Check for updates

Received: 6 February 2025 | Accepted: 6 June 2025

DOI: 10.1111/1365-2664.70097

Journal of Applied Ecology

RESEARCH ARTICLE

# Demographic performance review of a reintroduction project: Iberian lynx in Extremadura

José Jiménez[1] | Matías Taborda[2] | Pablo Ferreras[1] | Maria Jesús Palacios[3] | Fernando Nájera[4,5] | Jorge Peña[3] | Marc Kéry[6] | Michael Schaub[6]

[1]Instituto de Investigación en Recursos Cinegéticos (IREC, CSIC-UCLM-JCCM), Ciudad Real, Spain; [2]Consejería de Gestión Forestal y Mundo Rural, Dirección General de Gestión Forestal, Caza y Pesca, Mérida, Spain; [3]Dirección General de Sostenibilidad, Junta de Extremadura, Mérida, Spain; [4]Wildlife Health Center, School of Veterinary Medicine, University of California, Davis, California, USA; [5]Department of Animal Physiology, Faculty of Veterinary Medicine, Complutense University of Madrid, Madrid, Spain and [6]Swiss Ornithological Institute, Sempach, Switzerland

**Correspondence**
José Jiménez
Email: jose.jimenez@csic.es

**Handling Editor:** Ardiantiono

## Abstract

1. Reintroduction is a widely used management tool for restoring wildlife populations, with the goal of creating functional and self-sustaining populations. Evaluating the success or failure of such programmes requires a thorough understanding of the dynamics of the reintroduced population.
2. The Iberian lynx (*Lynx pardinus*), an iconic conservation flagship species, illustrates the value of reintroduction initiatives. On the brink of extinction 25 years ago, this species has now recovered thanks to intensive conservation management. However, the demography underlying the dynamics of the reintroduced Iberian lynx populations is poorly known, which hinders future management decisions.
3. Using data from camera trapping and radio-tagging, we reviewed the reintroduced population in Extremadura, Spain (2014–2024), using an integrated population model (IPM). We conducted both retrospective and prospective analyses to identify the demographic drivers of population growth and evaluate management scenarios using IPM-based population viability analysis (PVA).
4. In 2024, 10 years after the reintroduction began, the Extremadura population was estimated at 164 individuals (95% CRI: 141–189), including 28 breeding females. Female population size was regulated by density-dependence, driven by subadult dispersal leading to increased roadkill mortality. During the early stages of the reintroduction programme, variation in population structure was the main driver of changes in growth rate. However, as the population increased, adult survival and recruitment became the dominant contributors to population dynamics. Meanwhile, female breeding propensity and litter size remained stable, having limited effects on growth rate variability. PVA projections suggest that the lynx population will stabilize around 32 breeding females within the next 15 years. To increase the stationary population size, it is

necessary to improve habitats to increase the number of breeding territories and reduce roadkill mortality.

5. *Synthesis and applications*. Demographic performance reviews are essential for understanding the drivers of population growth and for evaluating the outcomes of reintroduction initiatives. IPMs as exemplified by our Iberian lynx case study provide a powerful and flexible framework for quantifying reintroduction performance and addressing key research and management questions. By using insights from demography, conservation practitioners can better guide effective management strategies and ensure the long-term viability of restored populations.

**KEYWORDS**
demographic monitoring, demographic performance review, Iberian lynx, integrated population model (IPM), *Lynx pardinus*, population viability analysis (PVA), reintroduction, roadkill

## 1 | INTRODUCTION

Reintroduction, or translocation, is an increasingly used management tool to restore wildlife populations and ecological processes (Morris et al., 2021; Seddon et al., 2007). The ultimate goal of management is for both populations and processes to be fully functional (Morris et al., 2021; Schaub et al., 2004; Scott & Carpenter, 1987). Therefore, the key question that arises in any reintroduction project is when the key goal of self-sustainability is achieved. The ultimate judgement of the success or failure of any reintroduction project must rely on a rigorous population demographic analysis (Morris et al., 2021).

Long-term monitoring is essential for assessing population size, demographic rates and trends and forms the foundation for evaluating the demographic performance of a reintroduction project (Morris et al., 2021; Okahisa & Nagata, 2022; Seddon et al., 2007). Firstly, knowledge of demographic rates and population size allows population viability analysis (PVA) to project the likely future status of a reintroduced population (Morris & Doak, 2002) and assess the probability of extinction. Secondly, PVA can guide the evaluation of alternative management strategies both during and after reintroduction (Seddon et al., 2007). Lastly, demographic drivers of population change can be identified (Koons et al., 2017; Servanty et al., 2014), potentially uncovering hidden or poorly understood issues in the reintroduction process. With this knowledge, conservation efforts can be further focused on the most influential drivers. Although the importance of demographic analysis in guiding and assessing reintroductions is widely acknowledged, comprehensive demographic performance reviews that address these aspects thoroughly remain the exception rather than the rule among the thousands of reintroduction projects that have been conducted worldwide (Marino et al., 2024). This limitation is particularly evident for elusive species with large home ranges (Stepkovitch et al., 2022).

Within this context, integrated population models (IPMs; Abadi, Gimenez, Arlettaz, & Schaub, 2010; Abadi, Gimenez, Ullrich, et al., 2010; Besbeas et al., 2002; Brooks et al., 2004; Schaub & Kéry, 2022) have emerged as transformative analytical tools. By synthesizing multiple and diverse data sources—such as population counts, survival data and productivity metrics—into a unified analytical framework, IPMs improve the precision of inferences, allow the estimation of demographic processes for which explicit data are not available and account for all relevant sources of uncertainty. Thereby, they provide a comprehensive understanding of population dynamics (Besbeas et al., 2002; Schaub & Kéry, 2022). This integrative approach facilitates the estimation of demographic parameters and population size, the identification of density-dependent effects, the conduct of rigorous prospective and retrospective population analyses and the evaluation of underlying ecological processes, thereby vastly improving the assessment of conservation outcomes.

The Iberian lynx (*Lynx pardinus*) provides an excellent case study for a large-scale and cost-intensive reintroduction programme. This species is a specialized predator of European rabbits (*Oryctolagus cuniculus*) with a strong reluctance to shift to alternative prey (Delibes, 1980; Ferreras et al., 2011). While rabbits historically were widespread and abundant, the effects of infectious diseases, such as myxomatosis in the 1950s (Ratcliffe et al., 1952) and Rabbit Hemorrhagic Disease (RHD) in the late 1980s, reduced their numbers in most of their historic range (Villafuerte et al., 1995). Consequently, the current rabbit distribution in Spain is fragmented and dependent on targeted land management (Virgós et al., 2003). High rabbit densities are typically found in actively managed small game hunting estates and certain agricultural areas where food is abundant and management practices support continued rabbit presence (Delibes-Mateos et al., 2009; Marin-Sáez et al., 2025). The fragmented distribution of rabbits leads to a fragmented metapopulation structure in lynx populations (Gaona et al., 1998). This structure often exhibits a 'matrix expansion' dynamic—in contrast to 'contiguous dispersion'—as described by Glass et al. (2024), occurring in fragmented landscapes with patches of high rabbit density and extensive areas with zero or very low rabbit density (Delibes-Mateos et al., 2009).

Following the first outbreaks of RHD in the late 1980s, there was concern about the potential indirect impact of the reduction in rabbit populations on the already very small populations of the

Iberian lynx (Villafuerte et al., 1995). Between December 1999 and June 2002, a national survey revealed an estimated population of only 30 breeding females (Guzmán et al., 2004). Following a comprehensive conservation programme coordinated by the Spanish and Portuguese governments, including captive breeding and reintroduction through numerous projects co-funded by the European Union, by 2023 lynx populations had recovered in areas with high rabbit densities, with an observed pre-breeding population size of 1299 individuals (Life Lynxconnect Team, 2024).

