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Former range and decline of the Iberian lynx (*Lynx pardinus*) reconstructed using verified records

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The Iberian lynx (*Lynx pardinus*) is the most endangered wild feline species and the only feline listed as critically endangered by the International Union for the Conservation of Nature. Successful conservation actions rely on accurate knowledge of the species' distribution and decline. Anecdotal unverified reports have overestimated the distribution of the Iberian lynx and misrepresented the severity of its decline. We reconstructed the Iberian lynx range from 1940 to 2000 using only records verified with indisputable physical evidence. We collected data from the 2 major scientific vertebrate collections in Spain, trophies registered by hunting authorities, and miscellaneous private collections. Of 320 lynxes collected during 1940–2007, 261 contained adequate date and location information for this study. The overall species range in 1940 included 15 subpopulations occupying 65 verified 10- × 10-km grid cells. Three large subpopulations (Montes de Toledo, eastern Sierra Morena, and Doñana) accounted for 86.6% of records. The species had a steady decline from 1940 until the 1990s, when lynxes remained in only 2 isolated subpopulations. Our reconstruction of verified lynx distributions since 1940 illustrates how most local extinctions occurred before disease outbreaks among prey, previously assumed to be the principal cause of lynx declines. Rabbit diseases alone cannot account for observed lynx declines, and we suggest that human-caused mortality from direct hunting and indiscriminate predator control programs likely played a larger role in the species' decline. Our verified maps provide a more accurate history of the Iberian lynx distribution in Spain than was available previously. Ideally, this information can help managers outline priority areas for conservation and reintroduction programs to reinforce and restore important subpopulations.

Key words: distribution, former range, Iberian lynx, population decline, reintroduction, verified records

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The Iberian lynx (*Lynx pardinus*) is considered the most endangered wild feline species in the world and the only feline listed as critically endangered by the International Union for the Conservation of Nature (2010). By the turn of the century fewer than 200 individuals remained in 2 isolated subpopulations in southern Spain, Doñana National Park and the eastern Sierra Morena Mountains (Guzmán et al. 2004; Simón Mata 2006). Archaeological data show that this cat was once well distributed throughout the Mediterranean areas of the Iberian Peninsula and southeastern France (Rodríguez and Delibes 1990). By the 19th century the species was reduced to south-central Spain (Rodríguez and Delibes 2002) and Portugal (Sarmento et al. 2009), and during the second half of the last century the Iberian lynx global population was reduced further to its critically endangered status (Nowell 2002). Extensive conservation programs have been launched to conserve the last 2 remaining populations (Simón Mata 2006); however, supporting only those subpopulations cannot recover the species from its current critically endangered status. Natural expansion from current subpopulations to recolonize areas of the former range is highly limited due to habitat fragmentation and lack of dispersal corridors (Guzmán et al. 2002, 2004). One of the recently proposed conservation actions, and perhaps the most urgent, is a reintroduction program to restore extinct subpopulations throughout the species' former range (Breitenmoser et al. 2006). Reintroduction sites that will provide the best opportunities for species recovery must be carefully selected, and the most obvious approach is to release lynxes into the areas where they disappeared most recently (Breitenmoser et al. 2006), given that the current habitat attributes are deemed suitable to sustain lynx populations. Therefore, understanding the former distribution of the species is essential for selecting reintroduction sites. Moreover, examining the species' decline over time can help to identify key factors that contributed to the decline so that those factors can be assessed before conservation and reintroduction efforts (International Union for the Conservation of Nature 1995).

The only existing information on the species' distribution (1950–1988) has been collected through questionnaires and interviews on lynx sightings (Guzmán et al. 2002; Rodríguez and Delibes 1992, 2002; Sarmento et al. 2004); however, these sighting data are not consistent with recent empirical data from field surveys (Gil-Sánchez et al., in press; Sarmento et al. 2004). The latest interview-based survey of Spain recorded sighting reports throughout south-central Spain, including areas where lynx have been absent for decades (Guzmán et al. 2002). Only after applying a heavy evaluation filter to the data of Guzmán et al. (2002) did the sighting data match the current species' distribution. Records supported by physical evidence were found within only 21 of the original 80 10- × 10-km grid cells presented by Guzmán et al. (2002), all of which were located within the 2 extant subpopulations. Sighting data in Portugal continued to be quite common (Palma et al. 1999), even in areas where lynx presence was questionable at best (Sarmento et al. 2004). Follow-up investigation of 37 Iberian lynx sightings in Portugal from 1999 to 2004 failed to produce any verifiable information, and Sarmento et al. (2004) determined that 100% were false sightings. Following the conceptual framework for evaluating the reliability of occurrence records provided by Frey (2006), most data on Iberian lynx sightings should be considered only as possible or probable reports. Given the limitations of anecdotal sighting reports (McKelvey et al. 2008), the former range estimates on the basis of unverified data and inferences about the decline of Iberian lynx (Rodríguez and Delibes 1992, 2002) are doubtful and should be viewed with great caution.

Presumably due to the solitary, elusive nature of rare species and the prevalent culture mystique surrounding their presence, the true status and distribution of many endangered species remain poorly understood and the subject of much speculation (G. Chapron, Université de Neuchâtel, pers. comm.; Hatten et al. 2005; McCain and Childs 2008; McKelvey et al. 2008; O'Brien and Kinnaird 2001). Sarmento et al. (2004) discussed how the discrepancies between indirect and direct evidence can be the result of unreliable information, such as confusion with another species, false sightings, or temporal confusion if a recent regional extinction occurred during the lifetime of the observer. The use of anecdotal sightings tends to generate fictional scenarios that can lead to dangerous conclusions (Sarmento et al. 2004). McKelvey et al. (2008) warns against the use of anecdotal data in describing species occurrence and distributions, especially for rare and elusive species, and calls for evidentiary standards. The rarer the species, usually the more significant are the conservation implications, and therefore the higher the standards should be for occurrence data. Just as the scientific process requires experimental hypothesis testing, the status and distribution accounts of rare and endangered species must stand up to scientific rigor to ensure that limited resources can be allocated most appropriately to achieve the best possible conservation outcomes.

