to reduce illegal persecution through 1) awareness, 2) the creation of a relationship of trust with stakeholders and 3) a surveillance programme. The awareness campaign was focused on spreading the message that the Iberian lynx was the most endangered cat on earth and that it was a privilege to count with it in their areas. The relationship of trust was created through the involvement of the stakeholders (land owners and hunters) in the project through the abovementioned collaboration agreements. Finally, a surveillance programme was implemented in risky areas in order to detect potential methods of illegal persecution of carnivores (snares, legholds, poison, etc.) through routine transects (Simón et al. 2012b).
2. Fight against road kills: The strategy to mitigate road kills included creating (or adapting previous structures) secure passes in roads (under- or overpasses) and leading lynxes to cross through them, mainly by fencing adjacent segments. Moreover, the awareness campaign allowed both to raise perception of the drivers and to involve all competent administrations in the ILCP. Because 1) road network is large, 2) these actions are expensive and 3) lynx crosses take place in random sections, efforts were mainly dedicated to black spots (road segments accumulating several road kills along years). More than 200 secure passes have been created in roads since 2002.

Table 1. . Individual Iberian lynx extracted by the ARME to act as founders in the ESCP in the period 2003-2024.

Name	Year of birth	Sex	Population	Genetic origin	Year of extraction
Saliega	2002	Female	Andújar-Cardeña	Sierra Morena	2003
JUB	1999	Male	Andújar-Cardeña	Sierra Morena	2003
Cromo	2003	Male	Andújar-Cardeña	Sierra Morena	2003
Fran	2003	Male	Andújar-Cardeña	Sierra Morena	2003
Garfio	2001	Male	Andújar-Cardeña	Sierra Morena	2003
Artemisa	2004	Female	Andújar-Cardeña	Sierra Morena	2004
Aliaga	2004	Female	Andújar-Cardeña	Sierra Morena	2004
Almoradux	2004	Male	Doñana	Doñana	2004
Adelfa	2004	Female	Andújar-Cardeña	Sierra Morena	2004
Alhucemas	2004	Female	Andújar-Cardeña	Sierra Morena	2004
Boj	2004	Female	Doñana	Doñana	2005
Biznaga	2004	Female	Andújar-Cardeña	Sierra Morena	2005
Arcex	2004	Male	Andújar-Cardeña	Sierra Morena	2005
Azahar	2004	Female	Andújar-Cardeña	Sierra Morena	2006
Beta	2005	Male	Andújar-Cardeña	Sierra Morena	2006
Cardo	2006	Male	Andújar-Cardeña	Sierra Morena	2006
Candiles	2006	Male	Andújar-Cardeña	Sierra Morena	2006
Caña	2006	Female	Andújar-Cardeña	Sierra Morena	2006
Coscoja	2006	Female	Andújar-Cardeña	Sierra Morena	2006
Cuco	2006	Male	Andújar-Cardeña	Sierra Morena	2006
Córdoba	2006	Female	Andújar-Cardeña	Sierra Morena	2006
Ceniza	2006	Female	Andújar-Cardeña	Sierra Morena	2006
Barraca	2005	Female	Andújar-Cardeña	Sierra Morena	2006
Al-Andalus	2004	Male	Andújar-Cardeña	Sierra Morena	2007
Charqueña	2006	Female	Andújar-Cardeña	Sierra Morena	2008
Alfonso	2004	Male	Andújar-Cardeña	Sierra Morena	2008
Esparto	2008	Male	Andújar-Cardeña	Sierra Morena	2008
Calabacín	2006	Male	Andújar-Cardeña	Sierra Morena	2008
Era	2008	Female	Andújar-Cardeña	Sierra Morena	2008
Carea	2006	Female	Andújar-Cardeña	Sierra Morena	2008
DamanII	2007	Male	Andújar-Cardeña	Sierra Morena	2008
Azuel	2004	Female	Andújar-Cardeña	Sierra Morena	2008
Estela	2008	Female	Doñana	Doñana	2008
Espina	2008	Female	Doñana	Doñana	2008
Fausto	2009	Male	Andújar-Cardeña	Sierra Morena	2009
Gazpacho	2010	Male	Doñana	Doñana	2010
Gitanilla	2010	Female	Doñana	Doñana	2010
Flecha	2009	Male	Andújar-Cardeña	Sierra Morena	2010
Durillo	2007	Male	Doñana	Doñana	2012
Jandra	2012	Female	Doñana	Mixture	2012
Huerto	2011	Male	Doñana	Mixture	2012
Homer	2011	Female	Andújar-Cardeña	Sierra Morena	2012
Kilimanjaro	2013	Male	Guadalmellato	Mixture	2014
Madagascar	2015	Male	Doñana	Mixture	2015
Onuba	2017	Female	Doñana	Mixture	2017
Odiel	2017	Male	Doñana	Doñana	2017
Elipse	2008	Female	Andújar-Cardeña	Sierra Morena	2017
Nala	2016	Female	Doñana	Doñana	2017
Felipe	2009	Male	Andújar-Cardeña	Sierra Morena	2018
Damero	2007	Male	Andújar-Cardeña	Sierra Morena	2018
Idminas	Unknown	Male	C Sierra Morena	Sierra Morena	2020
Urania	2023	Female	Andújar-Cardeña	Sierra Morena	2023
Untxi	2023	Male	Doñana	Doñana	2023

3. Mitigation of the impact of diseases: Although the impact of infectious diseases was not recognised as a problem for the Iberian lynx in 2002, it arose a few years later thanks to the routine monitoring of the ICLP (López 2009). The small population size, the low genetic diversity and the coexistence with domestic species made the Iberian lynx especially sensitive to this threat. The ICLP implemented a sanitary programme included: 1) routine epidemiological risk assessments, 2) health monitoring of the population, 3) immunisation against hazardous pathogens and 4) decrease the sanitary risk of all conservation measures. In 2002–2024, 1,200 health evaluations of living animals and 500 necropsies have been performed. The impact of some diseases could be mitigated through this programme (Nájera et al. 2024).

Genetic management

The Iberian lynx is the most genetically eroded mammal on earth, and the remaining genetic diversity in 2002 was the lowest ever registered (Abascal et al. 2016, Casas-Marcé et al. 2017). Negative effects of inbreeding were detected in the Doñana population since the beginning of the ICLP, and so a genetic management strategy was implemented. Its goals were to reduce inbreeding and minimise the loss of diversity. At least, two different nuclei with slightly different genetic composition survived, and the genetic strategy relied in the admixture of both of them. A rescue programme of the highly inbred Doñana population was implemented after 2007 and the inclusion of genetics from Doñana in Andújar-Cardeña began by 2010 (Simón et al. 2013). Moreover, the captive breeding programme was managed since the beginning under a programme focused on minimising the inbreeding coefficient (see Godoy et al. 2024). Since 2007, 12 Iberian lynxes (8 wild and 4 captive-bred) with genetics from Sierra Morena have been released in Doñana. Reproduction of three of them has been confirmed. Moreover, the E Sierra Morena population has been strengthen with Doñana genes in the reintroductions of Guadalmellato and Guarrizas.

Ex situ conservation programme

The ESCP was born in 2003 and aimed both to maintain a genetically and demographically managed captive population and to create new Iberian lynx populations through re-introduction (Vargas et al. 2008). It is composed of four breeding centres (three in Spain and one in Portugal) with capacity for hosting around 100 breeders. In 2004–2024, the ARME has extracted 54 selected Iberian lynxes to act as founders (Table 1), and reproduction in captivity has been achieved with all of them. Thus, all the selected genetic lines are currently represented in the ESCP and the programme is genetically managed as a whole (see Godoy et al. 2024). The first litter born in captivity was in 2005, and since that, 686 Iberian lynxes have been produced. Nowadays, the ESCP produces 30–40 Iberian lynx for reintroduction every year.

Fig. 2. View of the first litter detected in the Guadalmellato reintroduction area during the first year after release. The wild-translocated female gave birth in an artificial den inside the soft-release enclosure (Photo JRS, LIFE Lince project).

Reintroductions

Once the first implemented measures reversed the decline of the species (Simón et al. 2012a), the following step was the recovery of former population nuclei. The reintroduction programme is aimed to re-stablish as many extinct Iberian lynx populations as possible. It is composed of 1) selection of best areas for reintroduction, 2) preparation of the areas, 3) selection of individuals to be released, 3) releases and 4) post-release monitoring (Simón et al. 2012b). The reintroduction programme started in 2006 (LIFE Lince project) with the evaluation of the first three areas. Through the LIFE Iberlince project, the ICLP began reintroductions outside Andalusia. Between 2006 and 2024, 18 areas have been evaluated for Iberian lynx reintroduction. Three of them were discarded because conditions were not good. Releases of individuals began in 2009 and have taken place in nine areas so far, whereas the other six are still under evaluation (Fig. 1). Six of the nine reintroduction areas that started the releases (Guadalmellato, Guarrizas, Montes de Toledo, Matachel, Campo de Montiel and Vale do Guadiana) are already considered completed and no more individuals will be released there. In 2006–2024, 441 (402 captive bred and 39 translocated; Fig. 2) Iberian lynxes have been released in the reintroduction programme.

As a result of the selection procedure, all the selected areas displayed high rabbit density, suitable habitat, good social perception and low level of threats. The preparation of the areas included agreements with land owners and hunters and awareness campaigns. The selection of the individuals considered origin (wild or captive), age and genetics.

Likewise, measures to improve trophic resources were mostly abandoned in favour of reintroductions, which proved to be much more efficient in terms of cost-results.

Enhancement of the connectivity

Once new population nuclei were created through reintroduction over the SW quadrant of Iberia, achieving an effective connectivity among them was considered crucial to their long-term conservation. So that, the ongoing Lynxconnect LIFE project main goal is to achieve connectivity among remnant populations and all nuclei created through reintroduction. For that, small nuclei acting as "stepping stones" are being created within the most probable connection routes (Blázquez-Cabrera et al. 2019). The selection process was similar to the reintroductions, but requirements of surface were smaller (Lynxconnect 2022). Releases in the "stepping stones" began by 2022, and 15 individuals in 6 nuclei have been released so far.

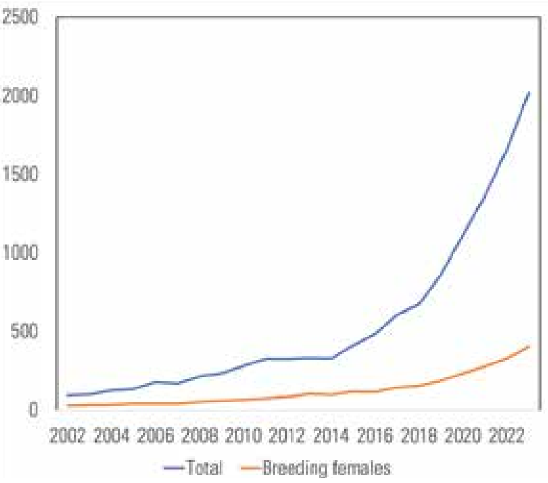

Fig. 3. Evolution of the Iberian lynx population since the beginning of the ICLP (2002-2023). Releases of the LIFE Iberlince project began by 2014, when the population growth increases.

On the other hand, both the remaining and the reintroduced populations have expanded through the colonisation of nearby areas, significantly increasing their occupied area. Montes de Toledo and Vale do Guadiana even reached physical continuity with other populations. Gudalmellato, Andújar – Cardeña, Guarrizas, Guadalmez and Campo de Montiel currently make up a single population with full connectivity, resembling the E Sierra Morena nuclei described in the 80s (Rodríguez & Delibes 1992).

Monitoring

Altogether, the abovementioned measures of the ICLP were focused on the recovery of the Iberian lynx population. To be able to evaluate their results, a routine monitoring of the population has been conducted since 2002, mainly based of photo-trapping (Garrote et al. 2011, Simón et al. 2012b).

Results and discussion

The ICLP was proven effective since the beginning of the programme in 2002 (Simón et al. 2012b), and a maintained increasing trend in the Iberian lynx population has been observed (Fig. 3). During the LIFE Lince-Andalucía and the LIFE Lince projects (2002–2011), the Iberian lynx population grew from 94 to 310 individuals. The increase in this period was mainly achieved by the enhancement of trophic resources and the reduction of mortality (Simón et al. 2013; López et al. 2014). Genetic management and reintroductions affect the population growth only the last years (after 2009). During the LIFE Iberlince and the LIFE Lynxconnect projects (from 2011 on), the Iberian lynx population increased from 310 individuals in 2011 to 2,021 individuals in 2023. The increase of the Iberian lynx population between 2011 and 2023 was mainly the result of the reintroduction strategy (based on both the ESCP and the genetic management). Natural spreading of Doñana population naturally occupied El Aljarafe, whereas that of Andújar-Cardeña occupied southern edge of Sierra Morena (C Sierra Morena and Montoro-Marmolejo and Zocueca), the Guadalmez valley, the nearby Guadalquivir River and some spots in the Baetic Mountains (Fig. 1).

Table 2. Different successful conservation measures implemented by the ICLP in 2002–2024, their estimated overall cost and their conservation effectiveness.

Measures	Subtype	Cost	Conservation effectiveness
Enhancement of trophic resources	Habitat management	Expensive	Low
	Rabbit restocking	Expensive	Low
	Supplementary feeding	Inexpensive	Moderate
Reduction of mortality	Illegal persecution	Inexpensive	Moderate
	Road kills	Expensive	Low
	Diseases	Inexpensive	Low
Genetic management	Wild population	Inexpensive	Moderate
	Captive population	Inexpensive	Moderate
Ex situ conservation program		Expensive	High
Reintroductions		Moderate	High
Enhancement of the connectivity		Inexpensive	Expected high

The effectiveness of the conservation measures implemented by the ICLP in 2002–2024 is not homogeneous (Table 2). Measures focused in the enhancement of trophic resources are expensive and their result is limited in time and space. These measures were necessary in the beginning of the ICLP (since the Iberian lynx remained in suboptimal trophic areas) but have been decreased in favour of other more cost-effective measures. Measures aimed to reduce illegal persecution and diseases are inexpensive and have shown the effective in reducing mortality rates. Measures aimed to reduce road kills are very expensive, but their implementation in black spots is still considered necessary. The genetic management programme of the population is also considered essential due to the huge genetic erosion suffered by the species. The ESCP is costly, but it is a strategic tool that allowed the creation of nine genetically-healthy reintroduction areas (see Fig. 4). In fact, only 2–3 reintroduction areas would have been created if the ESCP had not existed. Moreover, the genetic management of the ESCP allowed the preservation of almost all the remnant genetic diversity in 2002, and nowadays, the captive population holds the higher genetic diversity of all populations. Reintroductions in optimal selected areas allowed the faster rate of population growth due to capacity of the species to grow in high-rabbit-density scenarios (Sarmento et al. 2019).

To sum up, the conservation measures implemented in the ICLP have raised the Iberian lynx population from 94 individuals in 2002 to 2020 individuals in 2024. The current population size is probably similar to that in the mid-20th century. Once preserved both remnant populations in 2002, and considering the subsquent success of the reintroduction programme, the conservation measures should now be focused on 1) maintaining low levels of anthropogenic mortality, 2) creating new populations in optimal areas, using genetically-selected individuals and 3) maintain the flux among all existing populations.