Several studies have previously investigated the demography of the Iberian lynx (Ferreras et al., 2001; Palomares et al., 2005), but these have been limited in scope, relying on small sample sizes and focusing on a single natural population in the Doñana National Park (Southern Spain). So far, no published study has analysed the demography of a reintroduced Iberian lynx population. Despite the favourable trend in wild lynx numbers in recent years, it remains unknown whether the reintroduction has been successful in terms of the crucial goal of self-sustainability. Meanwhile, there is a concern about the long-term impact of the increasing number of documented road kills on the species. To address these issues, we used data from the Extremadura region, where standardized monitoring has been ongoing since 2014.

Through a demographic performance review based on an IPM, we gained comprehensive insights into population status, trends and the key drivers of population dynamics (Frost et al., 2023; Margalida et al., 2020). Our model enabled the estimation of lynx demographic parameters and population sizes, testing for density dependence, performing both prospective and retrospective population analyses and conducting a Bayesian PVA (Davis et al., 2023; Schaub et al., 2024). By integrating these demographic findings, we evaluated the performance of the reintroduction, assessed the impact of roadkill mortality on population viability and developed recommendations to guide future management strategies. Beyond evaluating the performance of this high-profile reintroduction project, the creative use of multiple population dynamics data within our IPM serves as a conceptual template for similar efforts and underscores the value of formal demographic performance reviews in improving the effectiveness and success of reintroduction projects as a central conservation strategy (Morris et al., 2021).

# 2 | MATERIALS AND METHODS

## 2.1 | Study area

Our study area comprised the Extremadura region (41,633 km$^2$) in SW Spain. The natural vegetation consists of Mediterranean holm oak (*Quercus ilex*) and cork oak (*Quercus suber*) forests with subclimax shrublands in the mountains, fragmented between the agricultural areas and open oak woodlands managed for livestock and agriculture ('dehesas') in the plains.

The exact date of the lynx's extinction in Extremadura is unknown. The last recorded sighting was in 1991, and Guzmán et al. (2004) reported no evidence of lynx in their survey. Lynx reintroduction in Extremadura began in 2014 and continues to date. The first release site was in the southern Matachel Valley (Jiménez et al., 2019, Figure 1). Typically, each year between 5 and 11 captive-bred, 1-year-old lynx were released. Some individuals dispersed from southern Matachel to colonize further core areas with dense rabbit populations, reaching Ortiga (2016), Sotillo, Valdecigüeñas and northern Matachel (2018), Valdecañas (2019) and Cornalvo (2022) (Rueda et al., 2021). The population in Cornalvo established naturally, but was translocated to other cores in 2023 to avoid road-kill mortality. Since 2019, reintroductions have been made in all these breeding areas to increase their genetic diversity and maintain a sex ratio as close to parity as possible. A total of 92 individuals (43 females and 49 males) were released by 2024. In 2024, the spatial structure of the lynx population in Extremadura consisted of one primary core (southern Matachel) and six secondary cores, with a total area of ca. 600 km$^2$. Immigration into Extremadura was observed from Castilla-La Mancha and Portugal, while emigration was recorded into Portugal, Castilla-La Mancha and Andalusia (Figure 1).

## 2.2 | Field data

The regional government gathered the data with the support of MITECO, CBD-Habitat and FOTEX, and provided it for the study. A database was created containing the individual history of all released and detected wild-born lynx in Extremadura during 2014–2024. Individuals were recognized based on their fur pattern, and released individuals were additionally monitored with GPS and telemetry collars. Camera traps were installed in all breeding areas and were operational during the breeding season (April–August). Breeding success is expressed as litter size and is measured as the ratio of offspring to breeding females recorded on visual and camera-trap observations during February–October. Dead animals were detected and recovered mainly using GPS/telemetry tracking, but some animals (tagged or untagged) were accidentally found by rangers, police and by the general public in Spain and Portugal. Apparent roadkills were necropsied to verify cause of death (see Appendix S1 in Supporting Information).

## 2.3 | Integrated population model

### 2.3.1 | Population model

The heart of our IPM was a stage-structured population model (Caswell, 2001), which related stage-specific population sizes to demographic rates and whose specific formulation was adapted to the lynx life cycle. Adult lynx exhibited intrasexual territoriality, as shown by their exclusive home ranges, with seasonal home range overlap between adult males and females, but not among individuals of the same sex (Ferreras et al., 1997). Yearlings (1-year-old)

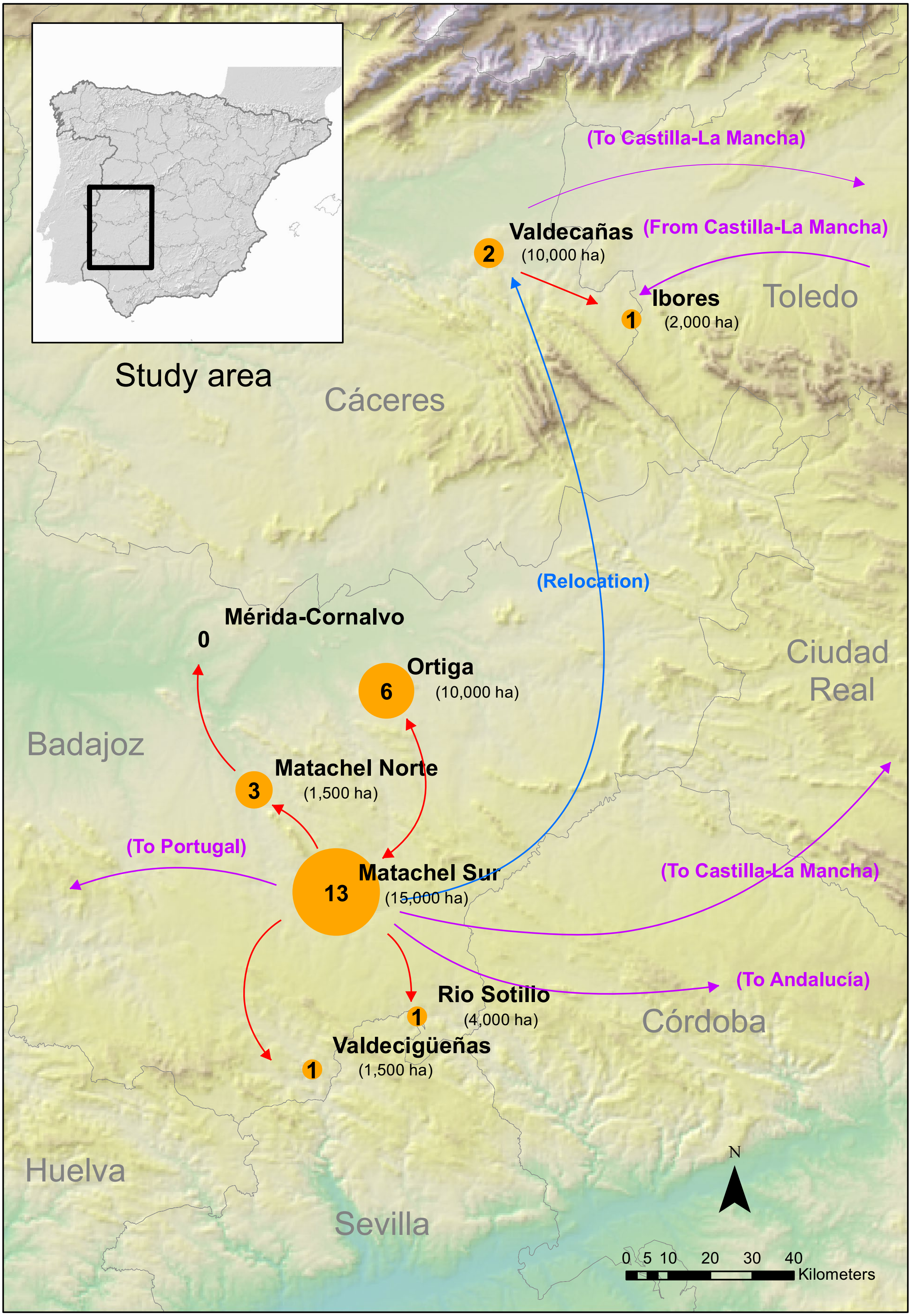
Study area
Cáceres
Toledo
Badajoz
Ciudad Real
Córdoba
Huelva
Sevilla
(To Castilla-La Mancha)
(From Castilla-La Mancha)
2 Valdecañas (10,000 ha)
1 Ibores (2,000 ha)
(Relocation)
0 Mérida-Cornalvo
6 Ortiga (10,000 ha)
3 Matachel Norte (1,500 ha)
(To Portugal)
13 Matachel Sur (15,000 ha)
(To Castilla-La Mancha)
(To Andalucía)
1 Rio Sotillo (4,000 ha)
1 Valdecigüeñas (1,500 ha)
N
0 5 10 20 30 40 Kilometers

**FIGURE 1** The study area (Extremadura; Cáceres and Badajoz) showing the breeding plots and movements (2014–2024) within the study area (in red), immigration-emigration routes (in magenta) and relocation paths (in blue). The orange circles show inside the observed number of reproductive females in each core population (2024). The area of each core is shown in parentheses, based on telemetry and GPS locations.