We provide an alternative approach to reconstructing the former distributional range and decline of the Iberian lynx in Spain using only verified records substantiated by physical evidence from reliable sources. We mapped all possible sources of verified specimens from the mid-1900s to 2000 to reconstruct the former range of the Iberian lynx in Spain. We discuss the decline of the lynx population range and numbers at 10-year intervals through time. We evaluate how the factors that potentially effected population declines coincided spatially and temporally with lynx population changes observed in this study.

Materials and Methods

Due to the critically endangered status of the Iberian lynx (Nowell 2002) and the resulting significance of conservation actions that can be influenced by our findings, we set high evidentiary standards for this study (McKelvey et al. 2008) and considered only verified records derived from preserved physical evidence, as defined by Frey (2006). We used information on existing lynx records (skins, bones and skulls, preserved specimens) from 3 sources. We first accessed databases of the 2 main scientific vertebrate collections in Spain, the Museo Nacional de Ciencias Naturales (MNCN) in Madrid and the Estación Biológica de Doñana (EBD) in Sevilla. These collections yielded information from a total of 212 individuals (63 and 149 respectively). Spanish government environmental authorities also registered 80 legal lynx trophies before species protection in 1973 (Instituto para la Conservación de la Naturaleza 1973). In addition, miscellaneous private collections provided information on 17 individuals from skins, bones, and preserved specimens. In a few distinct cases we considered highly probable lynx reports on the basis of an expert's accurate observations, but without physical evidence (Frey 2006). We included records from 5 dead lynxes cited in the scientific literature (Delibes et al. 1975; García-Perea and Gisbert 1986; Rodríguez and Delibes 1990; Valverde 1963) and 6 lynxes live-captured for zoological garden collections, of which we were unable to locate any physical remains (Aldama and Delibes 1990; J. Barasona, Zoológico Municipal de Córdoba, pers. comm.; Delibes 1980; J.M. Gil-Sánchez, pers. obs.; Valverde 1963). Also, information on several lynxes live-captured for research and monitoring programs in 1984 was located; however, these records were from within known subpopulations in Doñana National Park and eastern Sierra Morena Mountains. As these records did not provide any new information, to avoid redundancy we did not include them in our analysis.

Our investigation located a total of 320 lynx records, 261 of which contained adequate date and location information for

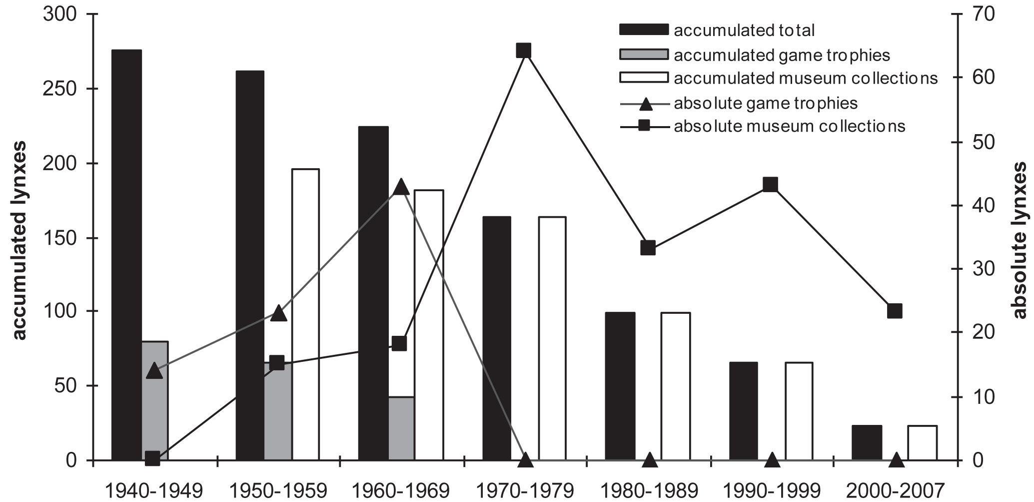

FIG. 1.—Temporal distribution of verified lynx records obtained from the two main data sources, the Museo Nacional de Ciencias Naturales (National Museum of Natural Sciences [MNCN], Madrid) and the Estación Biológica de Doñana (Doñana Biological Station [EBD], Sevilla). Verified records are expressed as ''absolute,'' representing lynxes collected during each 10-year interval, and following Rodríguez and Delibes (2002), ''accumulated'' contains all verified records from during and after each 10-year title period.

this study. A geographic information system (GIS; ArcView ESRI, Redlands, California) database was constructed to locate each individual geographically as accurately as possible. Museum specimens usually contained more precise (<1-km resolution) information, but some isolated cases listed only the municipality. In these cases we arbitrarily located these records at the center of the largest patch of scrubland habitat within the respective municipality (Palomares 2001). The MNCN contained 36 lynx records that were collected within the municipality of Los Yébenes in Montes de Toledo, where the best potential habitat patch consisted of approximately 430 km^2. Unfortunately, these accounts could not be mapped accurately; however, they were still useful at the subpopulation level. Legal trophy records contained only information on the estate where each lynx was killed. The location for these records was set at the center of the given property, yielding a mean accuracy of ± 2.6 km (largest mean length of 22 game properties = 5.27 km). Finally, the scattered samples from private collections usually offered detailed information directly from local sources, and thus locations were mapped using the same criteria.