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Regional Government of Castilla la Mancha: Regional Ministries responsible for the Environment and Roads: Administration of the Region of Murcia: Regional Ministries with competences in Environment; Spanish Administration: Ministries with competences in Environment, Roads and Autonomous Agency of National Parks; Portuguese Administration: *Instituto da Conservação da Natureza e das Florestas*, *Infraestructuras de Portugal and EDIA*; Local Administrations: *Diputación de Badajoz, Câmara Municipal de Moura and Comunidade Intermunicipal do Baixo Alentejo*; Research Centres: Doñana Biological Station, Clinical Laboratory, Leibniz Institute for Zoo and Wildlife Research, *Museo Nacional de Ciencias Naturales, Universidad Autónoma de Madrid*, University of Cordoba and University of Lisbon; Organisations representing landowners and hunters: Andalusian Hunting Federation, Extremadura Hunting Federation, Artemisam Foundation, Andalusian Association of Hunting Producers and ATECA hunting group; Conservation NGOs: CBD Hábitat Foundation, Ecologistas en Acción Andalucía, ADENA/WWF-Spain, *Asociación para la Defensa de la Naturaleza de Extremadura*, the Spanish *Sociedad para la Conservación y el Estudio de los Mamíferos* and Iberlinx association; Private companies: Acajú, AGROFOREX, FOTEX and FOMECAM.

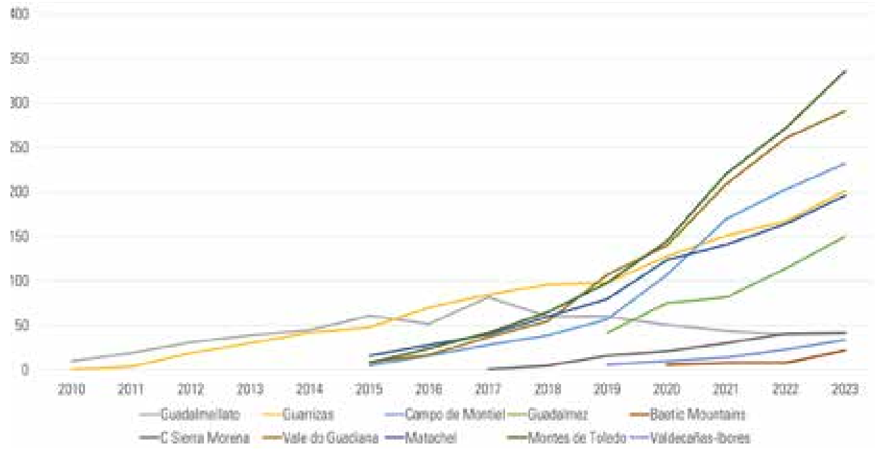

Fig. 4. Evolution of the population size of the different re-introduced and naturally-dispersed Iberian lynx populations after 2010.

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The Iberian lynx ex-situ conservation programme: from birth to release

The Iberian lynx *Lynx pardinus* ex-situ conservation programme was established in 2001, as the species was Critically Endangered, with the aim of maintaining a healthy, genetically sound captive breeding population to prevent extinction and provide a source for future reintroductions. After a slow early progress, the programme rapidly expanded after 2005 to a network of exclusive and associated breeding centres in Spain and Portugal. Extensive research advanced understanding of lynx reproductive biology leading to developments such as genus-specific pregnancy diagnosis, while assisted reproductive techniques and biobanking are being developed to optimise genetic management and reproductive output. The programme faced severe health challenges during its expansion - vitamin D toxicosis and disorders of likely genetic basis causing threatening clinical and demographic issues. When the programme reached its maturity, a specialised reintroduction training protocol for the Iberian lynx was implemented to promote natural behaviours critical for survival in the wild prior to release. By 2023, over 700 cubs had been produced across the breeding network from over 400 breeding events, and 403 lynxes have been released so far, playing a pivotal role in re-establishing 8 new free-ranging populations across the Iberian Peninsula and downlisting the species to Endangered and recently to a Vulnerable conservation status. Maintaining adequate population size, genetic diversity, and dealing with the overcrowding of enclosures due to the demographic challenge are priorities going forward as additional reintroductions are required to reach and maintain a favourable conservation status. Adapting the ex-situ programme to face other emerging challenges such as the rehabilitation of injured/orphaned or conflict generating free-ranging lynxes is necessary while upholding core principles that have enabled the program's success so far.

The historical context of Iberian lynx ex-situ conservation

The European Action Plan for the conservation for the Iberian Lynx (Delibes et al. 2000) states that individuals coming from captive stock could be required if the species reached critical levels in the wild. On the other hand, it questions if captive breeding could be a useful and effective conservation tool, both technically and in terms of use of resources eventually drawn from in-situ conservation, signalling some resistance to its use. The first Action Plan for the Captive Breeding of the Iberian Lynx was approved by the National Commission for the Protection of Nature (Spain) in 2001 and was modelled on the European Association of Zoos and Aquaria Ex-situ Programs. The Iberian lynx ex-situ conservation programme was to act as a "safety net" against extinction in the wild, support in-situ conservation and help raise social awareness about the threats to the survival of the species, relying on a Captive Breeding Committee with specialised working groups and in-situ representatives to advise it.

The El Acebuche Iberian lynx captive breeding centre (Huelva, Spain) was inaugurated in 1992. However, the first breeding attempt in captivity only took place in 2004. This happened immediately after an Iberian-wide census confirmed the absence of lynxes in Portugal and the presence of less than 200 lynxes in Spain [cross ref chapter 3 Rodríguez et al. 2024]. In July 2003, a Bilateral Commission was created between central Spanish and regional Andalusian governments to address coordination issues. By then the conservation status of the species was Critically Endangered. If the species was to be declared Extinct In the Wild at that time, there would be no "safety net" in captivity and the species would be considered effectively Extinct.

There were only four females in captivity in 2003 – and only one hand-reared adult female of breeding age – so males needed to be brought to "El Acebuche". Jerez Zoo came forth as an essential piece of the puzzle by hand-rearing two sub-adult females and holding one of the first wild-sourced males to become part of the breeding programme. This male was transferred to El Acebuche on the last day of 2003. With only a recently wild caught male and one hand-reared adult female at El Acebuche for the 2004 breeding season, it was no surprise that no litter was produced from the first breeding couple established. But gears were finally turning.

The first years of the ex-situ programme and its expansion

The year 2004 saw the captive stock at El Acebuche rise to the projected seven founders (3.4) only after the first mating season had occurred. In October, the IUCN's Conservation Breeding Specialist Group presented its recommendations for the genetic and demographic management of the captive breeding programme – the scenario selected aimed to maintain 85% of available genetic diversity for 30 years. A total of 60 breeding lynxes (30.30) were to be kept in captivity, by incorporating four wild-born cubs a year for five years and one adult from a rehabilitation centre every two years (Lacy & Vargas 2004). The population had to then grow exponentially and the ex-situ conservation action plan proposed a network of exclusive Iberian lynx captive breeding centres (Fig. 1) and associated breeding centres in zoos. On 28 March 2005, the first litter was born in captivity and the captive breeding programme did grow exponentially after that, with the "La Olivilla" exclusive breeding centre (Jaén, Spain) opening in early 2007.

The exponential growth of the programme ultimately led to its internationalisation, allowing the Iberian lynx to return to Portugal from where it disappeared in the early 90s. Portugal proposed a national ex-situ conservation action plan to the Captive Breeding Committee in 2005 (Serra et al. 2005), but only in 2008 did Portugal formally approve a national conservation action plan for the species (Sarmento et al. 2009). This happened in the wake of the construction of the National Breeding Centre for Iberian lynxes (CNRLI, Algarve) in 2008, a compensation measure decreed by the European Commission for the construction of the Odelouca Dam in a Natura 2000 classified site. Several agreements were signed between Spanish and Portuguese governments for Iberian lynx conservation, most notably in July 2009 to formalise the transfer of lynx between the two countries for captive breeding purposes. The CNRLI received its first animals in October 2009, paving the way for Iberian lynx reintroduction to Portugal in 2015.

The "Zarza de Granadilla" exclusive breeding centre (Cáceres, Spain) received their first lynxes in March 2011, and the programme reached the current conformation of its network – four exclusive breeding centres, where only Iberian lynxes are bred onsite; and one associated breeding centre at Jerez Zoo (Fig. 2). The close technical and scientific cooperation between this network of breeding centres - managed by different regional and national authorities - has been key to achieve common goals and relevant milestones. The ex-situ programme currently provides over 80 enclosures for captive breeding and reintroduction training, holding approximately 150 animals every breeding season.

Genetic and demographic management of the ex-situ population

The first main goal of the ex-situ programme is to maintain a genetically and demographically managed captive population (Vargas et al. 2008). The genetic diversity of the species was already greatly depauperated at the start of the ex-situ programme, seriously threatening its survival. Maintaining the maximum diversity possible has been central to the management of the captive breeding programme, achieved through the definition of breeder priority and mating schemes using minimum mean kinship and known genealogy. Captive-born lynxes are generally less inbred than their wild-born counterparts, and less inbred individuals appear to be more likely to survive and more successful in reproduction. The registered increase in survivability and reproduction output most likely played a role in forcing the revision of the early demographic projections of the ex-situ programme (Godoy et al. 2024).

As the breeding programme expanded its projections also grew: from keeping 60–70 breeders and producing 12 animals for reintroduction projects from 2011 onwards, to finally holding approximately 100 breeders and producing 40 surviving cubs, on average, every year since 2012. The start of the reintroduction projects using captive bred animals in 2011, their expansion to 6 new populations in Spain and Portugal by 2014–2015 and the need for a continuous yearly supply of lynxes to feed those projects seriously impacted the demographic dynamics and structure of the programme. This resulted in a combination of 1) the need to hold back a greater number of cubs a year to replace breeders in order keep the programme demographically viable and genetically sound; and 2) an accumulation of geriatric and surplus animals at the breeding centres overcrowding its enclosures. The resulting overpopulation threatens to collapse the ex-situ programme and constitutes one of its greater immediate challenges.

Fig. 1. Example of an exclusive Iberian lynx breeding centre. 1) Breeding enclosures; 2) Coordination and video-surveillance centre; 3) Clinic / laboratory, industrial kitchen and neonatology buildings; 4) Live prey enclosures; 5) Quarantine and rehabilitation enclosures; 6) Reintroduction training enclosures.

Fig. 2. Map of the current network of exclusive and associated breeding centres of the Iberian Lynx Ex-situ Conservation Programme.

Reproductive physiology, assisted reproduction and the Biological Resource Bank

At the beginning of the 21st century not many studies were published on Iberian lynx reproductive physiology and endocrinology. The captive breeding programme has fostered extensive research on these subjects since its creation. From then onwards, a disproportionately high number of studies have been

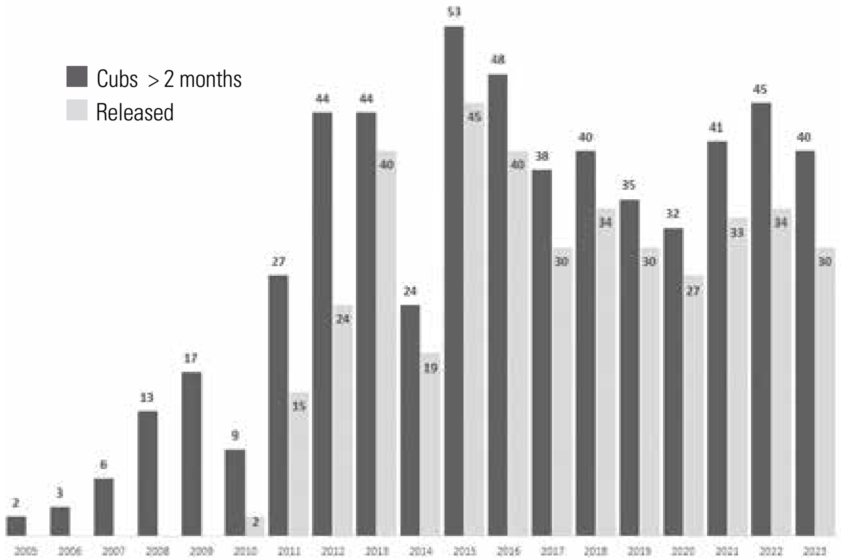

Fig. 3. Number of weaned cubs and lynxes released per year from 2005 to 2023.

conducted on Iberian lynx reproductive physiology relative to its geographical distribution when compared to other Iberian carnivores (Rosalino et al. 2023).

The reproductive physiology of the Iberian lynx was mostly unknown before the captive breeding programme and limited information was available on its reproductive cycle (e.g. Palomares et al. 2005). The assessment of Iberian lynx ovarian life-cycle through endo crinological and ultrasonographic analysis uncovered a "non cat-like" oestrus cycle due to the persistency of its corpora lutea CL, observed as being persistent in the *Lynx* genus (Goeritz et al. 2009, Jewgenow et al. 2014). The persistency of the CLs and high progesterone levels in blood, faeces and urine throughout the year (Dehnhard et al. 2009) led to the development of accurate genus-specific pregnancy diagnostic tests, especially needed due to the propensity shown by lynxes to develop pseudo-pregnancies (Finkenwirth et al. 2010). Female lynxes have been observed to be seasonally polyoestrous, mating only during the winter and spring months, whereas males vary in their breeding capacity, with sperm production between November and May and little or no sperm production during the summer (Gañán et al. 2010).

Ongoing efforts are being directed to the development of assisted reproductive techniques such as semen cryopreservation, artificial insemination and embryo production to maximise genetic management and reproductive output (e.g. Gañán et al. 2009). Attempts at influencing the natural ovarian cycle through luteolysis of persistent CL have failed so far (Painer et al. 2014), as have attempts at chemically inducing oestrus. Preserving somatic cells, blood, serum, and gametes in biological resource banks to maintain maximum genetic diversity – and developing assisted reproduction techniques – is an ongoing priority of the ex-situ programme (Roldán et al. 2009).

Health management and challenges faced

One of the first priorities of the veterinary advisory group was to develop working protocols and the establishment of a biomedical database. The information thus gathered allowed for the determination of baseline reference values for critical clinical parameters and the identification of the main causes of mortality and relevant infectious disease threats. A retrospective study of the morbidity and mortality in the ex-situ programme using the medical records of 120 lynxes highlighted three pathologies of note: chronic vitamin D toxicosis, juvenile idiopathic epilepsy and cryptorchidism (Martínez et al. 2013). Vitamin D intoxication affected over 50% of the ex-situ population and caused at least 28 cases of renal failure (Lopez et al. 2016). The analysis of mineral and vitamin supplements administered during that period showed approximately 30 times the vitamin D3 content indicated in the label of those batches.

Juvenile idiopathic epilepsy, most likely with a genetic basis, reached a prevalence of 7.44% of cubs born between 2005-2012 and caused the death of 50% of affected animals (Mínguez et al. 2021). Cryptorchidism, also likely genetic in origin, reached a prevalence of 5.63%. Avoiding mating of identified "carriers" significantly diminished the prevalence of both these conditions and no cases have been registered since 2018. One of the highest causes of morbidity detected, with associated mortality, was sibling aggression of cubs - starting with the first litter ever to be born in captivity in 2005 (Antonevich et al. 2009). Sibling aggression is seen in almost all litters with only rare exceptions, takes place mostly between days 38 and 63 after birth, and has resulted in at least seven fatalities to date.

The reintroduction training protocol

To reach the second main goal of the ex-situ programme – to create new Iberian lynx free-ranging populations through reintroduction - the husbandry protocols used for captive lynxes had to be re-directed. If Iberian lynx husbandry in captivity is generally aimed at striking a balance between fostering natural behaviours and creating a stress-free environment for successful mating, reintroduction training aims to provide a more challenging environment to increase the chances of successful adaptation and survival in the wild. The training protocol is directed to ensure that all lynxes released have the following skills: 1) prey identification and application of correct hunting techniques; 2) predator identification and avoidance; and 3) displaying correct natural, social behaviours conducive to territory acquisition and defence.