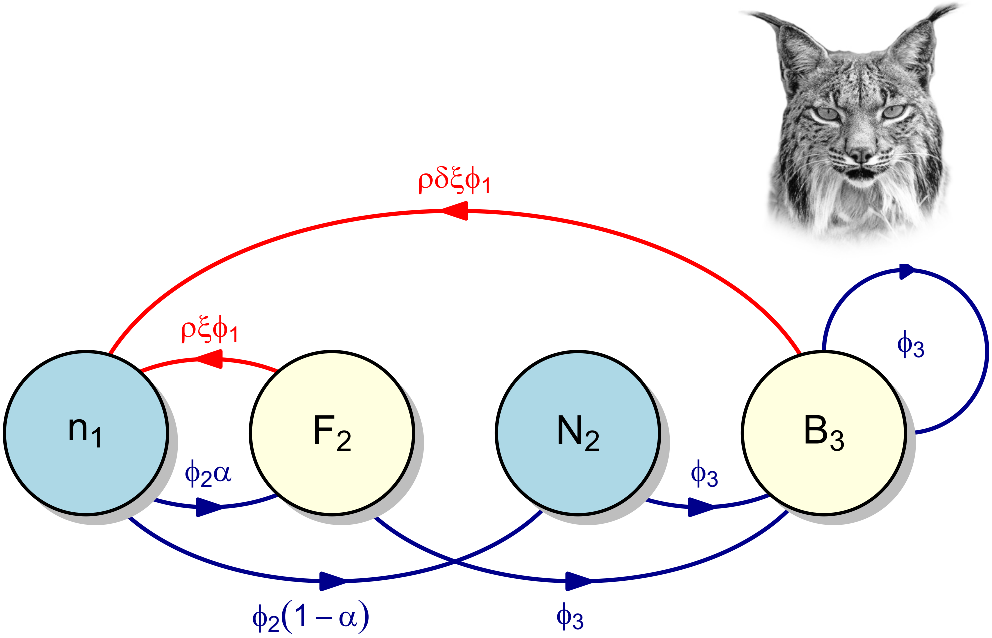

**FIGURE 2** Simplified life cycle graph of the stage-structured pre-breeding model used in the integrated population model (IPM) for the Iberian lynx. We show the submodel of wild-born females. Stages: $n_1$: 1-year-old non-breeders; $F_2$: 2-year-old first-time breeders; $N_2$: 2-year-old non-breeders; $B_3$: Females three-years-or-older that all reproduced. Transitions between stages are governed by demographic rates; $\phi_1, \phi_2, \phi_3$: Juvenile, subadult and adult survival; $\alpha$: Probability of a 2-year-old female to start breeding; $\delta$: Breeding propensity; $\rho$: Fecundity; $\xi$: Kitten sex ratio. See parameters in Table S1. Full model in Figure S1.

either remained in the natal area or became dispersers. Dispersal distance differed between sexes, with males dispersing further, as is typical for mammals (Ferreras et al., 2004). Female lynx could begin reproducing at age 2, and from age 3 on, they typically gave birth to 2 to 5 kittens in a single litter per year (Palomares et al., 2005). To capture this life cycle, we used a pre-breeding, two-sex model (Figure 2, Figure S1), with stages defined based on a combination of age (1, 2 and 3 years and more), breeding status (breeder, non-breeder), sex and release status (released, wild-born) (Tables S1 and S2). Transitions among states were governed by stage-specific demographic rates, including productivity, recruitment, survival, dispersal, immigration and emigration, all of which were allowed to vary over time. Individuals remaining in Extremadura either stayed in their natal or release area and were called philopatric, or they could disperse to another area within our study area, in which case we called them dispersers. Therefore, we defined two parameters representing dispersal: the probability to disperse within the study area and the probability to emigrate from the study area. Details are in Appendix S3.

To assess its impact on population growth, we investigated whether roadkill mortality could be compensatory—that is, whether it might at least partly replace other causes of death with reduced impact on overall mortality and hence on population dynamics. We distinguished between roadkill and other ('background') mortality due to all other causes. Survival was specified in terms of cause-specific mortality hazard rates (Ergon et al., 2018; Schaub & Kéry, 2022), which allowed us to estimate whether and by how much roadkill mortality was compensated for by reduced background mortality (Ergon et al., 2018). We estimated roadkill mortality hazard rates ($M^{RK}_{i,s,t}$) and background mortality hazard rate ($M^{BG}_{i,s,t}$) for each sex $s$, age class $i$ and year $t$; from these, we obtained the annual survival probability as $\phi_{i,s,t} = \exp\left(-\left(M^{RK}_{i,s,t} + M^{BG}_{i,s,t}\right)\right)$, the probability of mortality due to roadkill as $rk_{i,s,t} = (1 - \phi_{i,s,t})\frac{M^{RK}_{i,s,t}}{M^{RK}_{i,s,t} + M^{BG}_{i,s,t}}$, and the probability of background mortality as $b_{i,s,t} = (1 - \phi_{i,t})\frac{M^{BG}_{i,s,t}}{M^{RK}_{i,s,t} + M^{BG}_{i,s,t}}$. To test for compensatory processes, we assessed the correlation between roadkill and background mortality (Schaub & Kéry, 2022).

### 2.3.2 | Likelihood of each data set

We integrated three different datasets into the IPM: population counts, live encounter-dead recovery data and productivity data, each of which was represented by a different submodel with some parameters that are shared across submodels (see Appendix S3):

a. *Count submodel*: We analysed a time series of population counts with a state-space model whose state-process model corresponds to the above population model (Figure 2 and Figure S1). To separate process variability from observation errors, we modelled the counts of breeding females and males aged at least 2 years using Gaussian distributions. Counts of immigrants were modelled with Poisson distributions.
b. *Capture-recapture submodel*: We used live encounter-dead recovery data, which were jointly analysed using a multinomial multistate capture-recapture model (Burnham, 1993; Lebreton et al., 1999). This submodel enabled the simultaneous estimation of cause-specific survival, site fidelity and other parameters (Table S1), while accounting for imperfect detection.
c. *Productivity submodel*: For the dataset containing direct information about reproduction, we used a Poisson regression to estimate productivity, expressed as litter size per reproductive female.

#### 2.3.3 | Joint likelihood

The IPM is represented by a joint likelihood that is given by the product of the three individual data likelihoods. This likelihood construction assumed the data are statistically independent (Schaub & Kéry, 2022), though we note that the violation of this assumption hardly affects the inferences (Abadi, Gimenez, Ullrich, et al., 2010; Weegman et al., 2021). Estimates obtained from the IPM included stage-specific population sizes and all demographic rates described in the model (Tables S1 and S2). We used Bayesian MCMC (Markov Chain Monte Carlo) methods to fit the IPM (Kéry & Schaub, 2012; Schaub & Kéry, 2022) using the R package NIMBLE (de Valpine et al., 2017). We specified vague or weakly informative priors for all parameters (see Appendices S4 and S5) and ran three chains for 350,000 iterations, with a burn-in of 100,000 and thinning of 1 in 25, resulting in 30,000 posterior samples per parameter. Convergence of all chains was deemed adequate from visual inspection and by values of $\hat{R} < 1.1$ (Brooks & Gelman, 1998). To assess goodness-of-fit we used posterior predictive checks for all three component likelihoods and calculated the resulting Bayesian *p*-values (see Figure S2). For point estimates we reported posterior means, except for population size, where we used posterior medians due to their skewed distribution. We expressed estimation uncertainty by 95% Bayesian credible intervals (CRIs). Data and the R code for analyses performed are available in the Zenodo repository (https://zenodo.org/record/14825099).