The distribution range maps were constructed using the same 10-km projection grid as that of Rodríguez and Delibes (2002, 2003) so that results could be directly comparable. Given the accuracy of the location database, some lynxes might be placed in the incorrect 10-km grid cell; however, any such error can be only 1 grid cell away from the correct cell, and we considered this error minor given the broad scale of this study. Subpopulation boundaries were inferred from the grid cells containing positive records, considering natural barriers and the maximum known distance of dispersal (Ferreras et al. 2004; Rodríguez and Delibes 1992).

The temporal distribution of lynx records was different according to the 2 main data sources (museum and hunting collections; Fig. 1). This likely was due to any 1 of 4 sources of bias: legal protection of the species beginning in 1973; increased museum collecting activity after the 1970s; implementation of scientific monitoring and conservation programs in the early 1980s and 2000, respectively (see increase during 1990s in Fig. 1); and changes in occupied lynx range over time.

Verified records were mapped according to important temporal milestones for the Iberian lynx. Following Rodríguez and Delibes (2002), the distribution of the species was mapped from 1940 to 2000. Another map was generated using locations from 1973, when legal protection was granted for the species, to 2000. To compare our findings directly with those of Rodríguez and Delibes (1992, 2002, 2003) a semicurrent range was estimated from locations before 1980. Data from 1990 to 2000 illustrated lynx distribution during the period of maximum scientific collection (Fig. 2). Each map is constructed using the entire database, accumulating records from during and after the title year (Rodríguez and Delibes 2002). Finally, to illustrate population trends we present total lynx numbers at 10-year intervals beginning in 1940.

RESULTS

The combined database (1940 to 2000) yielded a former distributional range encompassing 65 occupied 10- $\times$ 10-km grid cells in 6 different geographical regions (pre-Pyrenean Mountains; Central Mountains, Sierra de San Pedro, Montes de Toledo; Sierra Morena Mountains, and Doñana coastal plains), with all but 1 located in southern Spain (Fig. 2). Fifteen different subpopulations were delineated, 3 of which (Montes de Toledo, eastern Sierra Morena, and Doñana) produced 86.6% of lynx records, with most others containing only 1–3 individual records (Table 1).

The posthunting-era map (1973–2000) depicted 32 cells with lynx presence, therefore describing a 33-cell decrease in total range since the period 1940–1972. Lynxes were found in