Reintroduction candidates are offered bigger, more complex and naturalised enclosures where they are fed exclusively live prey at randomised times and in irregular quantities, mimicking prey availability in the wild and building relative tension between siblings for access to resources, creating opportunities for social behaviour development. The prey is offered through indirect systems that disconnect prey supply from human presence, and predator avoidance is then strengthened by actively reinforcing fear responses towards humans (its main predator). Animal responses to this training procedures are then observed through CCTV systems, and behaviours recorded and evaluated according to specific protocols (Grupo asesor de manejo en cautividad 2016).

Candidates are then subjected to health checks and quarantine procedures, radio-collared and assigned to release areas following genetic criteria for population/genetic reinforcement or re-introduction purposes (Godoy et al. 2024). The majority of lynxes are released at around 11 months of age, in accordance with

Iberian lynx with her cub at El Acebuche breeding centre (Photo A. Sliwa).

the dispersion age registered for most subadults in the wild, opening space for the next cohort to be born and trained in captivity.

Global results and future directions for the Ex-Situ Conservation Programme

From 2004 to 2023, the Ex-Situ programme has established 405 breeding pairs, 372 of which have been observed mating (92%). We registered 316 pregnancies (85% of females mated) generating a total of 730 cubs, 2.5 cubs per litter on average. A total of 561 cubs (76.8%) survived to the age of two months old. Reintroduction and genetic reinforcement efforts started in 2011, and so far, 403 cubs born in captivity were released under the umbrella of LIFE+ projects. Captive lynxes trained for release have achieved approximately 70% yearly survival, have established territories and bred extensively, helping to create eight new populations of Iberian lynxes in the peninsula, playing a major role in the species spectacular recovery so far (Garrote et al. 2024). The programme's output of lynxes released to the wild has been 6.7 times greater than the number of lynxes extracted from it to establish the ex-situ programme.

The current proposal for an Iberian strategy for the conservation of Iberian lynxes establishes that at least another eight populations must be created to reach a favourable conservation status for the species, implying that the Ex-situ programme must keep breeding and training lynxes for release at the same rhythm of the previous decade. This implies facing pressing challenges such as the current demographic crisis successfully, finding suitable solutions for surplus lynxes in a timely manner to prevent the collapse of the programme while incorporating new breeders at the recommended pace to avoid losing genetic diversity. Expanding the ex-situ programme to an increasing number of zoological institutions is not only critical to meet the demographic and surplus challenge, it is also crucial for the long-term conservation of Iberian lynx genetic diversity.

The programme must also adapt to modern times while keeping its fundamental unity and technical and scientific cohesion. A revision of its action plan is overdue to clarify management models, research objectives and working groups to drive the programme forward, revisiting and improving standard operational procedures SOPs to maintain output and quality levels while maintaining budgetary stability. New challenges related to the exponential growth of free ranging populations need to be addressed, most notably the rehabilitation of the ever-growing number of orphans, injured or conflict-generating lynxes welcomed at ex-situ facilities without sacrificing proven biosecurity protocols and the ex-situ demographic balance.

The programme needs to keep working towards a favourable conservation status for the species, evolving and expanding SOPs, integrating zoological and rehabilitation institutions into the programme while ensuring appropriate resources, and to hold fast to the principles that have helped the Iberian lynx escape the extinction vortex through ex-situ conservation.

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Iberian lynx cub at El Acebuche breeding centre (Photo A. Sliwa).

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Genetic monitoring and management of Iberian lynx populations

The Iberian lynx *Lynx pardinus* is one of the most genetically depauperated species on earth. This is likely due to the combination of long-term small population sizes and serial historical bottlenecks. Conservation actions, including captive breeding, translocations and reintroductions, have minimised genetic risks through genetic management, which involved the admixture of the two remnant populations. Furthermore, a strategy based on the minimisation of mean kinship has succeeded in increasing genetic diversity and reducing average inbreeding in remnant, captive and reintroduced populations. To further support this genetic management, an ambitious monitoring programme based on the genetic individualisation of scats collected over known lynx territories was implemented, which is allowing to estimate census and to reconstruct the genealogies of the reintroduced populations. Thanks to this, current lynxes are less inbred and populations are more diverse on average than any of the two remnant populations were by the end of the 20th century. Preliminary evidence indicates that this has also contributed to population growth through the higher fitness of admixed individuals. As populations grow and systematic releases are eventually stopped, the intensive individual-based genetic monitoring and management should shift towards a population-based monitoring and management. Conservation actions should be maintained until its long-term viability is guaranteed, and this will require the establishment of at least three populations with effective sizes above 150, 10 subpopulations over 40, and migration rates close to 0.1 between neighbouring subpopulations.

Genetic status of Iberian lynx populations by 2002

The genetic status of Iberian lynx populations by the end of the 20th century, when only two small and isolated populations remained in Southern Spain, was evaluated first with microsatellite markers and short mitochondrial sequences and later with whole genome sequences. Early results raised concern by showing extremely low levels of genetic diversity when compared with other endangered felids, and high levels of inbreeding, especially so for the smaller Doñana population. These results also showed high levels of genetic differentiation between the two remnant populations. Furthermore, estimates of effective population sizes of around 10 in Doñana and 20 in Sierra Morena indicated that genetic diversity would be further reduced by 50% in less than 60 and 130 years, respectively, if the current situation persisted (Casas-Marce et al. 2013).

The concern for the viability of Iberian lynx increased with the accumulating evidence of deteriorated health, low survival and poor reproduction, which included: i) a decrease in litter size, and an increase in disease-associated mortality in recent years in Doñana, indicating that Doñana population may have already entered an extinction-vortex dynamics (Palomares et al. 2012); ii) high incidences of glomerulonephritis and lymphoid depletion (Jiménez et al. 2008, Peña et al. 2006), and a high virulence of a recent feline leukaemia virus epidemics (Meli et al. 2010).; iii) individual heterozygosity correlating with semen quality in both populations (Ruiz-López et al. 2012); iv) several deleterious traits that were observed at relatively high frequencies in the captive population, including cryptorchidism and idiopathic juvenile epilepsy (Martínez et al. 2013, Mínguez et al. 2021).

The critical genetic status of Iberian lynx by 2002 was further confirmed by whole genome sequences, which identified the species as one of the most genetically depauperated (Abascal et al. 2016). By reconstructing its demographic history, this study also suggested that the extremely low levels of genetic diversity were the consequence of both effective population sizes of a few thousands throughout most of its history and serial bottlenecks in the 16th and the 20th century. Subsequently, patterns of genetic diversity along the genome revealed a substantial accumulation of moderately deleterious variants due to the relaxation of purifying selection in Doñana in comparison to Sierra Morena (Lucena-Perez et al. 2021), and the reduction in the load of highly deleterious (partly) recessive mutations in Iberian lynx with respect to the more abundant Eurasian lynx due to purging (Kleinman-Ruiz et al. 2022).

Genetic patterns in historical and ancient populations

A retrospective analysis of historical populations based on specimens preserved in public and private collections revealed an already genetically structured population by mid-20th century, but with globally higher diversity than remnant populations at the end of the century (Casas-Marcé et al. 2017; Table 1, Fig. 1). The patterns of genetic diversity through time indicated varying levels of genetic drift and, thus, effective population sizes in different subpopulations, in general agreement with inferred census sizes and time in isolation. Whereas Doñana was estimated to have remained small ($N_e \approx 20$) and isolated for ca.

Table 1. Microsatellite genetic diversity in modern and historical Iberian lynx populations (Casas-Marce et al. 2017).

Epoch	Population	N	Dates range	H_e (SE)
Current	**Global**	**210**	**1991–2010**	**0.54 (0.13)**
Current	E. Sierra Morena	102	1991–2010	0.51 (0.14)
Current	Doñana	110	1991–2007	0.31 (0.20)
Historical	**Global**	**143**	**1856–1990**	**0.60 (0.13)**
Historical	Montes de Toledo	22	1939–1977	0.58 (0.17)
Historical	E. Sierra Morena	10	1960–1990	0.61 (0.17)
Historical	Far-E. Sierra Morena	13	1966–1989	0.44 (0.21)
Historical	W. Sierra Morena	3	1970–1972	0.51 (0.32)
Historical	Vale do Sado	8	1881–1956	0.55 (0.21)
Historical	Central Range	18	1916–1993	0.50 (0.15)
Historical	Doñana	64	1856–1990	0.41 (0.20)

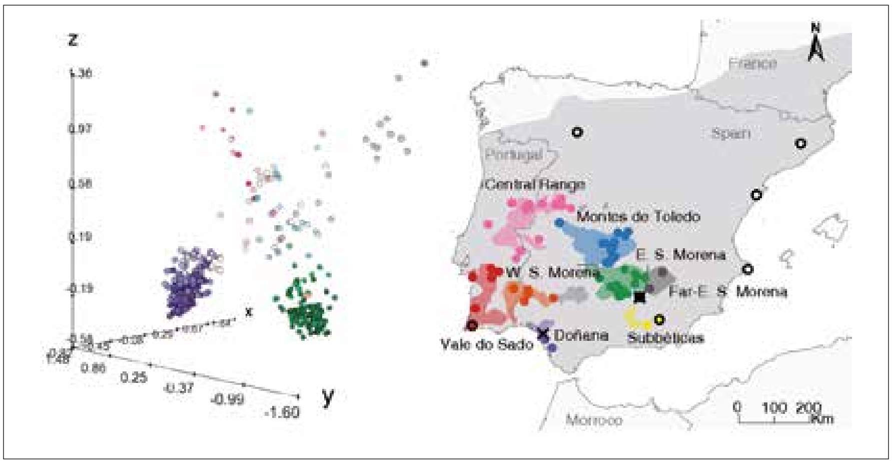

Fig. 1. Factorial Correspondence Analysis FCA of microsatellite variation in contemporary and historical Iberian lynxes. Populations are coded by colour (refer to map) and colour saturation increases with sample date (more saturated in recent samples).The pattern depicts a less structured historical population from which different subpopulations have progressively and independently differentiated through drift (Casas-Marce et al. 2017).

200 years, the Sierra Morena population became isolated at larger sizes ($N_e \approx 30$) more recently, around 1950. Interestingly, the large and central Montes de Toledo population showed highest and stable diversity levels until its extinction, indicating a fast demographic collapse (Casas-Marcé et al. 2017).

Ancient data, first obtained for ten whole mitogenomes, indicated similar diversity and less structure in the deeper past when compared to historical populations (Casas-Marcé et al. 2017), whereas three whole nuclear genomes more recently obtained revealed lower genome-wide diversity in ancient than in remnant populations, which was associated to increased introgression from Eurasian lynx in the latter (Lucena-Perez et al. 2024).

By showing that genetic differentiation between the two remnant populations was a consequence of recent population decline and isolation, and in the absence of evidence for adaptive divergences, historical genetics supported the consideration of the species as a single Evolutionary Significant Unit ESU and validated the joint management and eventual admixture of the two populations.

Genetic management of Iberian lynx populations

Conservation actions starting in 2002 have specifically addressed genetic risks through the implementation of a genetic management programme covering conservation breeding, translocations for genetic rescue, and reintroductions. The general strategy applied has been the minimisation of mean kinship, a well stablished strategy that has proven effective in minimising diversity loss and inbreeding accumulation in captive breeding.

Captive breeding

Through the recruitment of up to 60 founders over the years since its start in 2004, the captive breeding programme has succeeded in capturing most of the diversity in each of the two remnant populations, measured as the expected heterozygosity (H_e) as well as the allelic frequencies (Kleinman-Ruiz et al. 2019). Breeders were prioritised and mating schemes were designed based on minimum mean kinship. Being kinship proportional to the amount of genetic information shared between individuals, breeders with low levels of mean kinship harbours specific/unique information that deserves to be transmitted. Therefore, they have to be prioritised for yielding offspring. Additionally, the kinship between parents is equal to the inbreeding of their offspring. Consequently, the sensible methodology is trying to avoid the mating between relatives by arranging the couples as to provide the minimum mean kinship between couples. To conduct both strategies, kinship was estimated through a combined approach using molecular markers (36 microsatellite markers from 2005 to 2022 and 286 SNPs since 2023; Kleinman-Ruiz et al. 2017) to produce a kinship matrix among wild-caught founders, which was then incorporated to the known genealogy to calculate the kinship among all captive individuals. As the consequence of genetic management, captive born individuals are generally less inbred than wild-born individuals, and captive population heterozygosity is approaching the maximum expected heterozygosity achievable by mixing the two populations in optimal proportions (Kleinman-Ruiz et al. 2019). Preliminary results also indicate that less inbred admixed individuals are more likely to survive and are more successful in reproduction than non-admixed individuals.

Translocations and genetic rescue

In 2007, a first male was translocated from Sierra Morena to the highly eroded Doñana population in an attempt to restore genetic diversity and hopefully improve demographic parameters. This first translocated animal, named Baya, reproduced successfully in the following years, whereas only two of the eight subsequent releases reproduced. Translocations have succeeded in increasing genetic diversity in Doñana caused by the higher heterozygosity of admixed individuals (Fig. 2). Furthermore, genetic improvement has run in parallel to the first significant demographic growth in the last decades. This growth can be putatively attributed to higher reproductive success of admixed individuals, providing a potential example of a successful genetic rescue (López et al. 2015, Simón et al. 2012). However, the high success of Baya and its descendants has also produced subsequent inbreeding which may facilitate the expression of its genetic load and jeopardise the full recovery of the population. To minimise these risks, regular translocations are advised until natural gene-flow into Doñana is restored.

Reintroductions

Reintroductions started in 2010 and have been almost exclusively based on the release of captive-born, mostly admixed individuals (Fig. 2). Initial releases at selected sites were designed to maximise starting diversity in the release area by selecting animals minimally related among themselves, whereas subsequent annual releases at the same site selected animals that were minimally related to previously released animals. As the information on the current population coming from field monitoring based on radio-tracking and camera traps became available, the close genetic relationship between released animals and all the individuals living in the recipient population was also avoided. Rather than selecting individuals sequentially, a heuristic search was performed to find the optimal distribution of available cubs among all recipient populations at once, while accounting for any a priori restrictions on number, sex or identity of animals to be released at each site.

Non-invasive genetic monitoring

As the reintroduced populations grew fuelled by in situ reproduction, the completeness and reliability of field monitoring data was progressively reduced, severely jeopardising the effectiveness of genetic management. Starting in 2022, an ambitious non-invasive genetic monitoring programme was implemented to expand and curate field-based genealogies and provide marker genotypes for a precise individual-based management. Samples of faeces are collected in known lynx territories using cotton swabs and placed in barcoded tubes containing lysis buffer (Ramon-Laca et al. 2015), and sample information, including geographic coordinates, are recorded and submitted to a dedicated server using Cybertracker. Once in the lab DNA is extracted, a species-diagnostic assay is applied (Palomares et al. 2002), and samples passing a nuclear amplification test are genotyped for a panel of 94 highly informative SNPs (Kleinman-Ruiz et al. 2017) plus two sex-specific markers in a microfluidic platform (von Thaden et al. 2017). Genotypes are then compared to a reference genotypes database to identify previously sampled individuals, and called new genotypes when no match is found. Multigeneration genealogies are reconstructed from genotypes using Sequoia (Huisman 2017). At the date of writing (April 2024) more than 4000 faecal samples have been processed, yielding around 2000 reliable complete genotypes corresponding to more than 600 individuals, ca. 150 of which could be attributed to individuals typed previously from blood or tissue samples.

Genealogical and molecular information is being used to estimate and monitor population genetic and demographic parameters (e.g. census and effective population sizes), detect immigrants and estimate ongoing gene flow and, in general, to guide genetic management. Preliminary analyses of the available data suggest that reintroduced populations have retained a high proportion of the starting diversity represented in the captive stock. Nevertheless, they also have identified sites, usually isolated peripheral and recently colonised sites, where inbreeding is accumulating through the mating of close relatives. Genetic data has also confirmed cases of natural immigration followed by local reproduction, providing so far anecdotal evidence of gene flow between remnants and reintroduced, among reintroduced populations and between Portugal and Spain (Lopes-Fernandes et al. 2024).