### 2.4 | Test for density dependence

We tested whether the annual population growth rate of males and females decreased with increasing population size. We first compared the observed relationship between population growth rate and total population size with the theoretical relationship expected under exponential growth to test for the probability of density dependence, following the method of Schaub & Kéry (2022, p. 315). Second, in the IPM, we assessed density dependence a posteriori by regressing estimates of population size on estimates of demographic rates. The slope of these relationships provided an estimate of the strength of density dependence for each demographic parameter (Schaub & Kéry, 2022).

### 2.5 | Prospective and retrospective population analyses

We calculated the elasticities of realized population growth to temporal changes in demographic rates and in population structure (Koons et al., 2016, 2017). This prospective analysis told us by how much the population growth would change from one year to the next in response to an annual change in a demographic rate or components of the population structure. We also performed a transient life-table response experiment (tLTRE) analysis (Koons et al., 2016) to identify the drivers of the realized variation in population growth rates. First, we performed a decomposition of the temporal variance of the population growth rate. This informed us about the degree to which temporal variation in demographic rates and of population structure contributed to the observed temporal variation of the population growth rate during the study period. Secondly, we gauged by how much the annual changes in demographic rates and population structure contributed to the annual changes in the population growth rate. Given the evidence for density dependence in females (see Section 3 below), we developed a further IPM that incorporated density dependence and used it to conduct a Bayesian PVA (Schaub et al., 2024) to compare different management options in terms of the population sizes eventually reached. We tested a control scenario and four management scenarios over a 15-year projection horizon:

- Control: Ending lynx releases by 2024 without further additional management.
- Scenario 1 ('Release'): Annual release of five males and five females in every year, starting in 2025.
- Scenario 2 ('Mitigate roadkills'): Establish local mitigation measures, such as constructing fences, wildlife crossing tunnels and clearing rabbit burrows from roadsides, in a 5 km buffer around the population core. These actions are assumed—for illustrational purposes- to reduce juvenile and adult roadkill mortality by 50%. Note that subadult mortality is not assumed to be affected, because locally born subadults disperse to other areas.
- Scenario 3 ('Habitat management'): Reducing the strength of the density-dependence effect by 50% by implementing habitat improvements (see Delibes-Mateos et al., 2009) to establish rabbit populations in rabbit-free areas surrounding lynx territories.
- Scenario 4 ('Mitigate roadkills and habitat management'): A combination of scenarios 2 and 3.

For all scenarios, we estimated (2014–2024) and projected (2025–2039) the annual population size of breeding females. We also calculated the probability that the population size in 2039 would be less than in 2024 (i.e. that there will be a long-term decline), and the probability that each scenario will result in a population size greater than the control (i.e. long-term increase), based on logical tests applied to each MCMC draw.

## 3 | RESULTS

### 3.1 | Population size

The pre-breeding lynx population in Extremadura in 2024 was estimated at 164 (CRI: 141–189) individuals, with 75 (63–90) males and 89 (71–108) females, of which 28 (24–33) females (i.e. 32 [26–39] %) were breeders (Table S3). Of the total population in 2024, 22% were released and 78% were wild-born individuals. Estimates of detection parameters are shown in Appendix S5.

### 3.2 | Demographic parameters and density-dependence

The probability that a 2-year-old female became a breeder ($\alpha$) was estimated at 0.302 (0.206–0.404). For females aged three and older, the annual breeding propensity ($\delta$) was estimated at 0.686 (0.579–0.794). Mean litter size ($\rho$) was estimated at 3.004 (2.643–3.371) kittens per reproducing female (Figure S3 and Table S3).

Annual survival probability of juvenile females and males was estimated at $\phi_1^f=0.813$ (0.545–0.942) and $\phi_1^m=0.770$ (0.270–0.962), respectively, that of subadult females and males at $\phi_2^f=0.694$ (0.403–0.951) and $\phi_2^m=0.617$ (0.397–0.811), respectively, and that of adult females and males at $\phi_3^f=0.874$ (0.747–0.951) and $\phi_3^m=0.810$ (0.587–0.954), respectively. There was not much temporal variability in adult survival over the study period, and the background mortality rate remained nearly constant. The annual roadkill mortality rate for subadult females was low at the start of the study, but increased to 0.40 after the year 2021. Roadkill mortality rates for subadult males remained stable around 0.30–0.40 throughout the study period (Figure 3). There was a weak negative correlation between roadkill and background mortality for juvenile, subadult and adult females (posterior modes: −0.28; −0.36; −0.26) and males (−0.26; −0.37; −0.04), respectively, indicating weak compensation. For subadult females, the negative correlation increased to −0.77 during 2019–2023, suggesting that compensation may have become stronger during recent years.

Estimated rates of emigration and of immigration were low (Table S3). Site fidelity was similar for released and wild-born males, but differed in females (Figure S4). Released females were more likely to disperse within the study area ($\theta_f^2=0.318$; 0.136–0.510) than wild-born females ($\theta_f^1=0.099$; 0.032–0.175). Similarly, we estimated $\theta_m^2=0.254$ (0.101–0.417) for released males and $\theta_m^1=0.107$ (0.036–0.190) for wild-born males (Figure S4, Table S3).

The probability of density-dependence at the population level for females was high (0.946), but lower for males (0.836). Roadkill mortality in subadult females significantly increased with the female population size (Figure S5), while all the other demographic rates of females were unrelated to population size.

### 3.3 | Prospective and retrospective analyses

Adult survival was the demographic parameter with the highest elasticity, followed by the reproductive parameters (fecundity and breeding propensity), juvenile and subadult survival and the frequency of the breeder class in the population structure. According to the tLTRE analysis, temporal variation in population growth was primarily driven by changes in population structure (adults and released individuals), while temporal variation in demographic rates contributed less. In more recent years, as the population increased in size, annual variation in adult survival and breeding propensity began to play a more significant role in population growth. This shift coincided with a reduced relative contribution of the released individuals to population growth (Figure 4).

Population viability analysis revealed that with the current population structure, demographic parameters and environmental conditions and in the absence of any further releases ('Control'), the lynx population in Extremadura is expected to stabilize at 32 breeding females until 2039 ('Control'). Under the 'Release' scenario, the predicted population trajectory is hardly different. This suggests that, from a demographic point of view, further releases are unlikely to increase the size of the population. In contrast, under the 'Mitigate roadkill' scenario (where juvenile and adult survival is increased by reducing roadkill in the breeding areas), or if habitat management increased the size of the area available for new female territories ('Habitat management' scenario), the final resulting population sizes would be larger. The best option in terms of population size is the 'Mitigate roadkills and habitat management' scenario, with a 0.77 probability of achieving a higher future population size than the control, and only a 0.13 probability of falling below the 2024 size (Figure 5).

## 4 | DISCUSSION

We reviewed the demographic performance of a high-profile reintroduction experiment for the endemic Iberian lynx, identified the drivers of population change and assessed the impact of different management options on future population dynamics. This case study provides valuable insights into the recovery of this iconic species and advances reintroduction science and conservation practice in general. Findings from our study demonstrate how demographic performance reviews through IPMs can enhance reintroduction planning and guide adaptive management.