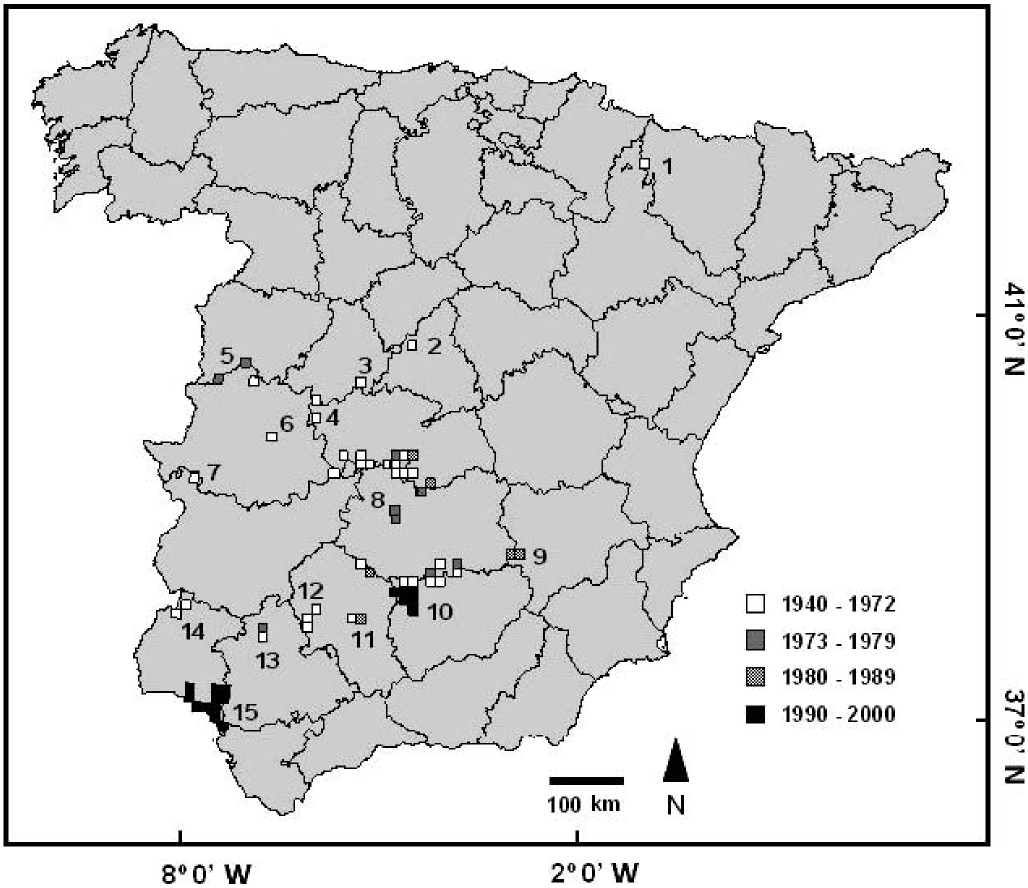

FIG. 2.—Former range of the Iberian lynx in Spain (represented in 10-km grid cells) based on verified records (physical evidence). Open squares represent all accumulated lynx records from 1940 to 2000; gray squares from 1973 to 2000; checked squares from 1980 to 2000; and solid squares from 1990 to 2000. Inferred subpopulations: 1) Sierra de Santo Domingo, 2) Sierra de Guadarrama, 3) Sierra de Gredos, 4) Tiétar River valley, 5) Sierras de Gata, Peña de Francia y Lagunilla, 6) Monfragüe, 7) Sierra de San Pedro, 8) Montes de Toledo, 9) Sierra de Relumbrar, 10) Guadalmez, Yeguas, Jándula, Rumblar, and Guarrizas river basins (eastern Sierra Morena), 11) Guadalmellato River valley, 12) Sierra de Hornachuelos, 13) Viar River valley, 14) Contiendas and Aroche, and 15) Doñana coastal plains. Spanish province boundaries are given.

TABLE 1.—Number of verified lynx records (physical evidence) found in each inferred subpopulation since 1940 and dates of last verified individual collected from each subpopulation and the first legal protection for lynx.

Subpopulation name (and number; see Fig. 2)	Trophies	Museum specimens	Other	Total	Occupied 10-km cells	Last record	First legal protection
Sierra de Santo Domingo (1)	0	1	0	1	1	1955	n. p.[a]
Sierra de Guadarrama (2)	0	0	1	1	1	>1950	1985[b]
Sierra de Gredos (3)	0	1	0	1	1	1968	1996
Tiétar River valley (4)	2	0	0	2	2	>1969	1996[b]
Sierras de Gata, Peña de Francia y Lagunilla (5)	0	5	2	7	4	1977	1973[b]
Monfragüe (6)	1	0	0	1	1	>1950	1979
Sierra de San Pedro (7)	1	0	0	1	1	>1950	n. p.
Montes de Toledo (8)	51	65	0	116	17	1985	1995[b]
Sierra de Relumbrar (9)	2	0	9	11	2	~1985	n. p.
Eastern Sierra Morena (10)	16	20	8	44	16	-	1989[b]
Guadalmellato River valley (11)	0	2	1	3	2	1981	n. p.
Sierra de Hornachuelos (12)	1	0	2	3	3	1963	1989
Viar River valley (13)	0	0	5	5	2	~1975	n. p.
Contiendas and Aroche (14)	0	3	0	3	2	1971	1989
Doñana coastal plains (15)	6	94	0	100	11	-	1969
Unknown subpopulation	0	20	0	20	-	-	-
Total	80	211	28	319	65	-	-

[a] n. p. = not protected.
[b] in part or all of each subpopulation.

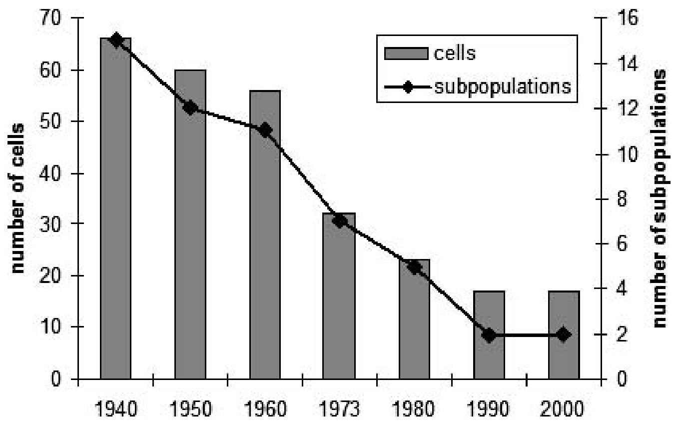

FIG. 3.—Decline of the Iberian lynx in Spain since 1940 expressed as the number of 10-km cells containing verified records (physical evidence) and existing subpopulations expressed as accumulated totals of all records from during and after each title year.

just 7 of the 15 subpopulations (Fig. 2). The subpopulations at this time included Sierra de Gata (2 lynxes in 1 cell), Peña de Francia (1 lynx in 1 cell), Montes de Toledo (47 lynxes in 6 cells), Guadalmellato River (1 lynx in 1 cell), eastern Sierra Morena (22 lynxes in 9 cells), Sierra de Relumbrar (9 lynxes in 2 cells), Viar River valley (1 lynx in 1 cell), and Doñana coastal plains (78 lynxes in 11 cells). This first noticeable decline was most apparent in Montes de Toledo (64.7% decline) and eastern Sierra Morena (43.7% decline), much of which was related to the loss of isolated squares or small adjacent subpopulations. Most of the former small subpopulations did not yield any lynx records after 1973, and many failed to produce lynx records after 1960 (Table 1).

The 1980–2000 distribution showed additional range decline since the 1970s (Fig. 2). Lynxes were recorded in 24 of the 32 cells from the previous decade and only 5 subpopulations: Montes de Toledo (7 lynxes in 2 cells), Guadalmellato (1 lynx in 1 cell), eastern Sierra Morena (17 lynxes in 8 cells), Sierra de Relumbrar (6 lynxes in 2 cells), and Doñana coastal plains (72 lynxes in 11 cells). Although 2 subpopulations had disappeared completely, lynx range at the 10-km grid scale had remained stable within the Sierra de Relumbar and Doñana coastal plains from 1973 to 1989.