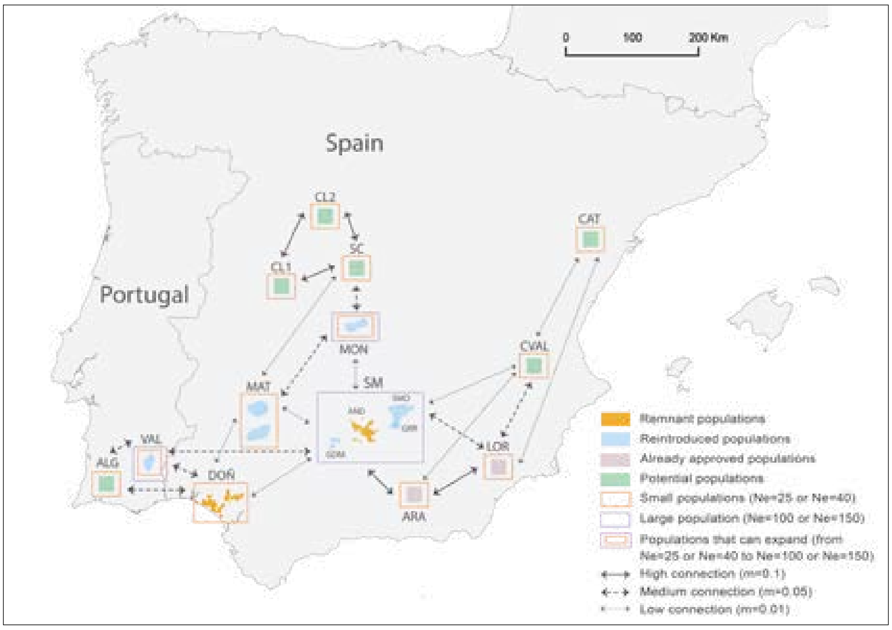

Fig. 2. Geographic distribution of remnant, reintroduced, approved and potential Iberian lynx subpopulations. Arrows show estimated migration rates between them, and rectangles delimit small (orange) or large (purple) subpopulations. Variants of this scenario with different population sizes and migration rates were modelled to evaluate the genetic viability of the species based on the expected trajectory of local and meta-population effective population sizes (Pacín et al. 2023).

Long-term genetic monitoring and management

The kind of intensive individual-based monitoring proposed for early stages of the reintroduction process will become unnecessary and unfeasible once the populations grow to their carrying capacity. Following the initial releases, the growth of reintroduced populations is mainly driven by in situ reproduction, survival and natural immigration and, therefore, releases will eventually be stopped. At the same time, genealogical and molecular information becomes more difficult to get with the intensity required for an individual-based management. This is the current situation of the reintroduced Iberian lynx populations in Vale do Guadiana, Montes de Toledo and Matachel (Extremadura). It is the same for the large and mostly interconnected nucleus in Sierra Morena formed by remnant Andújar-Cardeña together with neighbouring reintroduction sites at Guadalmellato (Córdoba), Guarrizas (Jaén), Campo de Montiel (Ciudad Real) and Guadalmez (Ciudad Real), with the other remnant population in Doñana being in an intermediate situation (Fig. 2).

Management during this phase should transition from an individual-based to a population-based approach, whereby monitoring can be limited to periodical estimation of population diversity (within- and between- subpopulations), inbreeding and gene flow (e.g. every 5 years, aprox. one generation), assisted, if necessary, by non-invasive sampling. Then, management will involve the occasional translocation of animals among populations whenever critical threshold values – yet to be defined – are surpassed.

Beyond the monitoring of genetic parameters, non-invasive genetic monitoring does provide an efficient and cost-effective way to monitor population size and density through spatial capture-mark-recapture approaches. Such approaches may prove a better alternative to current population monitoring based on camera-traps in the medium and long-term (López-Bao et al. 2020).

Defining genetic goals and evaluating demographic scenarios

Demographic goals for endangered species are often defined as the minimum viable population MVP. On the other hand, EU legislation defines the favourable reference population FRP as the minimum population size considered necessary to ensure long-term viability of the species. A recent evaluation estimated a total FRP of 750 breeding females for the Iberian lynx, and concluded that it would require the establishment of eight additional subpopulations (https://wwfes.awsassets.panda.org/downloads/2019conclusions-of-the-conference-the-iberian-lynx-looking-to-the-future.pdf). However, these demographic goals do not explicitly consider long-term genetic viability, which is usually defined as an N_e of 500. To fill this gap, we modeled population and metapopulation N_e under different metapopulation scenarios differing in number of subpopulations, census sizes and gene flow matrices (Fig. 2). Results indicated that achieving an $N_e \geq 500$ in a 100 years' time frame would require at least three populations with effective sizes above 150, plus 10 subpopulations over 40, and migration rates close to 0.1 between neighbouring subpopulations, resulting in a global population of 2,165 effective individuals (ca. 1,100 breeding females; Pacín et al. 2023). The spectacular recovery observed in the last decades allows for some optimism, but a premature triumphalism should be avoided and the current conservation efforts must be maintained to address this challenging goal.

Conclusions

When the Iberian lynx was at the brink of extinction by 2002, its extremely depauperated genetics, high inbreeding and poor fitness was perceived as an added heavy weight for a sinking ship. Only 20 years later the shipwreck has been avoided and the species seems to be safe afloat and navigating towards a better future. Such a remarkable recovery is the result of a sustained, efficient and multifaceted conservation efforts, as described in this Special Issue, which include the addressing of genetic issues through genetic management. Thanks to this, current lynx are less inbred and populations are more diverse on average than any of the two remnant populations were by the end of the 20th century. Preliminary evidences indicate that this has resulted in increased fitness and contributed to its spectacular recovery.

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The remarkable recovery of the Iberian lynx

By the early twenty-first century, the Iberian lynx *Lynx pardinus* was on the brink of extinction. As of 2002, conservation actions, including habitat management, reduction of mortality rates, reintroductions and genetic management, were implemented. As a result, about 700 Iberian lynxes were detected in the whole distribution area in 2018, and six new populations were created through reintroduction. At that point, the following step was to promote demographic and genetic connectivity among populations in order to assure the long-term conservation of the species. To this end, the LIFE Lynxconnect project is currently being developed with the goal of creating 10 more occupied areas functioning as stepping stones located among the existing populations. Moreover, new reintroduction projects are ongoing. In 2023, a total of 2021 individuals and 406 breeding females were detected. Of these, 92 individuals were detected in a total of ten stepping stones. Iberian lynx population has spread through the surroundings of the existing population nuclei, even in highly anthropised areas (such as agricultural lands) with high rabbit density and low levels of non-natural mortality. For example, the large olive groves surrounding the remnant Andújar-Cardeña population currently support more than 151 individuals. These findings suggest that the Iberian lynx holds greater ecological plasticity than previously thought, opening the door to new conservation strategies where habitat quality must be evaluated in a novel way. However, both non-natural mortality and rabbit population crashes can limit the growth and expansion of Iberian lynx populations. Road kills and poaching are the major causes of mortality, with average annual rates of 6.5% and 4.9%, respectively, for the entire geographic range. Too high mortality rates can locally hinder the settlement of the species in an area. Likewise, diseases continue to cause declines in European rabbit *Oryctolagus cuniculus* populations in some areas, thus limiting the suitable area for further Iberian lynx colonisation.

The conservation status of the Iberian lynx has undergone a remarkable transformation from the brink of extinction in the early twenty-first century to a population resurgence by 2023. This has been possible thanks to the development of a comprehensive conservation programme from 2002 on that encompassed 1) habitat management, 2) mortality reduction, 3) reintroductions, and 4) genetic management (López et al 2024). The next crucial step in this ongoing recovery effort is enhancing demographic and genetic connectivity among these populations to ensure the species' long-term survival.

This chapter provides a comprehensive and up-to-date account of the Iberian lynx's current status, and some lessons learned about the recovery of the species, focusing on three critical aspects: 1) the latest population numbers and distribution data as of 2023, 2) the goals and assessment of major conservation actions (with emphasis on reintroductions and connectivity between established populations) and 3) the spatial variation in cause-specific mortality rates. This examination elucidates the progress and ongoing challenges in the conservation of this iconic species, offering insights that are critical for future strategies aimed at securing both the survival and the expansion of the species across the Iberian Peninsula.

Current status and connectivity efforts for the Iberian lynx

As a result of the conservation strategy implemented in 2002 (López et al. 2024), the Iberian lynx population size at the end of LIFE Iberlince project was approximately 700 individuals by 2018 in eight populations (six of them were established through reintroduction; Iberlince 2018). The following step was to promote demographic and genetic connectivity among populations in order to ensure the long-term conservation of the species. To this end, the main goal of the ongoing LIFE Lynxconnect project is to create 10 more occupied areas that function as "stepping stones" among populations. Suitable patches (located between populations and holding enough habitat and prey to allow the settlement of a minimum of 2 reproductive females) were identified according to 1) ecological connectivity analysis for the Iberian lynx through analysis of minimum cost paths and circuit analysis (Blázquez-Cabrera et al. 2016), 2) distribution of the abundance of wild rabbit and 3) predicted habitat suitability for the Iberian lynx (Gastón et al. 2016). The actual suitability of these patches was evaluated by field sampling in a similar way to the selection of the reintroduction areas. A total of 16 areas were identified as eligible for selection as stepping stones. Simultaneously, reintroductions began in the new populations (Fig. 1) of Valdecañas-Ibores (Extremadura), Sierra Arana (Eastern Andalucía) and Lorca (Murcia). By 2023, a total of 2021 individuals and 406 breeding females were detected (Table 1, Fig. 1). Andújar-Cardeña, Guadalmellato, Guarrizas, Guadalmez and Campo de Montiel maintain a continuous exchange of individuals, functioning as a metapopulation in eastern Sierra Morena. The other populations created by reintroduction maintain their upward trend. Ten stepping stones were used by 92 lynxes, and reproduction was confirmed in six of them. Most of these stepping stones were colonised through natural dispersion and, when deemed necessary, they were reinforced by releasing individuals to facilitate the formation of reproductive pairs or to reduce inbreeding.

The lynx in agricultural areas

The Iberian lynx population has naturally spread through humanised areas with high rabbit density rather than through areas with presumed high-quality habitat, demonstrating it is not a habitat specialist. Thus, the species is nowadays occupying apparently suboptimal habitats such as anthropised areas. (Garrote et al. 2013, 2020). On the S and SW edges of the Andújar-Cardeña population, the Mediterranean scrubland borders vast extents of intensively cultivated olive *Olea europaea* groves. The first individual to establish there was detected in 2012 (Garrote et al. 2016). Since then, the Iberian lynx population inhabiting the olive groves has grown rapidly, and 151 lynxes and 28 breeding females were detected in 2023. Under these results, wild rabbit density, rather than habitat quality, seems to be the main predictor of occurrence of the Iberian lynx.

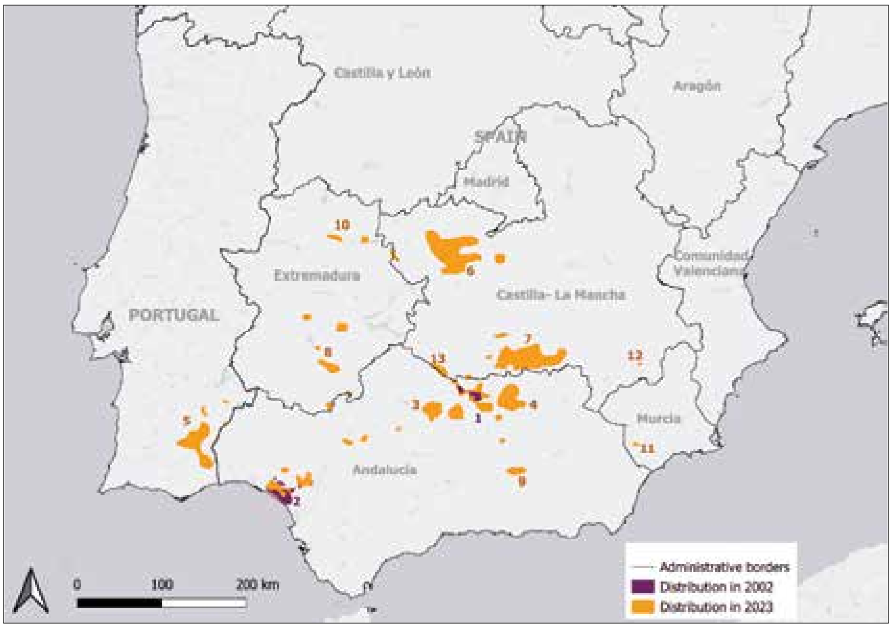

Fig. 1. Distribution range of the Iberian lynx in 2002 (Guzman et al. 2004) and 2023 (Lynxconnect unpub.data). Remnant populations: 1) Andújar-Cardeña and 2) Doñana. Reintroduced populations: 3) Guadalmellato, 4) Guarrizas, 5) Vale do Guadiana, 6) Montes de Toledo, 7) Campo de Montiel, 8) Matachel, 9) Sierra Arana, 10) Valdecañas-Ibores, 11) Lorca, 12) Campos de Hellín. Naturally funded populations: 13) Guadalmez Valle.

These olive crops in the Guadalquivir Valley are suitable for the species as long as there are good rabbit populations and low mortality rates (López-Parra et al. 2012, Garrote et al. 2013, López et al. 2014). The colonisation of these areas improved the connectivity among the nuclei of Andújar-Cardeña, Guarrizas and Guadalmellato. As a result, they are now considered a single metapopulation. Similar situations are found in cultivated areas of the foothills of Campo de Montiel and Montes de Toledo.

These findings suggest that Iberian lynxes hold greater ecological plasticity than previously thought (Fernández et al. 2000, 2006). Breeding females have been identified in olive groves whose territory was occupied by only about 2% scrub cover (Garrote et al. 2016). If management policies guarantee the existence of minimal shrub cover in agricultural areas, the Iberian lynx population would benefit. Given the current scarcity of wild rabbits in most of the Iberian habitats (Delibes-Mateos et al. 2014), ecotones between agricultural crops and scrubland could be the habitat with highest rabbit abundance in the Iberian lynx distribution range in the next decades (Calvete et al. 2004).

Table 1. Number of Iberian lynx individuals, breeding females and cubs detected in 2023. The Sierra Morena Oriental population is considered a metapopulation composed of the populations of Andújar-Cardeña, Guadalemellato Guarrizas, Campo de Montiel, and Guadalmez). Others: individuals detected outside the populations and stepping stones.

Population	Breeding females	Cubs	Individuals
Sierra Morena Oriental	190	315	913
Montes de Toledo	76	147	336
Vale do Guadiana	53	100	291
Matachel	33	64	168
Doñana - Aljarafe	27	41	130
Valdecañas/Ibores	4	14	34
Ortiga	7	9	28
Sierra Arana	0	0	13
Lorca	0	0	7
Stepping Stones	16	32	92
Others	0	0	9
Total	**406**	**722**	**2,021**

The reintroductions

The reintroduction programme allowed a much faster lynx population growth than any other conservation measure. This has been possible thanks to a detailed process of selection of the areas (Lynxconnect 2020), the preparation of the area for releases (Lynxconnect 2020b) and a successful captive breeding programme (Serra et al. 2024).

