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RESEARCH ARTICLE

Resident mortality determines grey wolf range dynamics

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Abstract

1. Large carnivores in Europe and North America are expanding their ranges, but the extent of expansion varies, with some populations showing a stable trend despite ample suitable habitat. Understanding such nuances requires dynamic modelling approaches that go beyond simple habitat association and account for interactions of resident and dispersing individuals.
2. We investigate how such interactions influence population dynamics and range expansion of grey wolves. We developed a high-resolution Spatially Explicit Individual-Based Model (SE-IBM) for the species in the Iberian Peninsula. Here, wolves remain isolated and have not expanded over the last decades despite ample suitable habitat, thus offering a unique opportunity to study the demographic constraints to range expansion.
3. We show that decreasing resident mortality by 10%, even when holding disperser mortality constant, increases group size (11%), reproductive success (8%) and dispersal distances (130%), and ultimately doubles the Iberian wolf distribution range in 30 years. The reduced group size and other mortality-induced group disruptions are associated with negative cascading effects on reproduction and dispersal, thereby limiting growth and expansion in wolf populations.
4. *Policy implications*. In the Iberian Peninsula, enabling recovery may require effective population-level protection. More broadly, down- and de-listing policies should be supported by explicit evaluation of the indirect demographic effects under alternative management scenarios. Our detailed, process-explicit modelling framework provides a robust tool for such assessments and highlights the need to strengthen and standardize demographic monitoring to progressively refine models and support adaptive, evidence-based conservation policy.

KEYWORDS
Canis lupus, dispersal, group size, individual-based models, large carnivores, mortality, range dynamics, reproduction

Maria Paniw and Eloy Revilla share senior authorship.

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1 | INTRODUCTION

Many large carnivore species now persist in only part of their former distributions, following historical eradication efforts across much of their ranges. Direct persecution, wild prey depletion or habitat loss currently hamper their recovery (Ripple et al., 2014; Wolf & Ripple, 2017). Yet, large carnivores in Europe and North America have remarkably expanded their ranges over the last few decades, including some recoveries into landscapes intensively used by people (Chapron et al., 2014; Thompson & Ryder, 2023). This has been possible due to several factors: the value of remnant wilderness areas acting as sources of individuals (Gilroy et al., 2015); a decrease in human persecution due to changes in human attitudes and legislation (Johnson et al., 2023; Linnell et al., 2001); some reintroductions (Hayward & Somers, 2009); and the flexible behaviour of these mammals towards habitat selection (Chapron et al., 2014; Cimatti et al., 2021; Gompper et al., 2015). In Europe, rural land abandonment has also contributed to large carnivore expansion through increased forest cover and availability of shelter (Cimatti et al., 2021).

However, not all populations of large carnivores in the northern hemisphere are currently expanding, some remain stable (e.g. wolves in the Iberian Peninsula and Idaho, brown bears in the Apennines) and some show an uncertain trend (e.g. wolves, brown bears and Eurasian lynx in the Balkans; Ausband et al., 2023; Kaczensky et al., 2024). These stable trends are not always explained by lack of habitat availability outside current ranges (Grilo et al., 2019; Recio et al., 2018). Identifying the constraints to range expansion also requires investigating the demographic mechanisms governing populations (Drake et al., 2022). This includes decoding the interplay between stage-specific survival, reproduction, population size and dispersal. Such mechanisms shape range dynamics and connectivity (Drake et al., 2022), but have rarely been assessed both in detail and at the population level (Revilla & Wiegand, 2008; Urban et al., 2016).

The grey wolf (*Canis lupus*) is widely distributed across the Northern Hemisphere and often experiences high mortality rates. A global review reported a median annual mortality rate of 0.31 across published estimates that represented overall mortality without separating by causes, with most data originating from human-dominated landscapes (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). Yet, it remains unclear how high overall mortality may constrain wolf expansion (Ausband et al., 2024; Creel et al., 2015; Tallian et al., 2023).

The species social structure may mediate the effects of mortality. Wolves live in family groups typically composed of a breeding pair (the basic social unit) and their annual offspring, although they can include multi-year offspring and rarely >1 breeding pair (Tallian et al., 2023). Group cohesion and role differentiation underpin key processes such as movement across the landscape, hunting prey, territory defence and pup rearing (Tallian et al., 2023). Offspring usually disperse upon reaching sexual maturity to form new groups or join existing ones, and may disperse multiple times over their lifetime (Morales-González et al., 2022).

Because range expansion ultimately relies on the successful establishment of new territories by dispersers, their survival plays a central role in shaping range dynamics (Morales-González et al., 2022; Revilla & Wiegand, 2008). The survival of dispersers is lower than that of residents (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). However, resident survival may also shape range expansion indirectly through its effects on group dynamics. The effects of mortality at the group level have been widely studied and higher mortality induces reductions in group size, breeder loss, decreased reproductive success and group dissolution (Brainerd et al., 2008; Cassidy et al., 2023; Sells et al., 2022; Tallian et al., 2023). In turn, these disruptions can influence dispersal patterns, with potential consequences for spatial expansion. For instance, a local study showed that disturbed groups are frequently maintained by the arrival of dispersers from neighboring groups (Nakamura et al., 2021).