By 1990 lynxes were detected in only 2 subpopulations, eastern Sierra Morena Mountains (14 lynxes in 6 cells) and Doñana coastal plains (46 lynxes in 12 cells), the latter again remaining stable since 1973 (Fig. 2). In the eastern Sierra Morena Mountains, however, the individuals collected were restricted to a well-defined area located in the Jándula and Yeguas river valleys, resulting in a 62.5% reduction of the known former subpopulation range in the previous decade at the 10-km grid scale. Between 1990 and 2000 (Fig. 3) lynxes were collected only from the Jándula and Yeguas river valleys in eastern Sierra Morena (6 lynxes) and the Doñana coastal plains (18 lynxes) within the same 12 grid cells as during 1980–1990 (Fig. 2).

The temporal progression of occupied cells and extant subpopulations highlights the major milestones of the Iberian lynx decline. An early crash during the 1950s heavily affected small populations and resulted in a 25% loss of all subpopulations. A second breakdown during the 1970s resulted in the loss of 42.8% of occupied cells and 36.3% of subpopulations. This was followed by a steady decline until the 1990s, which accounted for the accumulated loss of 43.5% of grid cells and 50% of subpopulations between 1973 and 1990. Finally, in 2000 serious conservation programs were undertaken by the European Union, and the decline appears to have been halted. During the 60-year period studied (1940–2000) the global Iberian lynx range decreased by 74.6% of occupied 10-km grid cells and 87.5% of subpopulations.

DISCUSSION

Assessment of method.—Potential bias in this study could result from differences in sampling effort represented by each data source over time (Frey 2006). The observed decline in occupied cells and subpopulations during the 1970s can be explained partially by lynx protection and the end of legal hunting (McCain and Childs 2008); however, this cannot account for the decline of individuals collected during the 1960s, when hunting was still legal. The increase in museum collecting activity during the 1970s might balance somewhat the effects of discontinued trophy hunting at that time, suggesting an actual decline in range and numbers despite a possible bias from data sources.

Spatial bias can also affect our results due to the limitations of obtaining physical evidence of specimens. Most specimens in the MNCN collection were from Montes de Toledo, and all lynxes in the EBD collection were from the greater Doñana coastal plains area. Aymerich (1982) collected stomach remains from a large number of European wild cats (*Felis silvestris*) and Iberian lynxes throughout Spain. Those records show wild cat distribution over a significantly larger range than the range of lynxes collected in the same study, which very closely matches our maps. Museums have collected multiple carnivore species throughout Spain, and despite obvious museum interest in the species, no lynxes have been recorded outside the subpopulations described. Hunting, legal and illegal, can be assumed to have been well distributed throughout the entire former range, as private hunting properties and rural inhabitants are common throughout every region of Spain. However, we recognize that lynxes killed in some rural areas might not have been registered by government authorities, and thus hunting records could be incomplete and potentially geographically biased.

We advise caution regarding the potential biases; however, several factors fully complement the results of our analysis of verified records. First, since the time of the last range estimate for the Iberian lynx in 1992 many field surveys have been conducted within the areas of the former range proposed by Rodríguez and Delibes (1992, 2002, 2003). None of the surveys verified lynx presence outside of the 2 remaining subpopulations; only a small handful of doubtful tracks or scats have been recorded in these areas (Gil-Sánchez et al.

1998; González Oreja and González Vázquez 1996; Ordiz and Llaneza 2004; Sánchez et al. 1998). Second, verified records, in the form of dead lynxes, have been collected continually since the middle of the 20th century within the 2 surviving subpopulations, despite small population size and low density in Doñana (Guzmán et al. 2004) and the lack of research programs in eastern Sierra Morena until 1993 (J. M. Gil-Sánchez, pers. obs.). Third, Guzmán et al. (2004) showed that scat surveys are a highly successful and efficient method for detecting the presence of territorial individuals, and in 1999 reliable genetic identification methods were developed (Alda et al. 2008; Fernández et al. 2006; Palomares et al. 2002; Pires and Fernandes 2003). During 2003–2007 395 potential lynx scat samples were collected in Montes de Toledo, 8 of which (2.0%) were genetically identified to be from lynx (Alda et al. 2008). Although we do not disregard the possibility of the presence of a few wandering individuals, these data do not likely represent a current subpopulation of territorial lynxes in Montes de Toledo. Furthermore, Palomares et al. (2002) reported a 7.4% error rate for this genetic technique, which easily could account for a few (2%) false positives in the Montes de Toledo samples. Finally, since the year 2000 approximately 100 camera traps have been monitoring within all of the former subpopulation ranges, including in Portugal; only Doñana and eastern Sierra Morena have produced lynx photographs (Guzmán et al. 2004; Sarmento et al. 2009).

The maps produced in this study are the first attempt to use only verified unequivocal data to describe the former Iberian lynx distributional range and population decline. Because these maps were constructed with solely verified records, they are conservative and offer only a minimum verified former range of the Iberian lynx. We acknowledge that it is possible that small populations could have escaped being sampled by museum collections or reported by hunters. However, if other subpopulations did exist during the period studied (1940–2000), we suggest that some verifiable evidence eventually should be recorded, and any undetected subpopulations were likely very small and of little overall importance. Our verified record-based maps represent the best available information on the subject to date and appear to describe accurately the actual range of the Iberian lynx at intervals from 1940 to 2000. By reconstructing the sequence of the various subpopulation declines and local extinctions we can infer how different potential impacts temporally coincided with the observed declines in lynx numbers and populations.