Both wild and captive-bred individuals adapted adequately to the areas where they were released. The average survival rate of lynxes from captivity during the first year since their release was 71% (Garrote 2019), higher than the average survival of 45% reported for reintroduced captive-born felines (Jule et al. 2008). The average survival rate of wild translocated individuals was 81%, whereas that of captive-born in the same areas was 60% (data from Guarrizas and Guadalmellato populations). A similar pattern was also reported in reintroduced Canada lynx *Lynx canadensis* (Devineau et al. 2011) and other carnivore species (Mathews, et al. 2005) where specimens born in the wild had higher survival rates than lynxes born in captivity.

There are two basic methods of releasing specimens in reintroduction programmes: direct release or "hard release" and release after a period of confinement to guarantee the adaptation of the specimens to the new area or "soft release" (Fritts et al. 1997). Whenever logistically possible, the first Iberian lynx releases in a new reintroduction area were carried out using the soft release system in pre-adaptation enclosures, in order to promote the survival of the specimens and guarantee their settlement, avoiding dispersal and return behaviours. Once lynxes were established in the area, they were released through hard releases. Regarding the release method, analysis of the GPS location data of the released animals suggests that the released lynxes that remain at least 30 days in the acclimatisation enclosures travel shorter distances and settle closer to the release point than other individuals (Garrote et al 2023). Likewise, 80% of soft released individuals establish their territory in the first year in comparison to 40% of hard released. Likewise, it has been demonstrated that if the releases conducted during the initial years of reintroduction are concentrated in a single small area, population growth is faster compared to those areas where releases were carried out in two or more locations within the same reintroduction zone (Garrote 2019).

Spatially concentrating releases minimises the dispersive movements of individuals, thus

Table 2. Annual mortality rates (%) by causes in wild populations of the Iberian lynx during the period 2011–2018.

Populations	Disease	Fight	Poaching	Road kill	Drowing	Inadaptation	Unknown	Total
Doñana	1.4	1.4	5.9	5.9	1.4	0.0	2.2	**17.6**
Andújar-Cardeña	4.5	3.1	0.8	3.9	0.0	0.0	4.3	**16.5**
Guadalmellato	1.1	1.3	11.8	10.5	0.0	1.6	6.2	**32.6**
Guarrizas	0.8	0.9	9.4	8.0	0.8	3.6	1.8	**25.3**
C. Montiel	0.0	0.0	7.4	23.4	0.0	0.0	7.5	**38.3**
Extremadura	4.2	0.0	2.5	5.8	0.0	0.0	2.6	**15.0**
M. de Toledo	0.0	0.0	0.0	8.5	2.2	0.0	3.6	**14.2**
V. do Guadiana	3.6	0.0	5.5	8.2	0.0	0.0	12	**29.4**
Total	**2.9**	**1.4**	**4.9**	**6.5**	**0.4**	**0.6**	**3.6**	**20.3**

reducing their probabilities of death (Berger-Tal & Saltz 2014). Similar conclusions have been previously obtained in various reintroduction projects of other species of the *Lynx* genus (Wilson 2018).

Mortality

A detailed study of the recent mortality rates in the Iberian lynx population was developed, with the information obtained from a total of 358 radio-tagged individuals during the period 2011-2018. Mortality events were evaluated to identify causes, and cause-specific annual mortality rates AMR were obtained using the nonparametric cumulative incidence function (Heisey & Patterson 2006). It must be taken into account that the mortality rates obtained in the case of the populations of Campo de Montiel, Matachel, Montes de Toledo and Vale do Guadiana, correspond to the first 3-4 years since the first releases were carried out. These populations were not yet consolidated and much of the information comes from released young individuals. An average annual mortality rate of 20.3% was identified (Table 2). By population, these values ranged between 14% in the Montes de Toledo and 38.3% in Campo de Montiel. The historical populations of Doñana and Andújar-Cardeña reached values of 17.6% and 16.5% respectively. The main causes of mortality were road-kills (AMR of 6.5%; 32% of deaths) and poaching (AMR of 4.9%; 24% of deaths). By population, the AMR due to road kills ranged between 3.9% in Andújar-Cardeña and 23.4% in Campo de Montiel. The AMR due to poaching ranged from 0% in Montes de Toledo to 11.8% in Guadalmellato. Interestingly, AMR due to poaching was higher than that due to road-kills both in Guadalmellato and in Guarrizas.

The AMR due to anthropogenic causes was the main one at an Iberian scale (11.7%). This pattern is repeated in all populations but the Andújar-Cardeña one, where natural AMR (7.5%) was found to be higher than anthropogenic AMR (4.6%). Mortality due to anthropogenic causes is nowadays more than twice from that identified in the period 2006–2011. This increase in non-natural mortality rates is probably a consequence of the expansion process of the species. An exponential increase of the distribution area implies a parallel increase in the length of roads within this enlarged range. Although actions continue to be carried out to reduce the number of casualties, the needs are increasingly greater, and it is not possible to act in all areas with a high roadkill risk. It is necessary to further implement defragmentation policies in large infrastructures, especially transport infrastructures. These infrastructures must be both safe and permeable for wildlife. There are currently tools available to build these infrastructures by assessing the least impact options, reducing the barrier effect and at the same time making them safe for wildlife. The pending issue is threats linked to existing infrastructures where society as a whole should make a greater effort. Major stakeholders include road managers and people using roads, who sometimes do not respect speed limits, thus reducing the effectiveness of the defragmentation efforts.

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo T. Pérez).

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo T. Céron).

In a similar manner, AMR due to illegal persecution has increased. Firstly, the Iberian lynx has settled in areas where illegal persecution of carnivores (snares, legholds, poison, etc.) is still present. Moreover, conflict with livestock (Garrote et al 2013) is now higher than 10 years before, and kills in revenge have been largely documented. In the current scenario of an expanding population, conservation managers should anticipate the potential conflicts that could arise as lynx colonise more humanised areas and implement preventive measures (preventing attacks to livestock, performing intensive surveillance and increasing awareness).

Not everything is a resounding success: The case of Guadalmellato

The recovery of the Iberian lynx has been a successful story at a global scale. However, the evolution of the population size has not been as positive as desired in all cases. In Guadalmellato population, releases began in 2010 and the expected carrying capacity was calculated to be 135 individuals. The population growth occurred as expected up to 2017, when 82 individuals were detected. However, the population declined since then, and as few as 41 individuals were recorded in 2023. Two main factors could explain this regression: 1) the abundance of rabbits drastically decreased in 2016 due to a new strain of the rabbit haemorrhagic disease virus (RHDV2, also known as Lagovirus europaeus GI.2; hereafer GI.2; Le Pendu et al. 2017). As a result, the average abundance decreased from 300 rabbits/km^2 in 2015 to 100 rabbit/km^2 in 2023; 2) AMR due to anthropogenic causes amounted to 18.2% in the period 2011-2018, exceeding the Iberian average of 11.7% and close to the global AMR in the Iberian Peninsula (20.3%). The global AMR in Guadalmellato was 32.6%

These factors affected demographic parameters of the population such as survival and reproduction. The apparent survival (accounting for both survival and emigration) of adults remained at mean values of 78% (min: 63%, max: 90%). The survival of subadults between 2010 and 2014 was 81% (min :73%, max: 100%), while in the period 2015-2020 the estimated apparent survival was 31% (min: 10 %, max: 54%). Regarding reproduction, with a maximum production of 27 cubs in 2015, it was reduced to 13 cubs in 2023. However, the number of breeding females remained relatively stable since 2015, varying between 13 and 18.

In a similar way, the outbreak of GI.2 in 2011 led to a decline of 60–70% in the rabbit populations in the scrubland areas of Andújar-Cardeña, which was followed by a fall of 45.5% in lynx breeding rates (Monterroso et al 2016). To this day, fecundity in the affected area continues to be conditioned to the application of supplementary feeding.

Conclusion

With more than 2,000 individuals, the current situation of the species makes us optimistic. The released individuals have shown a great capacity to adapt to the environment, as demonstrated by their high survival rates in the first stages of the creation of new populations, and their subsequent growth. The ecological plasticity of the species has contributed to its expansion and favored connectivity even cross habitats considered hostile for the species in the past. Poor habitat quality in these areas were more related to mortality risk than to the lack of resources. Currently, the impact of limiting factors, such as non-natural mortality and rabbit diseases, appear not to be limiting population growth at the range scale. However, it is necessary to monitor the factors limiting the survival of the species, since these can have an impact at the local level, causing a significant decline in some populations. A future challenge is the achievement of a viable Iberian lynx metapopulation, connected both genetically and demographically, in order to ensure the long-term conservation of the species.

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Iberian lynx recovery potential: results of the first Green Status of Species assessment

The reduction in the extinction risk of the Iberian lynx *Lynx pardinus* from Critically Endangered to Vulnerable is proof that conservation can work to bring species back from the brink. However, that does not mean that the work of conservation is over; preventing extinction is merely the first step on the road to recovery. In 2021, the International Union for Conservation of Nature IUCN expanded the Red List of Threatened Species assessment to include a standardised assessment of species recovery: The IUCN Green Status of Species. The Green Status of Species assessment assigns species to recovery categories, complementary to the classic extinction risk categories. In addition, the Green Status of Species provides a method to evaluate the impact of past conservation, and the potential for future conservation impact, on species' status. In 2023, the first-ever Green Status assessment for the Iberian lynx was conducted. Though the species' status has improved greatly over the past decades, its Green Status has nonetheless been assessed as Largely Depleted, indicating that there is more work to do to restore the species to pre-impact levels. However, the assessment also indicates that without past conservation actions, the species would likely be Extinct in the Wild today. The assessment also indicates a high Recovery Potential, meaning that it would be possible to recover the species across much of its former range with concerted conservation effort.

The downlisting of the Iberian lynx from Critically Endangered to Vulnerable (Breitenmoser & Breitenmoser-Würsten 2024) is a conservation triumph. In the decades since 2002, when the Iberian lynx was first assessed as Critically Endangered (Cat Specialist Group 2002), herculean efforts have been made to pull the species back from the brink (Serra 2024, Godoy et al. 2024, López et al. 2024a). While the change in Red List Category reflects those efforts, it does not tell the full story of the species' conservation. Firstly, it does not fully communicate the large reduction in range that has occurred within recent centuries (López et al. 2024b, Rodríguez 2024); although increasing lynx numbers are a sure sign of the species' diminishing extinction risk (as shown by its downlisting to Vulnerable), numbers are not yet increasing across all of the historical distribution. The change in Red List Category also does not fully capture the impact of conservation action for the Iberian lynx; with conservation, the extinction risk has been reduced, but these actions also averted further declines.

Developed in response to a 2012 IUCN Members Resolution (IUCN 2012a), the Green Status of Species (previously known as the Green List of Species; Akçakaya et al. 2018), provides a widely applicable, objective, and practical framework to assess species recovery. The Green Status of Species recovery definition considers the viability, ecological functionality, and representation of the species relative to a baseline representing these criteria prior to major human impacts on the species (IUCN 2021). This information about species condition relative to the "fully recovered" state complements the Red List Category (Grace et al. 2021a) and can be used to inform and incentivise more ambitious conservation goals. The assessment also measures the impact of conservation actions on a species' progress toward recovery, helping inform conservation planning (Grace et al. 2021b).

To fully understand the conservation story of the Iberian lynx, the first IUCN Green Status of Species assessment for this species was completed at a workshop in Sevilla, Spain, in November 2023 (Fig. 1). Here, we present the assessment process and results of this Green Status of Species assessment for the Iberian lynx.

Methods

Green Status of Species assessment

The methods for conducting an IUCN Green Status of Species assessment are documented thoroughly in a number of existing publications (i.e., IUCN 2021, IUCN SCSTF 2020). For full details, those publications should be consulted, but here we provide a brief summary of the assessment process:

The primary output of a Green Status assessment is a Species Recovery Score SRS and accompanying Species Recovery Category. The SRS reflects the species' level of recovery on a scale from 0% (category: Extinct or Extinct in the Wild) to 100% (category: Fully Recovered or Non-Depleted). To calculate the SRS, assessors carry out the following steps:

1. Determine the species' indigenous range (the range prior to major anthropogenic impacts on distribution or abundance);
2. Divide this range into a set of biologically relevant sections called spatial units. These spatial units are used to reflect any variations in status across the range and can be defined, for example, by biological or ecological divisions;
3. Assess the state of the species in each spatial unit. For each spatial unit, the state could be Absent (the species has been extirpated in the spatial unit), Present (the species occurs in the spatial unit, but is not Viable), Viable (the spatial unit meets the Regional Red List criteria (IUCN 2012b) for Least Concern or Near Threatened and not declining), or Functional (the species is Viable in the spatial unit and is also performing its ecological functions). Each of these states is assigned a weight (Functional = 9, Viable = 6, Present = 3, and Absent = 0, which are used to calculate the SRS:

$$SRS = \frac{\Sigma_S W_S}{W_F \times N}$$

Where s = each spatial unit, W_S = the weight of the state in the spatial unit, W_F = the weight of the Functional state, and N = the number of spatial units. $W_F \times N$ represents the maximum possible value (i.e., the species is functional in every spatial unit) and recovery is calculated as a percentage of this.

The Species Recovery Score and Species Recovery Category reflect the recovery condition of the species at the time of the assessment. However, the Green Status assessment also allows assessors to estimate scores under different scenarios to evaluate the impact of past conservation action, as well as the expected impact of future conservation. These scenarios are:

1. Counterfactual scenario: no past conservation actions;
2. Future-without-conservation scenario: all conservation actions are halted;

3. Future-with-conservation scenario: conservation actions continue as planned over the next 10 years;
4. Long-term aspiration scenario: conservation actions are improved and sustained over the next 100 years.

The scores estimated under these scenarios are used to calculate four conservation impact metrics (Fig. 2): Conservation Legacy (impact of past conservation); Conservation Dependence (expected impact of halting all conservation in the short term); Conservation Gain (expected impact of continuing conservation in the short term); and Recovery Potential (maximum possible recovery within 100 years).

Fig. 1. Participants of workshop for the first IUCN Green Status of the Species assessment for the Iberian lynx in November 2023 (Photo U. Breitenmoser).

Iberian lynx Green Status assessment process
In November 2023, the IUCN SSC Cat Specialist Group in collaboration with the Life Project LynxConnect convened a workshop at the Consejería de Sostenibilidad, Medio Ambiente y Economía Azul (Ministry of Sustainability, Environment, and the Blue Economy) in Sevilla, Spain to discuss the Red List reassessment for the Iberian lynx and to conduct the first-ever Green Status assessment for the species. Over the course of 2 days, the Green Status assessment of the Iberian lynx was drafted. Subsequently, it was reviewed by species experts. The process was supported by the IUCN Green Status of Species-SSC Integration Task Force, with Elliot Carlton and Molly Grace facilitating. The full assessment with all documentation can be viewed at the Red List website.

Results

Indigenous range and spatial units
The indigenous range of the Iberian lynx was determined to be much larger than the area it currently occupies. While the severe declines in the twentieth century are well-documented and have been accounted for when assessing the Red List category of the Iberian lynx (Rodríguez 2024), the Red List assessment does not consider earlier reductions in range (i.e. reductions occurring more than 3 generations ago; López et al. 2024b) when assessing extinction risk. These declines are, however, relevant to the Green Status recovery assessment.
Evidence of a genetic bottleneck indicates that significant declines in abundance occurred between the 1400s and 1600s (Abascal et al. 2016). While some of these declines may be naturally attributed to climatic changes associated with the Little Ice Age, there was also a direct and extensive fur trade for Iberian lynx in this period, as well as expansion of agricultural lands in the Iberian Peninsula (Villalpando-Moreno 2020). Prior to these declines, the Iberian lynx was found throughout the Iberian Peninsula in non-forested areas; the species has long been associated with scrubland within the Mediterranean bioclimatic region of the peninsula. Thus, the indigenous range does not include the Atlantic and Alpine bioclimatic regions in the north and northwest.
Dividing this indigenous range into spatial units was less straightforward. There are currently many subpopulations/nuclei of Iberian lynx existing in a metapopulation, and connectivity continues to increase. Prior to the aforementioned bottleneck, it is likely that connectivity between lynx nuclei was very high throughout the Iberian Peninsula. Therefore, spatial units were defined based on a mix of: major geographic barriers (e.g. rivers); strength of connectivity; and differences in climate/vegetation (which affect environmental favourability for rabbits, the lynx's primary prey item; Ferreras et al. 2010, Simón et al. 2012). This resulted in six spatial units: Southwestern Lowlands, Southern Plateau, Toledo Mountains, Northeast Spain, East Spain, and Northwest Iberia (Ortiz et al. 2024 for further description of the areas covered by these spatial units).