The differential effects of resident and disperser mortality on range dynamics remain poorly understood because empirical studies have often examined only a few demographic parameters in isolation, measured at local areas within large, continuous populations (Ausband et al., 2024). Similarly, dynamic population models have only tested the ultimate effects of high mortality on range expansion (Recio et al., 2020), without exploring the intermediate effects on the dynamics of resident and dispersing individuals. For a holistic understanding, large spatial scale frameworks integrating detailed feedbacks between demographic processes and the landscape are needed (Revilla & Wiegand, 2008).

In this study, we investigate the demographic constraints to range expansion in wolves. We hypothesize that wolf range expansion is prevented by high mortality of resident individuals, rather than disperser mortality, because social disruption of groups can indirectly constrain dispersal. In particular, we expect that decreases in the mortality of residents in stable populations, even if disperser mortality remains unchanged, will simultaneously: (i) increase group sizes; (ii) increase the reproductive success of groups; (iii) increase dispersal distances; and (iv) increase population growth and range expansion. To test our hypothesis, we developed a robust Spatially Explicit Individual-Based Model (SE-IBM) for wolves in the Iberian Peninsula, integrating resident and disperser dynamics with landscape heterogeneity at the population scale, using detailed ecological and demographic data available in the literature on the grey wolf across its distribution range. We modelled overall mortality by using stage-specific daily per capita probabilities. We then project how changes in the mortality of residents and dispersers influence population demographics and range dynamics.

2 | METHODS

2.1 | Studied wolf population

We used the population of wolves in the Iberian Peninsula as a case study because it provided a unique opportunity to study the demographic constraints to wolf expansion: the population

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remains isolated (i.e. we can project the dynamics of the entire population which is the appropriate scale to avoid non-informative results; Creel et al., 2015) and, in contrast to other areas in Europe and North America, has shown minimal spatial changes in its distribution range for the last 30 years despite suitable habitat (Grilo et al., 2019; Ordiz et al., 2022). Under Article 17 assessments of the Habitats Directive (European Environment Agency, 2020), the conservation status of the population is 'Unfavourable' across most of its range, being 'Favourable' only in a limited area of the Atlantic region in Portugal. According to the IUCN, the wolf is listed as 'Vulnerable' in Spain (Morales-González, Ruíz-Villar, Ordiz, et al., 2025) and 'Endangered' in Portugal (Pimenta et al., 2023).

Overall mortality rates are largely unknown for wolves in the Iberian Peninsula. Three local studies reported different annual rates of 0.459 in northwest Portugal (0.28 and 0.47 for adults and pups; Nakamura et al., 2021, 2026) and 0.18 in northcentral Spain (0.14 and 0.31 for residents and dispersers; Blanco and Cortés (2007)). Cause-specific mortality rates are not available. However, the information outlined below suggests that human-related causes may be important.

Wolves in the Iberian Peninsula were legally hunted and/or culled throughout most of their range until 2021 (Ordiz et al., 2022). The only areas where lethal management was not permitted were Portugal and south of the Douro River in Spain, where wolves have been legally protected since 1988 and 1995, respectively. In 2021, wolves north of the Douro River in Spain were also listed as protected, resulting in the cessation of lethal management across the entire distribution range. Yet, in 2025, legislative changes introduced by Law 1/2025 (final provision 19 and a transitional provision adopted to align with EU legislation; BOE, 2025) modified the legal framework in Spain, and wolves are no longer protected nationwide, remaining protected only in some regions under regional legislation. Following this change, lethal control has been implemented in some areas, although it has been temporarily halted by the Supreme Court.

A high number of wolves were legally killed in Spain prior to the species' legal protection in 2021 (Quevedo et al., 2019). No official government-reported estimates exist, but information compiled by Quevedo et al. (2019) shows that at least 623 wolves, from approximately 360 groups, were legally killed (hunted and culled) during 2008–2013. Very roughly, this may have represented approximately 6% of the winter population in the Iberian Peninsula each year, based on a mean group size of 4.9 individuals in early winter (Fernández-Gil et al., 2020). We do not know how such mortality was distributed across the different life stages.

Morales-González, Ruiz-Villar, Quevedo, et al. (2025) also compiled data on mortality causes in the Iberian Peninsula, mostly based on opportunistically found carcasses and more rarely on radio-collared wolves. Detection probability of illegal killings and natural deaths is particularly low when relying on opportunistically found carcasses (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). Still, some patterns are noteworthy. Reports of illegal killing generally outnumbered those of legal killing, despite its cryptic nature, suggesting that illegal killing may be prevalent. Illegal killing was also important in protected areas (see also Rio-Maior et al. (2018)), and reports of intentional killing (legal and illegal) generally outnumbered those of vehicle collisions. These results go in line with global patterns (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). The magnitude of natural mortality due to intraspecific aggression, disease or starvation remains unknown.