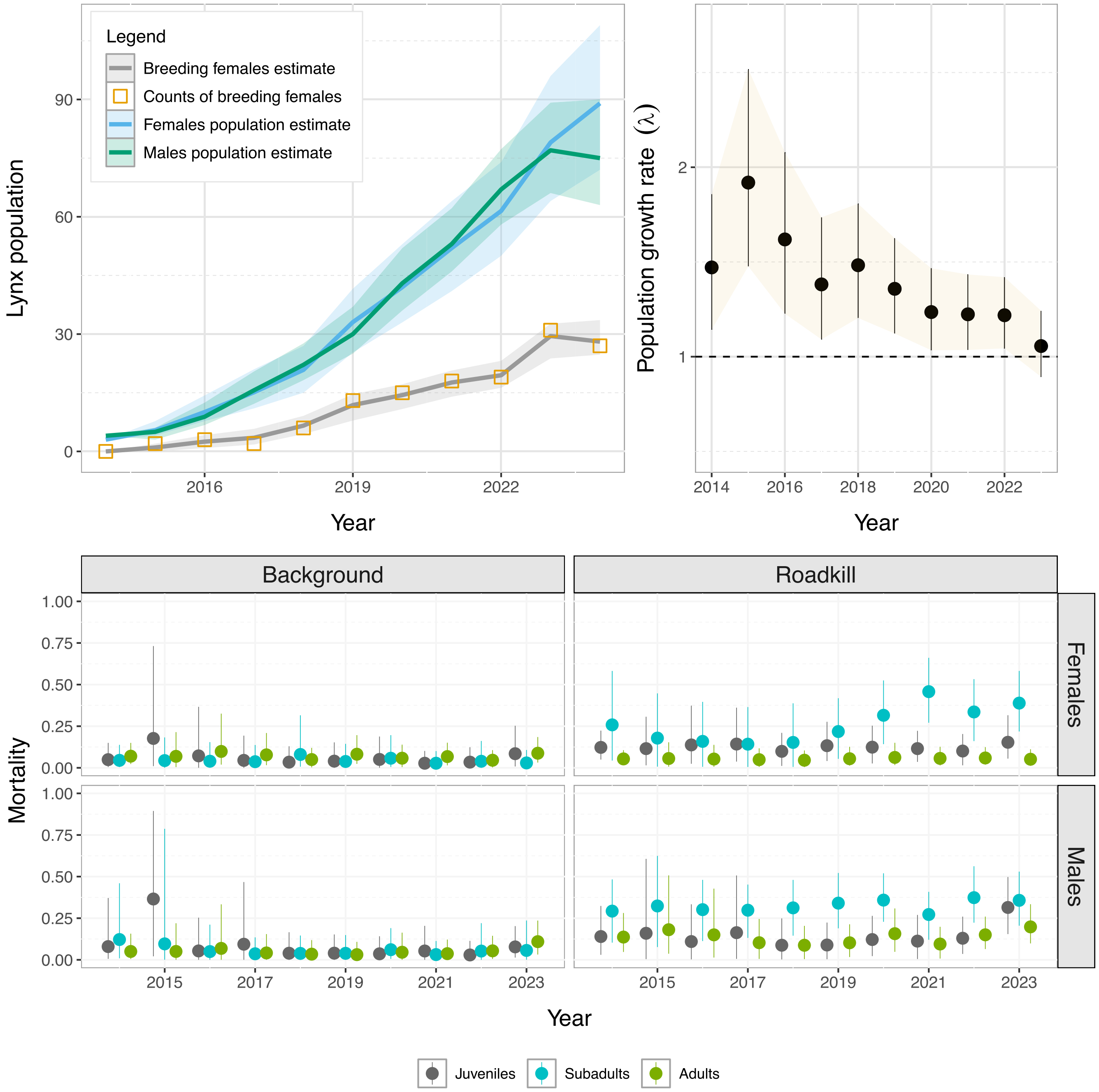

FIGURE 3 Demographic parameters of the reintroduced Iberian lynx in Extremadura (2014–2024). Top left: Pre-breeding population size; annual counts of breeding females (gold squares) and predicted female and male population sizes from the integrated population model (IPM) (blue and green, respectively). Top right: Inter-annual population growth rates of total population size. Bottom: Annual variation in cause- and age-specific mortality hazard rates: Background (left) and roadkill mortality rates (right). Top, females and bottom, males. Points and lines/shaded areas show posterior means and 95% CRIs.

## 4.1 | Dynamics of the reintroduced lynx

The growth of the reintroduced population is most sensitive to changes in adult survival, fecundity and the proportion of adults in the population. However, the dynamics of the population were predominantly driven by changes in population structure, and not so much by temporal variation in the demographic rates. Perhaps not surprisingly, the release of young individuals had a significant impact on population structure when the population was small and appeared to be the primary driver of population dynamics. As population size increased, the effect of releases on population structure decreased, while temporal variation in demographic rates (survival and breeding propensity) became more important as drivers of population dynamics, as expected for a naturally functioning population (Koons et al., 2016).

Female population size was regulated by density-dependence, mediated by subadult dispersal that led to increased roadkill