Verified data versus sighting data in describing lynx decline.— Verifiable physical records of Iberian lynxes collected since the middle of the 20th century suggest that the species was very rare outside of eastern Sierra Morena, Doñana, and Montes de Toledo, and by the 1990s only the eastern Sierra Morena and Doñana populations remained, offering a fragmented range similar to the range estimates by Valverde (1963) and later by Delibes (1979). More recently, Rodríguez and Delibes (1992, 2002, 2003) used sighting reports from mail-out surveys to portray a more continuous and widespread distribution than was described previously by Valverde (1963), and far different from our findings. This range estimate based on sighting reports encompassed basically all of Mediterranean Spain and consisted of 406 occupied 10-km grid cells (compared with our 65 cells), including an additional 48 broadly distributed areas located outside of the species' range later proposed by the same authors (Rodríguez and Delibes 2002). To arrive at this estimate Rodríguez and Delibes (1992) accepted many grid cells with only 1 or 2 sightings reported between 1950 and 1985 as occupied (228 cells with 0.028–0.057 reports/100 km^2 $year^{-1}$). This is not a realistic approach, and the doubtful results highlight the unreliability of sighting data and the use of isolated cells containing low sighting report rates.

One interesting finding was a lynx skull from 1951 in the external Pyrenees Mountains in the Sierra of Santo Domingo (Huesca Province). This is a Mediterranean area that Rodríguez and Delibes (2002) did not include as occupied by the species during the 20th century; however, Valverde (1963) and Rodríguez and Delibes (1992) did draw 1 subpopulation within this area at the middle of the last century. Rodríguez and Delibes (1990) reported some sighting data from these mountains, but this was never supported by any consistent information. Therefore, the history of lynx presence in this area remains somewhat unclear.

Rodríguez and Delibes (1992, 2002) listed a subpopulation inhabiting the Betic Mountains of southeastern Spain during the 1980s (Fig. 4). Our research found 3 former verified lynx records within those mountains. Two were museum specimens from the late 19th century (Padre Suarez Institute and Universidad de Granada), the other a jawbone of unknown age, but reported as very old, found in a cave (Gil-Sánchez et al. 1998). Several specimen investigations revealed European wildcats misidentified as lynxes, and intensive field studies during the early 1990s failed to detect any further verified information in that region (Gil-Sánchez et al. 1998). Therefore, despite common sighting reports from the area, which continue at present (J. M. Gil-Sánchez, pers. obs.), the best available verifiable information indicates that this subpopulation likely became extinct before 1940.

The verified reports compiled for this study suggest that most of the small scattered subpopulations seem to have become extinct during the late 1950s and 1960s. However, Rodríguez and Delibes (1992, 2002, 2003) reported these subpopulations to be extant during the 1980s. This disagreement between our verified data and sighting report data of Rodríguez and Delibes also can be observed in the larger population trends. According to verified records, the Doñana and eastern Sierra Morena subpopulations had great reductions in numbers and area from 1960 to 2000; however, Rodríguez and Delibes (1992, 2002) reported larger ranges during the 1980s. The case of the Montes de Toledo population is especially dramatic. The last verified lynx was collected in 1985 (MNCN), whereas Rodríguez and Delibes (1992) assumed a 1988 population of 272 lynxes, with reproduction and kittens. Because the sighting data (Rodríguez and Delibes 2002) depicted a much broader distributional range, these data also show a greater decline, in the form of occupied cells lost,