Recovery outlook
The Iberian lynx was assessed as being Largely Depleted, with a Species Recovery Score of 22%, in 2023 (Fig. 2). This is because the species was Present in four of the six spatial units (but not Viable or Functional), and Absent in two spatial units (Northeast Spain and Northwest Iberia). This result indicates that even though the Red List category has improved, there is still work to do to restore viable (and functional) populations throughout the indigenous range.
Just as the change in Red List Category from Critically Endangered to Vulnerable over the past decades demonstrates the positive impact of conservation, so too do the four conservation impact metrics of the Green Status assessment (Fig. 2). The Iberian lynx has a High Conservation Legacy, because it is estimated that in the absence of any past conservation efforts, the species' score would have been 22% lower in 2023 (range 11–22%), bringing the counterfactual score to 0% (Extinct in the Wild). The uncertainty around this estimate acknowledges that extinction was not an absolute certainty, in the absence of past conservation action, the Iberian lynx would most likely have become Extinct in the Wild by 2023.
It is expected that, if conservation continues as planned (including reintroduction efforts), within 10 years the Iberian lynx will be Present in all six spatial units, and Functional in the Southwestern Lowlands spatial unit (which is home to the largest current population, in Doñana) and the Southern Plateau spatial unit. This would bring the score to 44% (Largely Depleted), via a Medium Conservation Gain of 22% (range: 0–44%; Fig. 2). However, if all conservation actions were halted in 2023, it is expected that no spatial units would improve, and indeed that the East Spain spatial unit would likely be lost; this would result in an expected score of 17% and a Low Conservation Dependence of 6% (range: 0–6%).
Finally, the Recovery Potential reflects the biologically possible space for recovery within

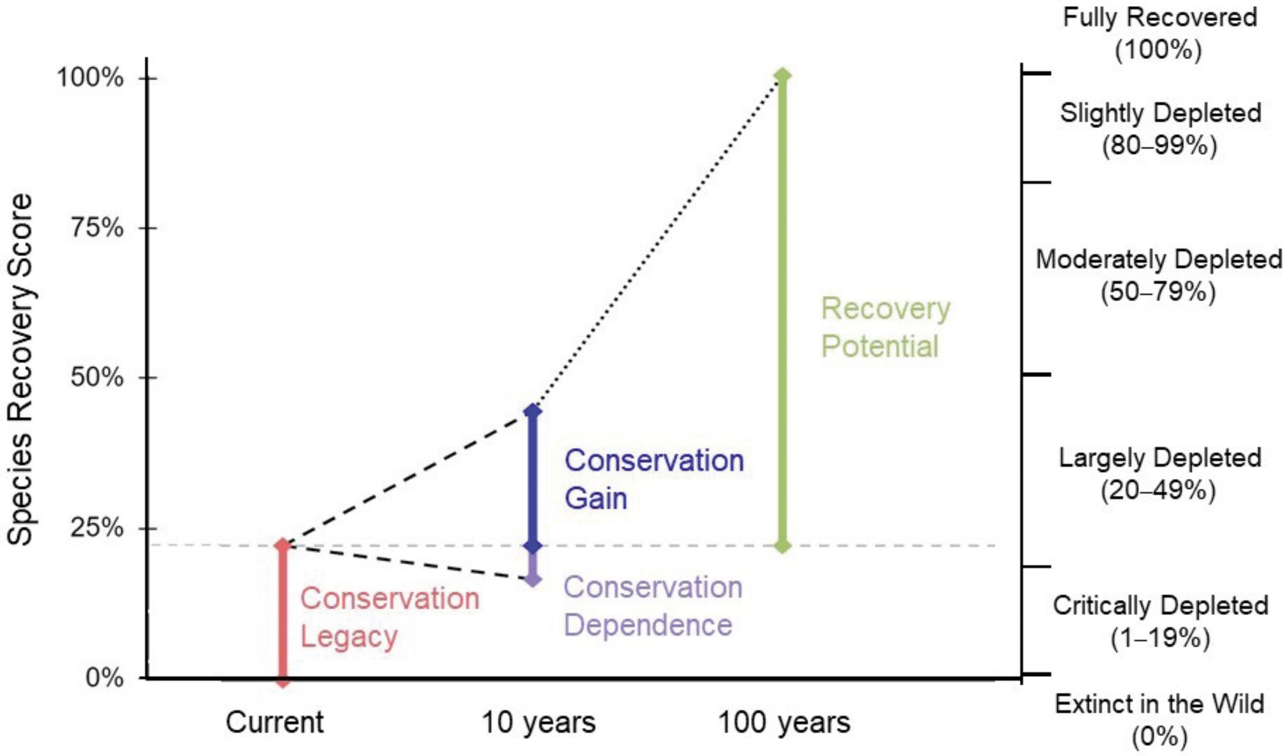

Fig. 2. Green Status results for the Iberian Lynx (best estimates; for uncertainty in these results, see text). The Species Recovery Score was estimated at the time of assessment (Current) under two conditions: the score based on observed status (22%), and based on expected status if no conservation had taken place to date (0%). The difference between these two values gives the Conservation Legacy (pink). The expected score ten years in the future was estimated under two conditions: a scenario of conservation continuing as planned (67%) and a scenario where all conservation stopped (17%). The difference between these values and the current observed score (represented by the horizontal grey dashed line) gives the Conservation Gain (blue) and Conservation Dependence (purple), respectively. The maximum possible score that can be achieved in the next 100 years was also estimated, giving the Recovery Potential (green). The Species Recovery Category that corresponds to different ranges of the Species Recovery Score are shown on the right; the Iberian Lynx is currently Largely Depleted.

the next 100 years: if funds were not an issue, what could conservation achieve for the Iberian lynx within that time period? Although large areas of native shrubland have been replaced by agricultural mosaics over the past two centuries, this change has increased rabbit abundance and therefore these areas are suitable for lynx occupancy (López et al. 2024a). Therefore, it would be possible to restore the species across much of its former range, and within 100 years to achieve Functional lynx populations over at least 50% of each spatial unit. Under this scenario, the Iberian lynx would be considered Fully Recovered (SRS = 100%; Fig. 2).

The full results of the Green Status assessment can be viewed on the Red List website (Ortiz et al. 2024).

Discussion

The results of the first Green Status assessment for the Iberian lynx demonstrate the tremendous impact of past conservation actions and help provide a glimpse of the possible future for the species. The result that, within 100 years, full recovery of the species is possible should galvanise the conservation community to sustain and augment their efforts for this iconic species. It is important to note that this assessment is not a conservation plan; nonetheless, the results can inform conservation planning. For example, the substantial Conservation Legacy indicates that past actions were effective, which can inform how similar actions are implemented across the range. The Conservation Gain, on the other hand, shows that the recovery score is expected to double within just 10 years if currently planned conservation actions are implemented. While this result is hopefully motivating in itself, conservation planners may also consider whether additional actions could be implemented in the same timeframe to have an even greater impact on recovery across the range.

The results can also help provide a horizon scan for threats that need to be addressed. In the Green Status assessment, assessors indicate uncertainty with lower bound, most likely, and upper bound estimates for states in each spatial unit. While the most likely estimate of Recovery Potential is that full recovery is achievable within 100 years, the lower bound estimate is more sobering. This is because rabbit disease outbreaks (rabbit haemorrhagic disease (RHD) and myxomatosis) remained a threat in 2023, with three disease outbreaks in the previous 75 years. These disease outbreaks in rabbits were accompanied by dramatic decreases in Iberian lynx populations (Delibes-Mateos et al. 2014). Therefore, in the lower bound estimate of Recovery Potential, assessors assumed that there could be as many as four rabbit disease outbreaks in the next 100 years, which would keep lynx populations at low levels. In this pessimistic scenario, which assumes disease affects all spatial units, the lowest expected score in 100 years would be 33%; an improvement over the score in 2023, but nowhere near the inspiring heights of full recovery. This indicates that disease management and treatment should be a key priority as part of the species recovery plan moving forward.

While this uncertain future should be kept in mind, it is also important to see this as a major opportunity for conservation of the species; over the next century, new data about these diseases and innovation in veterinary medicine can play a large role in helping the Iberian lynx achieve full recovery.

Iberian lynx from Sierra de Andújar (Cortijo Gato Clavo; Photo T. Pérez).

Conclusion

The Green Status of Species assessment complements the Red List assessment of the Iberian lynx to tell a powerful story of conservation success and hope for the future. Going forward, the two assessments will be re-evaluated in parallel at least every ten years, which will allow continued reflection on the recovery of the Iberian lynx and the role of conservation actions in its recovery.

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The rabbit beyond its role as lynx prey: improving knowledge on a keystone species

The Iberian lynx *Lynx pardinus* is a trophic specialist. Among mammals, its dependence on rabbits *Oryctolagus cuniculus* is paradigmatic. They account for more than 80% of the biomass of the feline's diet, up to 99% in some cases. Moreover, lynx productivity and the survival rates of cubs and sub-adults depend on rabbit population densities. Beyond its role as the main prey of the Iberian lynx, the rabbit deserves prominence for itself. European rabbit populations in their natural distribution range were classified as Endangered in 2018 by IUCN, after a sharp decline of more than 70% between 2008-2018. Rabbit population monitoring is the first essential step for an adequate management of both lynx and rabbit populations. Monitoring in the Iberian Peninsula has been characterised by the lack of common methodologies among regions, which prevents reliable, updated and comparable data from being obtained at the Iberian scale. This lack of information on the status of rabbit populations, the incidence of diseases or their impact on agriculture greatly complicates its management – and thus fuels the human-wildlife conflict. To address this complex situation, the LIFE Iberconejo project was launched in 2021. Up to date, LIFE Iberconejo has been able to develop 1) an European rabbit coordination committee ERICC, 2) a common, Iberian-scale monitoring system for the species, (population and health status and damage to crops), and 3) good management practices for the species. The goal of LIFE Iberconejo is to establish a long-term, evidence-based management of the European Rabbit. Preliminary monitoring results have helped identify "stepping stones" within the frame of LIFE LynxConnect.

The European rabbit, the main lynx prey, and a keystone species

The European rabbit is known across the world as prolific breeder, a pest species that is almost impossible to combat (Thompson & King 1994). Their takeover of Australia in the late 19th century has been described as the fastest colonisation rate for an introduced mammal ever recorded (Alves et al. 2022). But in the Iberian Peninsula, where the European rabbit originated, it stars in a very different story.

In the Mediterranean forest ecosystem where the Iberian lynx roams, rabbits are the keystone species, playing a critical ecological role (Delibes-Mateos et al. 2007). They are part of the diet of around 40 species of predators, and some of them are true rabbit-specialists (Delibes & Hiraldo 1981). Among mammals, the Iberian lynx dependence on rabbits is paradigmatic. They account for more than 80% of the biomass of the feline's diet, up to 99% in some cases (Aldama et al. 1991, Palomares et al. 2001, Gil-Sánchez et al. 2006). It is also known that in order to establish a breeding territory (around 5 km^2) and successfully raise a litter, a female lynx needs rabbit densities of between 100 and just under 500 rabbits per km^2 (in autumn and spring respectively; Life + IBERLINCE 2016). Moreover, lynx productivity (Monterroso et al. 2016) and the survival rates of cubs and sub-adults (Garrote et al. 2017) depend on rabbit population densities.

Most conservation efforts for the Iberian lynx have focused on fostering and monitoring rabbit populations. The status of rabbit populations is the primary indicator for selecting reintroduction areas and stepping stones, and for initiating the emergency plan in case of a rabbit population collapse.

However, there was no census of the species in areas without lynx presence, nor an Iberian consensus on large-scale rabbit monitoring methodologies. This gap in knowledge has been one of the great obstacles to select lynx reintroduction areas and stepping stones, as well as to evaluate the management of rabbit populations. On the other hand, despite decades of rabbit management, there is still no consensus among stakeholders on the best practices for managing the species.

Ecological relevance in its native range

In addition to its role as prey, the rabbit has been described as a true 'ecosystem engineer', thanks to its ability to modify its environment and thus the availability of resources for itself and other species (Delibes-Mateos et al. 2007, 2008, 2014). It is able to 'cultivate' its ideal habitat, promoting the maintenance of open scrub grassland through feeding and seed dispersal (Martins et al. 2002).

Rabbit latrines (accumulations of their droppings) have a demonstrable effect on soil fertility and plant growth, and provide new food resources for many invertebrate species (Galante & Cartagena 1999, Delibes-Mateos et al. 2007, Sánchez-Piñero & Ávila 1991). In addition, the burrows they excavate provide shelter and breeding sites for a multitude of species, from amphibians and reptiles to birds as the little owl *Athene noctua* (Delibes-Mateos et al. 2007, Dellafiore et al. 2008, Gálvez Bravo et al. 2009).

There are two genetically distinct subspecies of European rabbits, each with different ecological and morphological traits (Delibes-Mateos et al. 2008a, Díaz Ruiz et al. 2023), and they are geographically separated (Branco et al. 2000, Carneiro et al. 2014, Alda & Doadrio 2014). These differences suggest that the populations should be managed differently. However, no specific management recommendations for each subspecies currently exist.

For local communities, it has a great socio-economic relevance, as the main small game species in the Iberian Peninsula (Delibes-Mateos et al. 2008b). Historically, the great abundance of rabbits has been exploited as a food resource, while the skins were used to make clothes and, more recently, fur. The popular cuisine of many regions cannot be imagined without their flesh, and they are a fundamental ingredient in some of the most traditional dishes, such as paella or rabbit with garlic. Nowadays, although the number of hunting licenses is slowly declining, more than 5 million rabbits are captured per year in Spain (MITECO 2021). The other side of the coin concerning the economic impact of this species is the damage it causes to agriculture (Barrio et al. 2010, 2013, Delibes-Mateos et al. 2018). The rabbit is the species that causes the most damage to crops in Spain, accounting for 64% of agricultural insurance payments for wildlife damage (Agroseguro 2022). In an attempt to reduce this damage, the species is hunted intensively. For example, 308 of the 919 municipalities in the region of Castilla-La Mancha (South Spain) have been declared in 2024 as

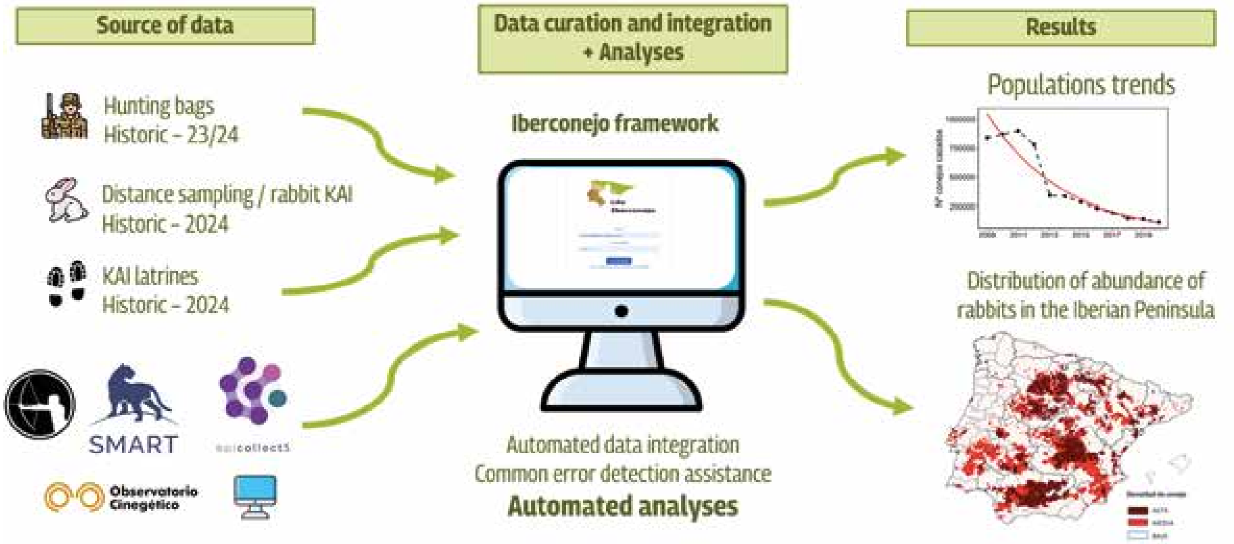

Fig. 1. Final work flow development in LIFE Iberconejo for the Iberian monitoring system of the European rabbit populations. Different data from different methodologies and data gatherings applications are integrated in an ad-hoc web platform. Hierarchical modeling framework and TRIM analyses were selected to obtain the abundance distribution maps and populations of the European rabbits at Iberian scale.