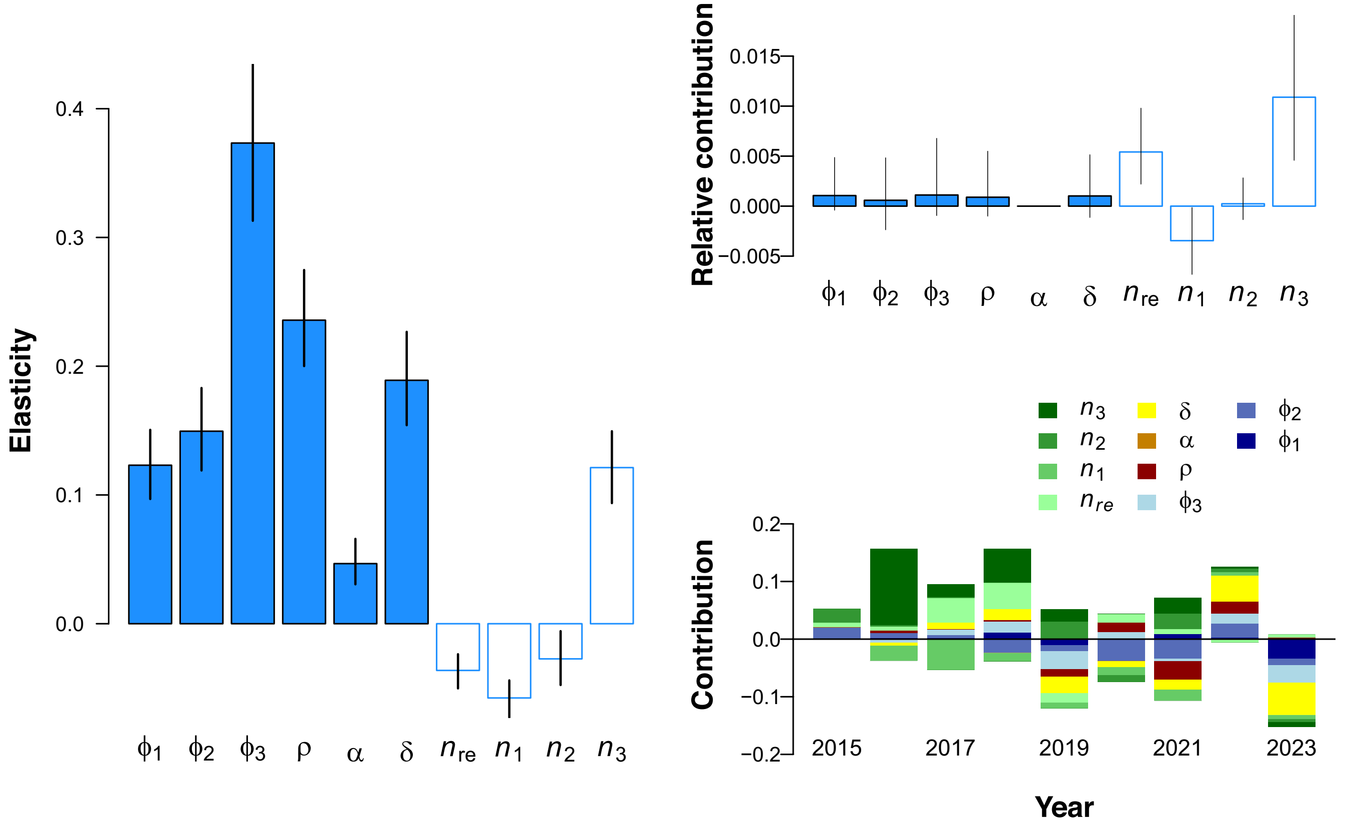

FIGURE 4 Elasticities and transient life-table response experiment (tLTRE) for the Iberian lynx. Left: Growth rate elasticities of the temporal variability in demographic rates (filled bars) and of the population structure (empty bars). Top right: Contribution of the realized temporal variation of the demographic rates and of the proportional population structure (*n*) to temporal variability in the realized population growth rate. Bottom right: Contributions of the annual changes in demographic rates and in population structure to annual changes in population growth rate. The vertical lines show the limits of the 95% credible intervals. Symbols of demographic rates are given in Figure 2. Population structure: $n_{re}$ (released yearlings), $n_1$ (wild-born yearlings), $n_2$ (2-year-old) and $n_3$ (individuals aged 3 or more).

mortality. As roadkill mortality was not fully compensated by background mortality, this resulted in a decrease in annual survival. The increase in subadult roadkill mortality with increasing population size was likely the result of increased dispersal due to the saturation of available breeding territories. Dispersal in both sexes occurred mainly as subadults, with males dispersing more than females, as is the rule in mammals. Roadkill accounted for 30%–40% of the annual mortality in subadult males. For subadult females, mortality started at 7% when the population was small and rose to similar values as in males (40% per year; Figure 3) by 2020 as density-dependence effects intensified. Male dispersal did not appear to be driven by density-dependent processes, but was an 'intrinsic' trait as described for other territorial felids (Robinson et al., 2008) and remained almost constant since the start of the reintroduction programme.

Although the data do not allow for definitive conclusions to be drawn, the correlations between roadkill and background mortality suggest that roadkill mortality of subadult females was additive at the start of the study period and partially compensatory at the end, when density-dependent effects predominate. A comparison of the dispersal behaviour of released females with the philopatric behaviour of wild-born females reveals that dispersal movements are more frequent in released females (Figure S4). The surplus of released females that became dispersers represents a 'reintroduction cost' (Jule et al., 2008) and should be taken into account in similar programmes to enhance effectiveness. Roadkill mortality appeared to be largely the result of frustrated dispersal by individuals in search of vacant territories with rabbit densities that are sufficient for reproduction. In Extremadura, most roadkills were recorded around natal areas (Appendix S1), suggesting a tendency to return to natal areas after frustrated dispersal (Maehr et al., 2002). Roadkill mortality is lower in adults than in subadults, probably because territorial adults are mainly restricted to the core areas of our study area, and these are in well-preserved areas with low road density.

We have found demographic rates that were largely consistent with those in previous studies. Ferreras et al. (2001) reported similar survival for subadults and adults as the current study, but slightly lower survival for juveniles. Palomares et al. (2005) found fecundity estimates close to ours that hardly varied over time, but a higher reproductive propensity. Ferreras et al. (2011) reported an inhibition of lynx reproduction following the collapse of rabbit populations as a result of the RHD outbreak. Links between population levels

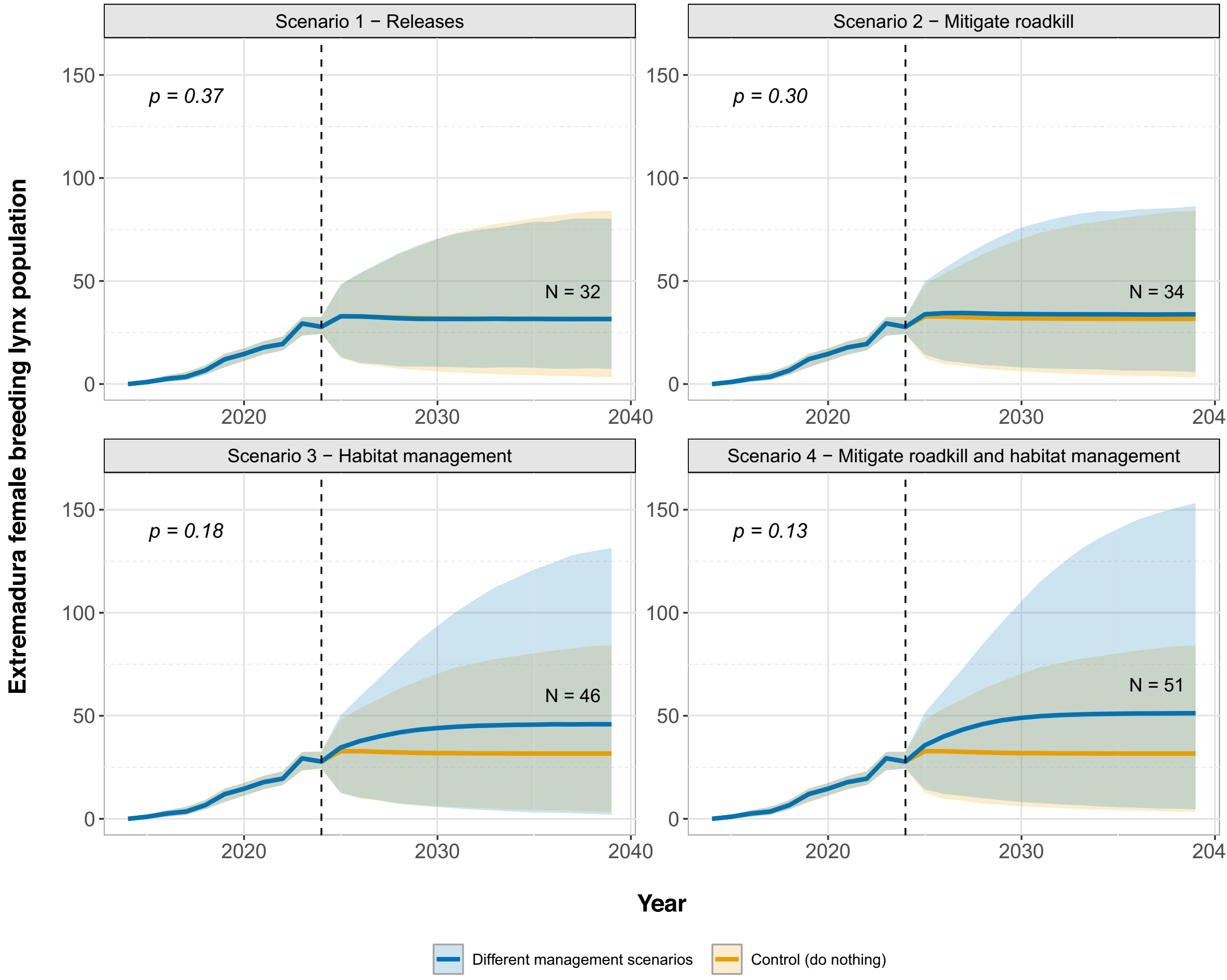

**FIGURE 5** Population viability analysis: Estimated (2014–2024) and forecasted (2025–2039) population sizes of the Iberian lynx population in Extremadura (breeding females). Solid lines show the posterior medians (blue: Active management scenarios; orange: Control) shadowed areas indicate 95% CRIs, and the dashed vertical lines show the year when the forecast period begins. Given in all scenarios, is the probability that the population size in 2039 will be smaller than in 2024 (*p*), and the predicted median number of reproducing females in 2039 (*N*).

of the main prey and fecundity are typical for carnivores (Fuller & Sievert, 2001). In our study, fecundity does not contribute much to population dynamics, since it hardly varied over time. However, we find a high growth rate elasticity of fecundity, which suggests a potentially important effect on population dynamics (Figure 4). If for some reason fecundity begins to vary more in the future, it would contribute strongly to population dynamics.