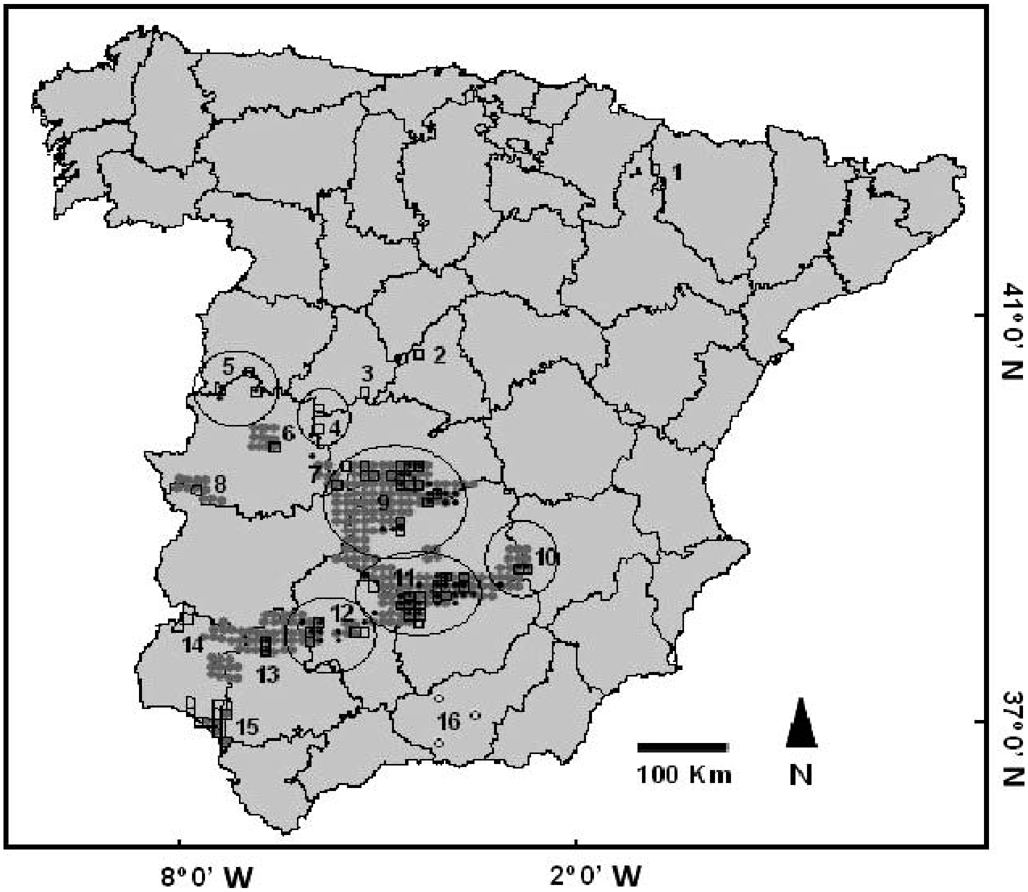

FIG. 4.—Distribution of the red deer (*Cervus elaphus*) in Spain in 1968 (gray circles, redrawn from Servicio de Pesca Continental, Caza y Parques Naturales [1968], reintroduced populations excluded), with overlaying Iberian lynx range since 1940. Lynx range is represented by verified data with physical evidence from the present study (squares) and heavily filtered sighting report data (cells with >10 records/35 years) redrawn as black dots from Rodriguez and Delibes (2002). Verified lynx records from before 1940 are represented as white circles. Inferred subpopulations: 1) Sierra de Santo Domingo, 2) Sierra de Guadarrama, 3) Sierra de Gredos, 4) Tiétar River valley, 5) Sierras de Gata, Peña de Francia y Lagunilla, 6) Monfragüe, 7) Villuercas, 8) Sierra de San Pedro, 9) Montes de Toledo, 10) Sierra de Relumbrar, 11) Guadalmez, Yeguas, Jándula, Rumblar, and Guarrizas river basins (eastern Sierra Morena), 12) Guadalmellato River valley and Sierra de Hornachuelos, 13) Viar River valley, 14) Contiendas and Aroche, 15) Doñana coastal plains, and 16) Betic Mountains. Spanish province boundaries are given.

occurring at a later date (after 1970) than our verified data (during 1960–1970).

The discrepancies between our data and those based on sighting reports by Rodríguez and Delibes (1992, 2002, 2003) are explained mostly by the differences in the evidentiary data standards used. Given the limitations of anecdotal sighting data used by Rodríguez and Delibes (1992, 2002, 2003), we suggest that only cells with the highest report rates should be acknowledged, especially considering the significant subjectivity problems of interview data (Frey 2006; Guzmán et al. 2002; McKelvey et al. 2008; Sarmento et al. 2004). Using only the grid cells containing more than 10 reports/35 years from Rodríguez and Delibes (2002), the number of cells decreases from 406 to 56, yielding a result much closer to the 65 cells in our verified data-based maps. With this filter applied, 27 cells overlapped directly with those in our maps (40.0% of verified cells and 48.2% of sighting cells), and the remainder were concentrated usually around the periphery of the same subpopulations. Therefore, by combining the 2 data sources (verified and filtered sighting reports), a new map containing 95 cells represents a more realistic description of the former Iberian lynx distribution (Fig. 4). Furthermore, by combining our verified data set with the filtered sighting data, we can begin to account for the spatial bias in our own data due to geographic

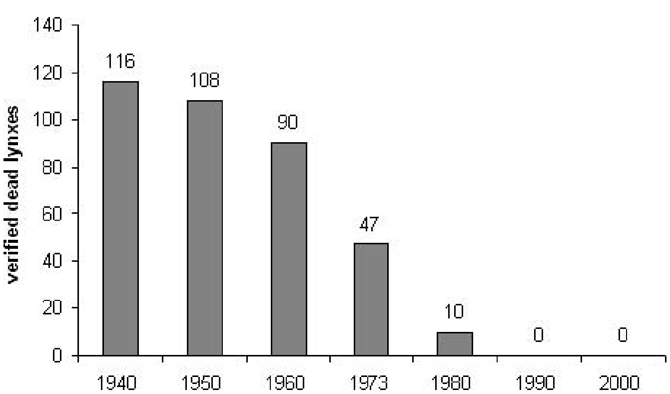

FIG. 5.—Decline of the Iberian lynx in Montes de Toledo since 1940, expressed as the accumulated total number of verified lynxes from during and after each title year.

limitations in museum collections and hunting records. In this combined map the total number of former subpopulations still was 15, as 1 new subpopulation becomes apparent (Villuercas) and another 2 (Guadalmellato and Hornachuelos) become combined into 1 subpopulation (Fig. 4).

McKelvey et al. (2008) described 3 cases where anecdotal sighting data created false understandings of endangered species distributions and misled conservation efforts. In the case of the fisher (*Martes pennanti*), needed habitat protection in the western United States was delayed because anecdotal sighting data suggested that the species was widespread and thriving. Reintroductions or other conservation actions for the wolverine (*Gulo gulo*) in California were postponed for the same reasons. The ivory-billed woodpecker (*Campephilus principalis*) was extinct for decades until unverified sighting reports stimulated the misallocation of scarce resources for conservation in the southeastern United States. The critically endangered status of the Iberian lynx calls for urgent and precise conservation actions, guided by the best available information to avoid species extinction.

Potential factors contributing to the observed declines.—The Iberian lynx is completely dependent on just 1 prey species, the European rabbit (*Oryctolagus cuniculus*—Delibes 1980; Gil-Sánchez et al. 2006; Palomares et al. 2001). Rabbit populations were decimated across the Iberian Peninsula by the introduction of myxomatosis in the late 1950s (Muñoz 1960) and rabbit hemorrhagic disease (RHD—Calvete et al. 2002; Villafuerte et al. 1995) in the late 1980s. The true spatial and temporal impacts of these diseases on lynx declines have not been shown clearly. A substantial crash in the lynx populations between 1960 and 1973 might coincide with myxomatosis-related rabbit population crashes; however, the potential impact of RHD on lynx numbers is not so easily inferred. Furthermore, our data show that many lynx subpopulations became extinct before either myxomatosis or RHD outbreaks occurred. Myxomatosis and RHD have highly limited rabbit populations and thus prey availability for lynxes, but prey diseases alone cannot entirely explain the extinction of most lynx subpopulations.