'Comarca de Emergencia Cinegética Temporal por daños causados por el conejo' (Temporary Hunting Emergency Region due to rabbit damage; JCCM 2024), allowing the extraordinary control of the species.

The decline of the rabbit

Beyond its role as the main prey of the Iberian lynx and its ecological and economical role, the rabbit deserves prominence for itself. European rabbit populations in their natural distribution range were classified as Endangered in 2018 by IUCN, after a sharp decline of more than 70% between 2008–2018 (Villafuerte & Delibes-Mateos 2019).

In a large part of the Iberian Peninsula the species has become very scarce (Delibes-Mateos et al. 2009, 2014). The decline of the rabbit began 70 years ago, with the arrival of a devastating disease - myxomatosis, introduced in France in 1950 by inoculation of wild rabbits to control crop damage. The disease spread rapidly across Europe, resulting in mortalities of up to 99% in many populations (Fenner & Ratcliffe 1965, Thompson & King 1994, Fenner & Fantini 1999). Although average mortality in the populations declined considerably in the following years, and the species seems to have developed some immunity, the formerly abundant rabbit populations were severely depleted (Villafuerte et al. 2017).

On top of that, a new disease - Rabbit Hemorrhagic Disease, RHD, which appeared in the Iberian Peninsula in the 1980s, caused mortalities of 50–80% (Villafuerte et al. 1994). Just as the species was starting to get back on its feet, a new strain from France emerged in Spain and Portugal in 2012, genetically differentiated from classical RHV (Le Gall-Reculé et al. 2011, Calvete et al. 2013). Unlike the latter, it also affected kits and young rabbits. This new strain caused very high rabbit mortalities, above 75%, both in dense and low-density populations (Delibes-Mateos et al. 2014a, Santoro et al. 2023).

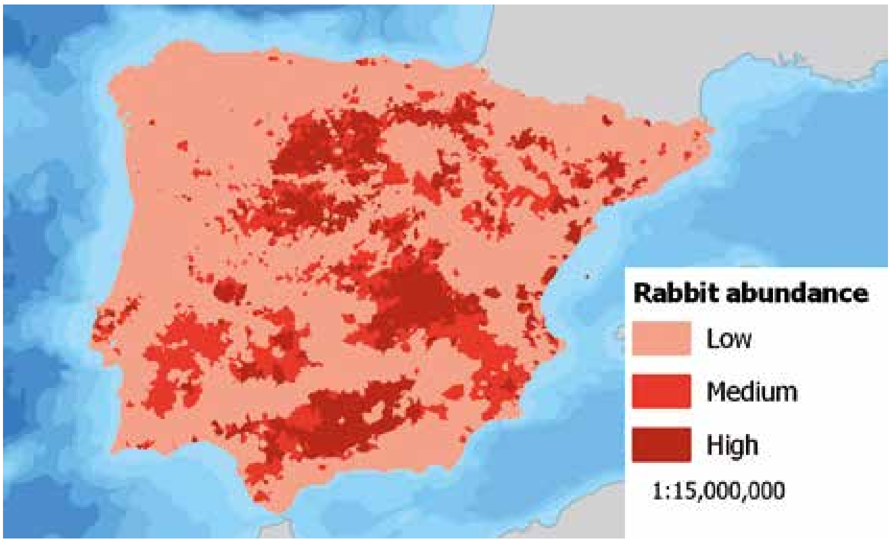

Fig. 2. Preliminary abundance distribution map of the European rabbit resulted by the hierarchical modeling of the hunting bags.

In addition to disease, many authors point to another key factor in explaining the decline of rabbit populations in the Iberian Peninsula: changes in land use in recent decades, which have drastically altered the rabbit's ideal habitat (Delibes-Mateos et al. 2010). Located in the southern half of the Peninsula, with a typically Mediterranean climate (with hot and dry summers and not too abundant rainfall in autumn and spring), this ideal habitat has been described as a mosaic. Trees are scarce and abundant patches of scrubland predominate (covering 40-50% of its surface; Silvestre et al. 2004), interspersed and alternating with clearings formed by pastures, small cultivated plots, streams or springs, rocky areas and bare soil (Moreno & Villafuerte 1995, Lombardi et al. 2003, Monzón et al. 2004). Habitat degradation and the abandonment of traditional land uses in mountain areas with low agricultural or livestock profitability, such as the Iberian lynx nuclei of Sierra Morena, have led to scrubland, damaging the rabbit and favouring species such as ungulates like the wild boar *Sus scrofa* (Carpio et al. 2014, Barasona et al. 2021).

Improving management with a LIFE project

Globally, it is estimated that during the 20th century the rabbit population in the Iberian Peninsula declined by more than 90% due to the combined impact of land use changes and disease (Villafuerte & Delibes-Mateos 2019). In the early 2000s, during the census that exposed the dire condition of the Iberian lynx (Guzmán et al. 2004, Sarmento et al. 2009), it was not uncommon to go days without spotting a single rabbit in some of the lynx's traditional strongholds. As other authors have explained in this Special Issue, much of the in-situ conservation efforts to prevent the Iberian lynx extinction have been linked to habitat management and, more specifically, to the recovery of rabbit populations.

Surprising as it may seem, because of its status as a 'pest' species in many areas of the planet where it has been introduced, recovering rabbit populations in the peninsula's Iberian lynx areas has proved to be an extremely complex task, and there was no consensus on the most effective promotion measures (Catalán et al. 2008, Ferreira & Delibes-Mateos 2010, Cabezas et al. 2011, Godinho et al. 2013, Guerrero–Casado et al. 2013, Marín-García & Llobat 2021).

In addition to that, and despite the importance of the rabbit, monitoring in the Iberian Peninsula has been characterised by the lack of common methodologies between regions - preventing reliable, updated and comparable data from being obtained at the Iberian scale. This lack of information on the status of rabbit populations, the incidence of diseases or their impact on agriculture greatly complicates its management.

With the goal of reversing its decline and coordinating conservation and management actions for the species, the World Wide Fund for Nature WWF drafted a National Wildlife Rabbit Strategy in 2017 (WWF España 2017). This call for action received significant support from the scientific world in 2018, when wild rabbit populations were classified as 'Endangered' by the IUCN (Villafuerte & Delibes-Mateos 2019). However, these efforts hit a wall.

The rabbit paradox and the human-wildlife conflict

As mentioned, although it is very scarce in a large part of the Peninsula, rabbit populations experience outbreaks and produce crop damages in some agricultural areas (Delibes-Mateos et al. 2018, Rouco et al. 2019). In Spain, between 2012 and 2017, damage by the species affected on average almost 420 km^2 of crops per year (Agroseguro 2022). This double-sidedness of the species has led to major conflict around the rabbit, and has greatly complicated its management (Barrio et al. 2013, Delibes-Mateos et al. 2014b). In many regions of Spain, the control of its populations has been one of the main demands of farming organisations (Williams et al. 2007, Latham et al. 2012, Ríos-Saldaña et al. 2013). And any mention of the need to protect the species raised the suspicions of farmers. Moreover, the lack of reliable, Iberian scale data on rabbits exacerbated this conflict.

A LIFE project to unite them all

After years of efforts to build bridges and seek common solutions, in 2022 a joint initiative was launched, bringing together all the agents involved in the management of the species: public administrations, universities and research centres, hunters, farmers and conservation NGOs.

With 15 partners from Spain and Portugal, and financed by the European Union's LIFE programme (within the Governance and Environmental Information sub-programme), the LIFE Iberconejo project (LIFE20/GIE/ES/000731) was born with the aim of drawing the baselines for the good management of the wild rabbit in the Iberian Peninsula.

These partners established the European Rabbit Iberian Coordination Committee ERICC, which will coordinate the management of the species after the end of the project. The ERICC counts with the participation of the institutions that hold the highest authority in the

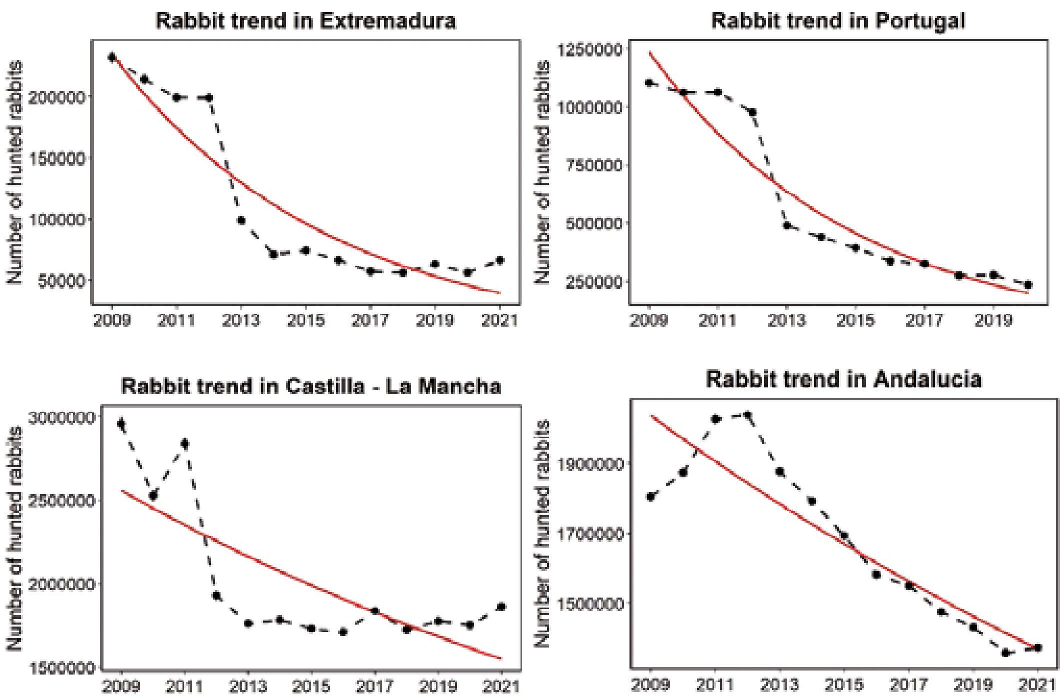

Fig. 3. Rabbit population trend by region partners of LIFE Iberconejo (Extremadura, Portugal, Castilla La-Mancha and Andalucía). Graphics obtained using TRIM for hunting bags data at hunting estate scale. TRIM calculates indices that represent the effect of change between years, which indicates relative variation of the total population size.

management of the species in the Iberian Peninsula, the Ministry of Agriculture, Fisheries and Food MAPA in Spain and the Instituto da Conservação da Natureza e das Florestas ICNF in Portugal. Five new entities have already joined the ERICC: a farming association, three hunting associations and the veterinary authority of Portugal.

Establishing effective management strategies for any species necessitates comprehensive knowledge of population status and the implementation of robust, standardised monitoring systems. Iberconejo's first objective, therefore, was to determine how many rabbits there are, where they are, and how their populations are changing, including the incidence of diseases and their impact on agriculture.

Monitoring of wild rabbits was already being undertaken in several regions, at different scales and with different methodologies depending on the objective pursued. As a starting point, information from previous monitoring was compiled and, as far as possible, efforts were made to give continuity to the monitoring already being carried out, and to standardise them with the others.

Up to date, LIFE Iberconejo has been able to develop a common, Iberian-scale monitoring system for the species, divided into three monitoring protocols – population status, health and diseases, and damage to crops. These protocols were approved in late 2023 by the ERICC, and they are already being implement by public game management authorities in both countries:

1. A population monitoring system based on the integration of different methodologies and data sources, merging hierarchical integrated models' framework with software tools to automate data gathering and analyses.
2. A health status monitoring system focused on detecting and preventing outbreaks (passive approach) and monitoring the prevalence of myxomatosis and RHD (active approach).
3. Finally, a damage crop monitoring protocol has also been developed to collect long term data. This data could help control and manage, at the local scale, the human-wildlife conflict around rabbit populations.

Additionally, good management practices for the species have been agreed upon by ERICC, both for population recovery and crop damage prevention, identifying key European financing schemes -including the Common Agricultural Policy- that could be used.

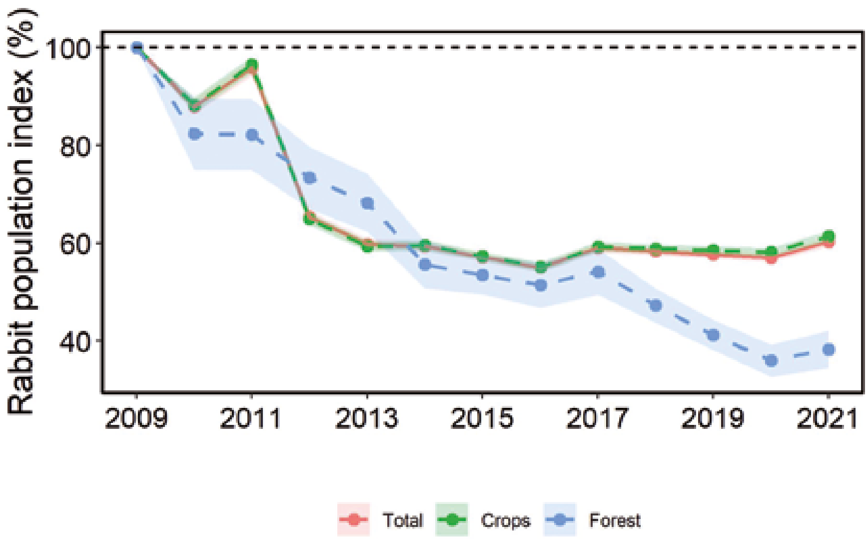

Fig. 4. Rabbit population trend by habitat in Castilla La-Mancha. Crops and forest show similar trends until 2017, when agrosystems populations began to stabilise.

Estimating the rabbit population status

Regarding the monitoring of the rabbit population, we integrated three different sets of data and methodologies – the first, data from hunting bags, has a wide coverage with low detail. The other two data - distance sampling and latrine counts - have better accuracy, but with a small coverage. The information is collected through SMART (Spatial Management and Reporting Tool), a conservation-tool that has been adapted for the project.