## 4.2 | Reintroduction assessment and management

Our demographic analysis provides clear evidence of the success of lynx reintroduction in Extremadura, confirming the establishment of a self-sustaining population that no longer requires additional releases. The probability of extinction within the next 15 years is essentially zero unless environmental conditions change strongly. However, due to habitat saturation, the population is predicted to remain small and therefore be vulnerable to changes in environmental conditions. A larger population size would increase its resilience to extinction. We investigated different scenarios to achieve this goal. Road modifications would increase adult and juvenile survival, but would not have a strong effect on the future population trajectory. This management practice would lead to increased dispersal and therefore shift the subadult mortality to other, more distant roads. A better option is to increase the amount of suitable habitat, which would result in higher female population sizes. The best option is to do both, reduce roadkill mortality and increase the amount of suitable habitat, which would result in a population size of 51 breeding females and a negligible probability of longer-term decline (Figure 5). While road modifications help to reduce mortality, they often displace threats unless combined with broader landscape-level strategies.

## 5 | CONCLUSIONS

The demographic performance review of the Iberian lynx reintroduction programme in Extremadura using an IPM has provided comprehensive insights into the population's demographic status, trends and drivers of population growth, while enabling the prospective evaluation of management activities. Our assessment has identified hard-to-detect mechanisms such as density-dependence, its underlying demographic pathways and cause-specific mortality. Our Bayesian PVA IPM-based model used these insights to evaluate management options under realistic population processes. IPMs are a flexible and robust framework for demographic inference, particularly for reintroduction/translocation projects. They can be tailored to the available data and the management actions being taken and can address both research and management questions, while supporting adaptive management. These findings highlight the utility of IPMs in optimizing conservation strategies for endangered species and provide a comprehensive approach to improving reintroduction success and long-term population viability.

### AUTHOR CONTRIBUTIONS

José Jiménez, Pablo Ferreras, Marc Kéry and Michael Schaub conceived the ideas and designed the methodology; Matías Taborda, Maria Jesús Palacios, Fernando Nájera and Jorge Peña collected the data; José Jiménez and Michael Schaub analysed the data; José Jiménez led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### ACKNOWLEDGEMENTS

We thank the Junta de Extremadura for logistical support and access to data. We wish to acknowledge the valuable comments of Antoni Margalida who kindly reviewed a first draft of the manuscript. We thank all the field workers from the Junta de Extremadura, CBD-Habitat and Ministerio para la Transición Ecológica (MITECO), who have contributed monitoring data of Iberian lynx over the years.

### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data available from the Zenodo Repository https://zenodo.org/record/14825099 (Jiménez et al., 2025).

### ORCID

*José Jiménez* https://orcid.org/0000-0003-0607-6973
*Pablo Ferreras* https://orcid.org/0000-0002-1116-6706
*Maria Jesús Palacios* https://orcid.org/0000-0002-9924-2290
*Fernando Nájera* https://orcid.org/0000-0003-4186-6217
*Jorge Peña* https://orcid.org/0000-0001-9470-1315
*Marc Kéry* https://orcid.org/0000-0001-7476-7616
*Michael Schaub* https://orcid.org/0000-0003-2745-0557

### REFERENCES

Abadi, F., Gimenez, O., Arlettaz, R., & Schaub, M. (2010). An assessment of bias, accuracy, and violation of the assumption of independence. *Ecology*, *91*(1), 7–14. https://www.jstor.org/stable/25661016

Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R., & Schaub, M. (2010). Estimation of immigration rate using integrated population models. *Journal of Applied Ecology*, *47*(2), 393–400. https://doi.org/10.1111/j.1365-2664.2010.01789.x

Besbeas, P., Freeman, S. N., Morgan, B. J. T., & Catchpole, E. A. (2002). Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, *58*(3), 540–547. https://doi.org/10.1111/j.0006-341X.2002.00540.x

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.1080/10618600.1998.10474787

Brooks, S. P., King, R., & Morgan, B. J. T. (2004). A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation*, *27*(1), 515–529.

Burnham, K. P. (1993). A theory for combined analysis of ring recovery and recapture data. In J. D. Lebreton (Ed.), *Marked individuals in the study of bird populations* (pp. 199–212). Academic Press.

Caswell, H. (2001). *Matrix population models. Construction, analysis, and interpretation* (2nd ed.). Sinauer Associates, Oxford University Press.

Davis, K. L., Saunders, S. P., Beilke, S., Ford, E. R., Fuller, J., Landgraf, A., & Zipkin, E. F. (2023). Breeding season management is unlikely to improve population viability of a data-deficient migratory species in decline. *Biological Conservation*, *283*(May), 110104. https://doi.org/10.1016/j.biocon.2023.110104

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2), 403–413. https://doi.org/10.1080/10618600.2016.1172487

Delibes, M. (1980). El lince ibérico. Ecología y comportamiento alimenticios en el Coto Doñana Huelva. *Doñana. Acta Vertebrata*, *7*(3), 1–128.

Delibes-Mateos, M., Ferreras, P., & Villafuerte, R. (2009). European rabbit population trends and associated factors: A review of the situation in the Iberian Peninsula. *Mammal Review*, *39*(2), 124–140. https://doi.org/10.1111/j.1365-2907.2009.00140.x

Ergon, T., Borgan, Ø., Nater, C. R., & Vindenes, Y. (2018). The utility of mortality hazard rates in population analyses. *Methods in Ecology and Evolution*, *9*(10), 2046–2056. https://doi.org/10.1111/2041-210X.13059

Ferreras, P., Beltrán, J. F., Aldama, J. J., & Delibes, M. (1997). Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*). *Journal of Zoology*, *243*(1), 163–189. https://doi.org/10.1111/j.1469-7998.1997.tb05762.x

Ferreras, P., Delibes, M., Palomares, F., Fedriani, J. M., Calzada, J., & Revilla, E. (2004). Proximate and ultimate causes of dispersal in the Iberian *Lynx pardinus*. *Behavioral Ecology*, *15*(1), 31–40. https://doi.org/10.1093/beheco/arg097

Ferreras, P., Gaona, P., Palomares, F., & Delibes, M. (2001). Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx. *Animal Conservation*, *4*(3), 265–274. https://doi.org/10.1017/S1367943001001317

Ferreras, P., Travaini, A., Cristina Zapata, S., & Delibes, M. (2011). Short-term responses of mammalian carnivores to a sudden collapse of rabbits in Mediterranean Spain. *Basic and Applied Ecology*, *12*(2), 116–124. https://doi.org/10.1016/j.baae.2011.01.005

Frost, F., McCrea, R., King, R., Gimenez, O., & Zipkin, E. (2023). Integrated population models: Achieving their potential. *Journal of Statistical Theory and Practice*, *17*(1), 6. https://doi.org/10.1007/s42519-022-00302-7

Fuller, T. K., & Sievert, P. R. (2001). Carnivore demography and the consequences of changes in prey availability. In J. Gittleman, S. M. Funj, D. W. Macdonald, & R. K. Wayne (Eds.), *Carnivore conservation* (pp. 163–178). Cambridge University Press.

Gaona, P., Ferreras, P., & Delibes, M. (1998). Dynamics and viability of a metapopulation of the endangered Iberian Lynx (*Lynx pardinus*). *Ecological Monographs*, *68*(3), 349–370.

Glass, T. W., Beausoleil, R. A., Elbroch, L. M., Kertson, B. N., Maletzke, B. T., Martins, Q., Matchett, M. R., Vickers, T. W., Wilmers, C. C., Wittmer, H. U., & Robinson, H. (2024). Limited cougar recolonization of eastern North America predicted by an individual-based model. *Biological Conservation*, *298*, 110756. https://doi.org/10.1016/j.biocon.2024.110756

Guzmán, J. N., González, F. J., Garrote, G., Pérez de Ayala, R., & Iglesias, C. C. (2004). *El Lince ibérico (Lynx pardinus) en España y Portugal*. Censo-diagnóstico de sus poblaciones. Dirección General para la Biodiversidad.