Iberian lynx habitat selection is not well studied outside of the Doñana coastal plains (Fernández and Palomares 2000; Fernández et al. 2003, 2007; Palomares 2001; but see Fernández et al. 2006; Real et al. 2009). However, we can infer from the species' former range that it once inhabited mixed pasture and Mediterranean scrubland landscapes with dense cover, which realistically could be comprised of several different vegetative communities (Rivas-Martínez 1987). Large areas of habitat types formerly inhabited by lynxes still are distributed broadly across the former range (Real et al. 2009), some of which overlap healthy rabbit populations (Guzmán et al. 2004). Habitat loss due to pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.) plantations and loss of Mediterranean scrubland diversity (Rodríguez and Delibes 2002) could have contributed to the reduction of some subpopulations but likely did not cause extinctions.

Direct hunting and human persecution might best account for the observed decline in lynx population range and numbers, especially between 1960 and 1980 (Fig. 5). Verified records show that 80 legal trophies were registered before 1970, and an additional 20 lynxes are known to have been trapped or shot in Montes de Toledo and eastern Sierra Morena between 1974 and 1983 (Fig. 5), after the species was legally protected (García-Perea 2000). The number of verified records representing human-caused mortality is certainly only a fraction of the lynxes actually killed in rural areas, and the implementation of legal protection in 1973 likely decreased the probability of specimens being reported after that date (McCain and Childs 2008).

Private and commercial rabbit exploitation has been a strong Spanish tradition and continues in some areas where rabbit populations escaped disease-caused extinctions. Snares and large steel-jaw traps were common methods for large-scale rabbit harvest until the 1980s (Rodríguez and Delibes 1990). Also associated with small-game hunting traditions, intensive predator control practices use leg-hold and box traps, snares, and poisons for carnivores. Many of these nonselective practices remain legal and continue to threaten lynx survival (Delibes-Mateos et al. 2009; Rodríguez and Delibes 2004; Villafuerte et al. 1998; Virgós and Travaini 2005). For instance, 8 radiotracked lynxes were killed by traps in Doñana between 1983 and 1989 (Ferreras et al. 1992), indicating that unprotected areas of good-quality habitat actually behaved as a sink for the important population within the nearby protected national park (Gaona et al. 1998). Fortunately, the potential risk from human persecution is assumed to be lower currently than in the past, considering the highly protected legal status of the species and the development of Spain's network of protected spaces. However, before conservation programs can be successful, more rigorous laws must address irresponsible trapping and predator-control practices.

Traditionally, big-game hunting has been limited to Spain's wealthy elite in restricted private big-game hunting reserves, and by the middle of the 20th century persecution by countryside people drove the red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), Iberian ibex (*Capra pyrenaica*), and roe deer (*Capreolus capreolus*) to virtual extinction outside of these reserves. Valverde (1963) assumed this to be the case also for the Iberian lynx. Our results confirm that most of the grid cells formerly occupied by lynxes were located within or near private big-game hunting properties.

Our temporal and spatial reconstruction of the lynx decline illustrates the importance of protected areas free from hunting, trapping, and predator control pressures. Apparently, the 1973 nongame/protected status for the species was not sufficient protection to avoid population declines. Further protective measures, which were imposed mostly during the late 1980s or early 1990s, arrived too late to protect most remaining populations. The Doñana coastal plains subpopulation was protected in 1969 when the Doñana National Park was founded and hunting forbidden. The relict subpopulation of eastern Sierra Morena Mountains represents a rare and fortunate case where key positive socioeconomic (private big-game reserves) and natural factors (high rabbit density) geographically overlapped at a suitable spatial scale to combine the elements necessary for lynx persistence: ample habitat and food resources, reduced levels of predator control (because small and mesocarnivore species have no negative impact on big game), and absence of commercial wild rabbit exploitation (to avoid trap damages to big game). It was only because of the special circumstances in Doñana National Park and the big-game hunting reserves of eastern Sierra Morena, where suitable habitat, protected from human persecution, coincided with healthy rabbit populations that the Iberian lynx avoided complete species extinction in the second half of the 20th century.

Conservation implications.—Heavy-handed conservation actions for the world's only critically endangered cat species must be intensified to avoid the first known feline extinction in modern times. The probability for natural dispersal to reestablish viable breeding populations is too low (Breitenmoser et al. 2006), and reintroduction programs appear to be essential for the long-term survival of the species. Our data can be best applied in comprehensive and detailed feasibility evaluations of potential reintroduction sites, following a well-based global conservation strategy designed by Spanish and Portuguese environmental authorities. The most obvious approach would be to focus first on areas where populations were most recently lost (Breitenmoser et al. 2006). If we then consider the key role that human persecution played on lynx population declines during the 20th century, we might be able to refine site selection for reintroduction. We then can examine rabbit availability among the recently occupied subpopulation ranges with reduced predator control and other human-caused threats. Finally, we must remember that a larger number of reintroduction attempts in different areas will yield a higher probability of success and species recovery. The Iberian lynx historically lived throughout the entire Mediterranean area of the Iberian Peninsula, and therefore reintroduction programs should be applied not only within the former range offered in this study but also eventually in other areas offering suitable habitat attributes in both Spain and Portugal (Real et al. 2009). The first reintroduction efforts for the Iberian lynx, currently underway in the Guadalmellato and Guarrizas river valleys (J.M. Gil-Sánchez, pers. obs.), were selected, in part, on the basis of the preliminary results of this study.

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