However, due to existing historical monitoring programmes and previous methodologies (i.e. kilometric abundance index) and gathering data apps in use (i.e. Epicollet, Cybertracker), it seemed necessary to integrate diverse data sources. Thus, we used novel methodologies in hierarchical modeling to pool different data sources (hunting bags, distance sampling and latrine counts) to estimate rabbit abundances at regional and Iberian scale (Fig.1). Those methodologies allowed us to take the strengths from each data source (spatial coverage, accuracy, etc.), minimising their weaknesses and thus making the most from existing monitoring programmes (Fernández-López et al. 2023).

As a result, we have been able to obtain a clear estimate of the rabbit population status – showing animal density on a 2x2 grid scale, and population trends across different landscapes. The project's preliminary hierarchical integrated model (Fig. 2) is already being shared with the LIFE Lynxconnect team, and it has helped identify and establish new lynx reintroduction areas that will serve as "stepping stones" between existing populations - one of the key actions to safeguard the cat's future.

For example, between the populations of Sierra Morena Oriental and Montes de Toledo, in Castilla-La Mancha, there is a sea of very homogeneous and intervened agricultural landscapes, and habitat selection models for the Iberian lynx were unable to find suitable areas for the species (Garrote et al. 2020). By adding the Iberconejo model, it was possible to locate 5 possible "stepping stones" - working with the humble rabbit, we achieved much more.

On the other hand, we evaluate changes in population estimates using TRIM (Trends and Indices for Monitoring data - Bogaart et al. 2016, Pannekoek &Van Striker 2005). These models allow us to evaluate trends by incorporating covariables, such as habitat type, helping us to understand what is happening at each site. These analyses can be very useful for assessing the effect of population promotion actions in Iberian lynx reintroduction areas.

Our preliminary results of rabbit population trends show a population decrease of between 30 and 87% in the last decade, depending on the region (Fig. 3). In Extremadura -a region in the centre-west of Spain that hosts 11,7% of the Iberian lynx population- the rabbit population decline is 80%, while it reaches 91% in Portugal, where 261 lynx individuals (15,7%) live (MITECO 2022).

But these population trends seem to be different depending on the type of habitat. For instance, we can focus on the Spanish region of Castilla-La Mancha, a stronghold of the Iberian lynx with 35% of the population (MITECO 2022), and critical to recover the cat's historic range. In woodland areas of

Iberian lynx from Sierra de Andújar having predated on a European rabbit (Cortijo Gato Clavo; Photo A. M. Morillas).

Castilla-La Mancha the decline of rabbits has been 60% in the last decade and populations are still in free fall (Fig. 4). However, in agricultural areas, where the human-wildlife conflict due to agricultural damage is very intense, the decline has not reached 40%, and populations seem to be slowly recovering (Fig. 4).

To update these results and validate the monitoring protocols and methods approved in LIFE Iberconejo, a census of rabbit populations will be carried out during the summer of 2024 in practically the entire Mediterranean region of the Iberian Peninsula. With this information we expect to publish an update of the species' abundance distribution and trends in 2025.

To achieve this goal, Iberconejo's partners are training all key stakeholders in rabbit monitoring methodologies. More than 800 people have been trained so far, including hunters, farmers, volunteers and environmentalists, so they can contribute to the monitoring effort.

Thus, during the summer of 2024 we expect all involved actors from several regions (including some that are not part of the project but have decided to join the initiative) will take part in the census. In times of confrontation, it is encouraging to see different sectors, so much at odds on other issues, working towards a common purpose.

The goal of LIFE Iberconejo is to establish a long-term, evidence-based management of the European rabbit. This information is essential for the effective management of the species. On one hand, from a socio-economic and social conflict point of view, assessing the evolution of populations where they cause damage to agriculture. On the other hand, to conserve biodiversity as a whole and its predators – including endangered species such as the Iberian lynx and the Spanish eagle. For example, habitat selection models for the Iberian lynx are of little use without a map of rabbit abundance, which is essential for calculating carrying capacity.

Acknowledgements

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Towards a long-term viability of the Iberian lynx

The conservation of the Iberian lynx *Lynx pardinus* has been a success. It is still necessary, however, to invest efforts to bring the species out of threat. To evaluate future conservation needs, a Favourable Conservation Status (FCS; minimum population size considered necessary to ensure long-term viability of the species according to the EU Habitats Directive) analysis was carried out for the Iberian lynx population by 2019. It found that the presence of 750 breeding females in the population was the main goal to reach the FCS. In order to reach that goal, the creation of eight more new populations would be necessary. Another recent study indicates that the long-term genetic viability of the metapopulation requires 1) 2,165 effective individuals (ca. 1,100 breeding females), 2) an increase in the subpopulation size of 50–200% and 3) migration rates close to 0.1 among neighbouring subpopulations. Again, these goals need the creation of at least 8 new subpopulations. To achieve the long-term viability of the Iberian lynx population, both studies identified the need of 1) incorporating new regions into the reintroduction programmes, 2) choosing those areas with the highest growth potential and larger expected carrying capacity (even if they are more poorly connected than other smaller areas) and 3) maintaining ex situ breeding centres at full capacity at least until 2030. After these two studies were conducted, four new reintroduction areas have been started: Valdecañas-Ibores (Extremadura), Sierra Arana (Andalusia), Lorca (Murcia) and Campos de Hellín (Castilla la Mancha). Moreovoer, there are five more areas that have been evaluated, one in Castilla La Mancha, two in Aragón and two more in Castilla y León. Finally, there are five more areas under evaluation nowadays, one Andalucía, two in Madrid, one in Comunidad Valenciana and another one in Catalonia. With these forecasts, the Iberian lynx could reach its FCS within the next 2 decades. Likewise, the number of administrations and entities involved in the conservation of the species is increasing, requiring a complex decision-making structure. Therefore, a common Strategy for the conservation of the Iberian lynx in Spain and Portugal has been developed.

Evaluating future needs in the light of the EU Habitats Directives

Achieving a Favourable Conservation Status (FCS; minimum population size considered necessary to ensure long-term viability of the species) is an obligation for the member states under the European Union's Habitats Directive (92/43/EEC). To evaluate future conservation needs of the Iberian lynx population, Pérez de Ayala (2019) analysed the FCS of the Iberian lynx. The starting point of this analysis was the situation of the species at the end of Life IBERLINCE in 2018 (Iberlince 2018, Lopez et al. 2024): 686 individuals and 160 breeding females distributed in eight subpopulations: Andújar-Cardeña, Doñana, Guarrizas, Guadalmellato, Campo de Montiel, Vale do Guadiana, Montes de Toledo and Matachel. To calculate the necessary population size to reach FCS, this analysis used the "Guidelines for Population Level Management Plans for Large Carnivores in Europe" (Linnell et al. 2008), and the approach suggested by Epstein et al. (2016). Growth rates and carrying capacities of the reintroduced populations were used as a reference The FCS was calculated using these approximations: (1) the size of the population is at least what it had been when the Habitat Directive came into force in 1992. (2) The species is still from the Minimum Viable Population Size. In the absence of a specific population viability analysis, the only criterion of common acceptance is criterion D of the IUCN red list criteria, implying that the number of breeding females would be 500. (3) The objective would be achieved when population is closer to the carrying capacity than to extinction. For the estimation of the carrying capacity, available information has been derived from habitat suitability models, rabbit abundance data, and the territory sizes of breeding females. It was found that 750 breeding females are necessary to ensure the FCS (target that can be reached when eight more new populations are created).

Pacín et al. (2023), starting from a population situation similar to the previous study, evaluated the genetic viability of the Iberian lynx metapopulation using the GESP software (predicting the effective population size and inbreeding accumulation over time) in order to find realistic scenarios granting the genetic viability of the species. They conclude that long-term genetic viability of the metapopulation requires 2,165 effective individuals (ca. 1,100 breeding females) and migration rates close to 0.1 among neighbouring subpopulations. Interestingly, these goals were estimated to happen when eight further populations are created.

The conclusions of the previous two works must be taken with caution, since they both assumed that the smallest populations would reach a minimum of 50 breeding females. With the current rabbit abundances (the main factor determining the carrying capacity of a lynx population) there is a risk that some population nuclei will not reach the necessary population sizes. The status of rabbit populations is highly defined by diseases, and their possible emergence of in any of the extant or futures populations could limit or reduce their estimated carrying capacity (Monterroso et al. 2016).

Pacín et al. (2023) found that reaching the long-term genetic viability implies the exchange of 8–15 individuals per generation between neighbouring subpopulations. The effective connectivity and migration between populations will have to be carefully monitored, as well as its effect on the genetic diversity. If a too low migration rate between adjacent populations is detected, they will have to be human-managed for a longer time.

Actions towards the long-term needs to secure the Iberian lynx conservation

In response to the findings of the abovementioned studies, releases have been started in four new areas (Fig. 1): Valdecañas-Ibores (Extremadura), Sierra Arana (Andalusia; Fig. 2), Lorca (Murcia) and Campos de Hellín (Castilla la Mancha). Five additional areas have been evaluated and their approval is expected take place by late 2024. Hopefully, releases will begin between 2025 and 2026. These areas are: Cuenca (Castilla la Mancha), Arribes del Duero and Cerrato Palentino (Castilla and León; Fig. 3) and Las Planas and Sierra de Alcubierre (Aragón). Five more areas

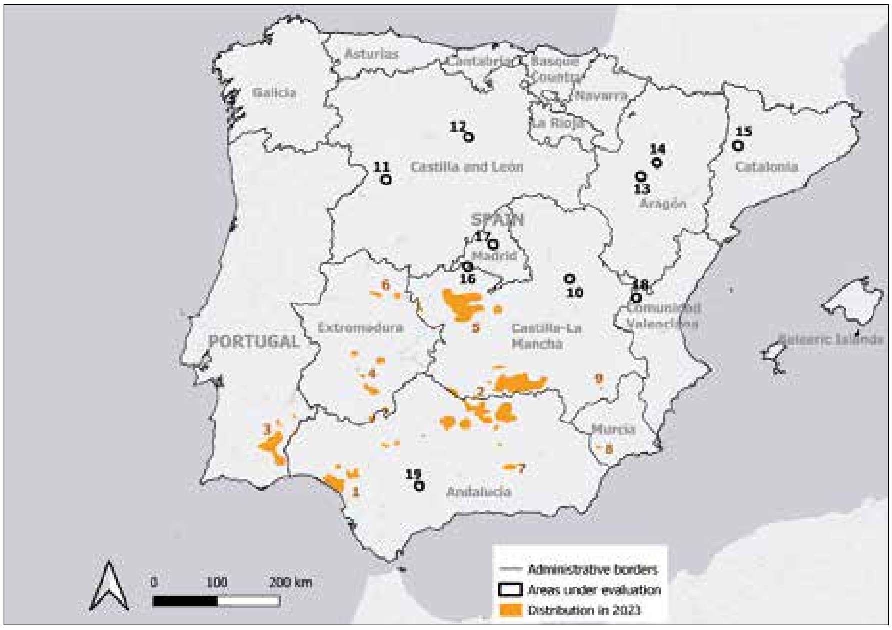

Fig. 1. Map of current populations, and additional reintroduction sites (under evaluation): 1) Doñana, 2) Sierra Morena Oriental (metapolation composed by Andujar-Cardeña, Guadalmellato, Guarrizas, Guadalmez and Campo de Montiel), 3)Vale do Guadiana, 4) Matachel (composed by Matachel y Ortiga), 5) Montes de Toledo, 6) Valdecañas-Ibores, 7) Sierra Arana, 8) Lorca, 9) Campos de Hellín, 10) Cuenca, 11) Arribes del Duero, 12) Cerrato Palentino, 13) Las Planas, 14) Sierra de Alcubierre, 15) Cataluña, 16) Sierra Oeste, 17) El Pardo, 18) Comunidad Valenciana y 19) Andalucía central.

Fig. 2. Sierra Arana landscape (Photo G.López/ Agencia de Medio Ambiente y Agua/ Consejería de Sostenibilidad, Medio Ambiente y Economía Azul de la Junta de Andalucía).

are under different phases of evaluation: two in Madrid, and one in each Andalucía, Cataluña and Comunidad Valenciana (Fig. 1).

With these additional populations, the entire metapopulation should be able to reach the FCS (e.g. no longer to be in the threatened categories in the IUCN Red List). Furthermore, the creation of populations in the northern half of the Iberian Peninsula would also take account for the possible effects of climate change on the Peninsula (Fordham et al. 2013).

To achieve these objectives, of the following recommendations were derived from the studies presented above:

1. The new regions should be incorporated into the reintroduction programme;
2. The ex situ conservation programme must be maintained at full capacity at least until 2030. Both captive-bred and wild-to-wild translocated individuals will be necessary for reintroductions;
3. Efforts should also be directed towards the expansion of extant subpopulations, rather than only the creation of new ones;
4. Areas with the highest growth potential and larger expected carrying capacity should be prioritised, even if they are more poorly connected than other smaller areas;
5. Directing resources to the creation of small populations with no prospects of connection to adjacent subpopulations should definitively be avoided, since they contribute little to the over-all effective population size and risk to rapidly accumulate inbreeding.

Despite this hopeful situation, further work is needed to monitor and reduce the potential threats limiting the conservation of the Iberian lynx, e.g. (1) the status and evolution of rabbit populations (Pérez de Ayala et al. 2024), (2) the anthropogenic mortality (road kills and illegal persecution; Garrote et al. 2024), (3) the low genetic diversity (Godoy et al. 2024) and (4) the isolation of subpopulations. Otherwise, regression and extirpation of population nuclei could happen again.

New Iberian conservation strategy for the Iberian lynx

To reach the current situation of the species, joint work has been necessary since the beginning of the century. A clear and decisive commitment was made to the conservation of the species. During the first decade, this work was under the leadership of the Junta de Andalucía with the support of Ministerio para la Transición Ecológica y el Reto Demográfico MITECO and the participation of different interest groups and NGOs. More entities and regions such as Castilla-La Mancha, Extremadura and Portugal have gradually joined (Simon et al. 2012; Garrote et al. 2020). The conservation programme has been mainly supported by four consecutive EU LIFE projects, under which institutions from both countries have carried out management actions in a coordinated manner. By 2004, a cooperation agreement in the conservation of the Iberian lynx was signed between Spain and Portugal (MMA 2004). Likewise, a cooperation agreement regarding the captive breeding programme was signed in 2007 (BOE 2009). Based on these documents, a "Comisión Mixta" was established between Spain and Portugal to make common decisions regarding the conservation of the Iberian Lynx. The main technical discussion forum for the conservation of the Iberian lynx today is the Iberian Lynx Working Group, which integrates Spanish and Portuguese representatives.

With both the gradual expansion of the species' range and the future perspectives, the number of administrations and other involved entities is increasing, entailing a multitude of decision-making structures. This situation will make decision-making extremely difficult in the future, so finding efficient solutions will be necessary. Hence, a common "Strategy for the Conservation of the Iberian lynx in Spain and Portugal" has been developed. This document provides guidance to work in a harmonised and coordinated manner with regard to the legal and administrative protection of the species, the monitoring of populations, and the conservation measures (genetic management, connectivity, measures aimed to reduce mortality rates, captive breeding and reintroduction projects). Effective compliance with the guidelines and measures included in this Strategy requires close coordination between the administrations of the two countries and all sectors involved, especially between institutions responsible for its implementation. To work towards a common goal requires that each unit involved develops its competencies. Therefore, it is necessary to define a clear governance model helping to organise the conservation work of the Iberian lynx, which is also reflected in the new Iberian Strategy.


Fig. 3. Cerrato Palentino landscape (Photo G. Carmona/ Fundación Patrimonio Natural de la Junta de Castilla y León).

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