Jiménez, J., Nuñez-Arjona, J. C., Mougeot, F., Ferreras, P., González, L. M., García-Domínguez, F., Muñoz-Igualada, J., Palacios, M. J., Pla, S., Rueda, C., Villaespesa, F., Nájera, F., Palomares, F., & López-Bao, J. V. (2019). Restoring apex predators can reduce mesopredator abundances. *Biological Conservation*, *238*, 108234. https://doi.org/10.1016/j.biocon.2019.108234

Jiménez, J., Taborda, M., Ferreras, P., Palacios, M. J., Nájera, F., Peña, J., Kéry, M., & Michael Schaub, M. (2025). Data from: Demographic performance review of a reintroduction project: Iberian lynx in Extremadura. *Zenodo Repository*. https://zenodo.org/record/14825099

Jule, K. R., Leaver, L. A., & Lea, S. E. G. (2008). The effects of captive experience on reintroduction survival in carnivores: A review and analysis. *Biological Conservation*, *141*(2), 355–363. https://doi.org/10.1016/j.biocon.2007.11.007

Kéry, M., & Schaub, M. (2012). *Bayesian population analysis using WinBUGS. A hierarchical perspective*. Academic Press/Elsevier.

Koons, D. N., Arnold, T. W., & Schaub, M. (2017). Understanding the demographic drivers of realized population growth rates. *Ecological Applications*, *27*(7), 2102–2115. https://doi.org/10.1002/eap.1594

Koons, D. N., Iles, D. T., Schaub, M., & Caswell, H. (2016). A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology Letters*, *19*(9), 1023–1031. https://doi.org/10.1111/ele.12628

Lebreton, J. D., Almeras, T., & Pradel, R. (1999). Competing events, mixtures of information and multistratum recapture models. *Bird Study*, *46*, S39–S46. https://doi.org/10.1080/00063659909477230

Life Lynxconnect Team. (2024). Censos de lince ibérico. https://lifelynxconnect.eu/censos/

Maehr, D. S., Land, E. D., Shindle, D. B., Bass, O. L., & Hoctor, T. S. (2002). Florida panther dispersal and conservation. *Biological Conservation*, *106*(2), 187–197. https://doi.org/10.1016/S0006-3207(01)00245-2

Margalida, A., Jiménez, J., Martínez, J. M., Sesé, J. A., García-Ferré, D., Llamas, A., Razin, M., Colomer, M., & Arroyo, B. (2020). An assessment of population size and demographic drivers of the Bearded Vulture using integrated population models. *Ecological Monographs*, *90*(3), e01414. https://doi.org/10.1002/ecm.1414

Marino, F., McDonald, R. A., Crowley, S. L., & Hodgson, D. J. (2024). Rethinking the evaluation of animal translocations. *Biological Conservation*, *292*(March), 110523. https://doi.org/10.1016/j.biocon.2024.110523

Marin-Sáez, C., Delibes-Mateos, M., Cooke, B., Santoro, S., Castro, F., & Villafuerte, R. (2025). Negative trends in Rabbit populations in 'Pest' and 'Non-Pest' areas of central Spain after the outbreak of rabbit hemorrhagic disease virus 2. *European Journal of Wildlife Research*, *71*(1), 8. https://doi.org/10.1007/s10344-024-01888-y

Morris, S. D., Brook, B. W., Moseby, K. E., & Johnson, C. N. (2021). Factors affecting success of conservation translocations of terrestrial vertebrates: A global systematic review. *Global Ecology and Conservation*, *28*, e01630. https://doi.org/10.1016/j.gecco.2021.e01630

Morris, W., & Doak, D. F. (2002). Quantitative conservation biology: Theory and practice of population viability analysis. In *Quantitative conservation biology: Theory and practice of population viability analysis*. Sinauer Associates.

Okahisa, Y., & Nagata, H. (2022). Evaluation of ongoing Crested Ibis (*Nipponia nippon*) reintroduction using an integrated population model and Bayesian population viability analysis. *Ibis*, *164*(4), 1104–1122. https://doi.org/10.1111/ibi.13071

Palomares, F., Revilla, E., Calzada, J., Fernández, N., & Delibes, M. (2005). Reproduction and pre-dispersal survival of Iberian lynx in a subpopulation of the Doñana National Park. *Biological Conservation*, *122*(1), 53–59. https://doi.org/10.1016/j.biocon.2004.06.020

Ratcliffe, F. N., Myers, K., Fennessy, B. V., & Calaby, J. H. (1952). Myxomatosis in Australia: A step towards the biological control of the rabbit. *Nature*, *170*(4314), 7–11. https://doi.org/10.1038/170007a0

Robinson, H. S., Wielgus, R. B., Cooley, H. S., & Cooley, S. W. (2008). Sink populations in carnivore management: Cougar demography and immigration in a hunted population. *Ecological Applications*, *18*(4), 1028–1037. https://doi.org/10.1890/07-0352.1

Rueda, C., Jiménez, J., Palacios, M. J., & Margalida, A. (2021). Exploratory and territorial behavior in a reintroduced population of Iberian lynx. *Scientific Reports*, *11*, 1–12. https://doi.org/10.1038/s41598-021-93673-z

Schaub, M., & Kéry, M. (2022). *Integrated population models theory and ecological applications with R and JAGS*. Elsevier.

Schaub, M., Loercher, F., Hegglin, D., & Arlettaz, R. (2024). Demographic assessment of reintroduced bearded vultures in the Alps: Success in the core, challenges in the periphery. *Ecological Solutions and Evidence*, *5*(2), 1–13. https://doi.org/10.1002/2688-8319.12347

Schaub, M., Pradel, R., & Lebreton, J. D. (2004). Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable? *Biological Conservation*, *119*(1), 105–114. https://doi.org/10.1016/j.biocon.2003.11.002

Scott, J. M., & Carpenter, J. W. (1987). Release of captive-reared or translocated endangered birds: What do we need to know? *Auk*, *104*(3), 544–545.

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, *21*(2), 303–312. https://doi.org/10.1111/j.1523-1739.2006.00627.x

Servanty, S., Converse, S. J., & Bailey, L. L. (2014). Demography of a reintroduced population: Moving toward management models for an endangered species, the Whooping Crane. *Ecological Applications*, *24*(5), 927–937. https://doi.org/10.1890/13-0559.1

Stepkovitch, B., Kingsford, R. T., & Moseby, K. E. (2022). A comprehensive review of mammalian carnivore translocations. *Mammal Review*, *52*(4), 554–572. https://doi.org/10.1111/mam.12304

Villafuerte, R., Calvete, C., Blanco, J. C., & Lucientes, J. (1995). Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. *Mammalia*, *59*(4), 651–659. https://doi.org/10.1515/mamm.1995.59.4.651

Virgós, E., Cabezas-Díaz, S., Malo, A., Lozano, J., & Lopez-Huertas, D. (2003). Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. *Acta Theriologica*, *48*(1), 113–122.

Weegman, M. D., Arnold, T. W., Clark, R. G., & Schaub, M. (2021). Partial and complete dependency among data sets has minimal consequence on estimates from integrated population models. *Ecological Applications*, *31*(3), e2258. https://doi.org/10.1002/eap.2258

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Roadkill protocol and necropsies.
**Appendix S2.** Figures and tables.
**Appendix S3.** Integrated population model (IPM).
**Appendix S4.** Priors distributions of all parameters in the integrated population model (IPM).
**Appendix S5.** R+NIMBLE code.
**Appendix S6.** Detection and dead-recovery probability.

**How to cite this article:** Jiménez, J., Taborda, M., Ferreras, P., Palacios, M. J., Nájera, F., Peña, J., Kéry, M., & Schaub, M. (2025). Demographic performance review of a reintroduction project: Iberian lynx in Extremadura. *Journal of Applied Ecology*, *62*, 2189–2201. https://doi.org/10.1111/1365-2664.70097