Ethics Statement: Ethical approval was not required for this study because no fieldwork was conducted and no animals were captured, handled, disturbed or experimentally manipulated.

2.2 | Setting up baseline conditions for future projections

We modelled the dynamics of the wolf population in the Iberian Peninsula during 1991–2021, the period of apparent population stability that defines the baseline conditions for future projections. We assessed variations in life-history processes, that is, growth, mortality, reproduction and dispersal, between 1991–2002, 2002–2013 and 2013–2021. These three periods were defined based on snapshots of the number and distribution of groups in the Iberian Peninsula in 1991, 2002, 2013 and 2021, which we reconstructed from national and regional estimates available for Spain and Portugal (Table S1).

To model the dynamics of the population, we built a novel SE-IBM for wolves in the Iberian Peninsula. IBMs are dynamic models that simulate populations by following individuals and their properties, and are particularly suitable to simulate group dynamics and dispersal (Paniw et al., 2021). This is essential to investigate the demographic constraints to range expansion in social species, as processes such as dispersal or abundance changes emerge from interactions among individuals within and among social groups (Paniw et al., 2021). As the internal organization of our model includes robust probabilistic and deterministic functions to simulate demographic processes, it allows us to make reliable inferences on how demographic parameters interrelate to shape population growth and range dynamics (Paniw et al., 2021). We developed the model in R version 4.2.1 (R Core Team, 2022). The code and input data required to run the model and reproduce the study outputs have been deposited in the Dryad Digital Repository (Morales-González et al., 2026).

2.2.1 | SE-IBM structure

The structure of the SE-IBM is detailed in Supplementary Methods. We built a unique initial population for each of the three study periods: we located groups according to the corresponding reconstructed snapshot of the number and distribution of groups in 1991, 2002 and 2013, respectively; we estimated the territory

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of each group; and we generated individuals defined by state variables such as sex and age (Figures S1–S3). We used the map of habitat quality from Grilo et al. (2019) to locate individuals, where a total of 5,831 grid cells of 100 km^2 cover the Iberian Peninsula. Habitat quality values represent the predicted probability of wolf occurrence based on environmental variables related to topography, water availability, vegetation, prey availability and human disturbance.

For each period, simulations start on March 10, and each day individuals follow a sequence of stage-specific life-history processes that determine their fate (Figures S4–S6). All processes are influenced by individual state variables, such as age and sex, and social conditions, such as group size and relatedness. We defined 'group' as at least two individuals settled in a territory. Group territory size depends on habitat quality, with a minimum size of 100 km^2. The non-spatial life-history processes were partially adapted from a previous wolf IBM, which used annual time steps (Bauduin et al., 2020). We updated the processes based on the literature and to match our higher temporal resolution. Throughout the Supplementary Methods, we indicated the conditions that we maintained from Bauduin et al. (2020).

Breeding females may become pregnant on March 10, and pups may emerge from the den and be added to the population on July 15. All other processes occur daily. Resident wolves are updated first. In order, residents may die; if one or both breeders died, the remaining members may disperse (group dissolution); if the group remains, lost breeders may be replaced by subordinates; and finally, residents ≥8 months old may disperse. After resident updates, each disperser is processed in random order. First, the disperser may move up to six cells in a single direction (Table S2), with direction correlated with the previous day's direction and habitat quality. At each cell, the disperser may either remain as disperser or become resident by forming a new group or by filling a breeding vacancy in an existing group. Lastly, we simulate disperser mortality during the daily travel. The conditions of replacements favour daughters and dispersers to fill female and male breeding vacancies in groups, respectively. Group formation arises from different dispersal behaviours of females and males: dispersing females tend to restrict their movements to most nearby suitable vacant areas, whereas males move in search of these females to form new groups. Groups can terminate either through dissolution or if all members die. Suitable habitats and breeding positions are preferentially filled by mature individuals (≥3-year-old females and ≥2-year-old males). Individuals ≥8 months may take over when no competitors are available, but they do not reproduce until they are mature.

Mortality is implemented as a daily per capita probability of death, which varied by age class and individual status of resident versus disperser (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). We did not model cause-specific mortality rates because our goal was not to investigate the differential effects of mortality types. Apart from that, separating by causes is not possible because no estimates exist for the study area, and such data are also very scarce at the species level (Milleret, Dupont, et al., 2025). However, we modelled overall mortality because, although robust estimates are also lacking for the study area, extensive information is available from other wolf populations (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). This allowed us to explore the biologically plausible range of mortality values using Pattern-Oriented Modelling (see Section 2.2.2). Our overall stage-specific mortality rates implicitly captured important underlaying demographic mechanisms. For example, we assigned a higher probability of death to senescent individuals, indirectly reflecting their increased susceptibility to natural mortality. Similarly, dispersers had higher mortality than residents, reflecting their greater vulnerability even though we could not distinguish the relative contributions of natural and human-related causes. As in real populations (Brainerd et al., 2008), the demographic consequences of an individual's death in the model depend on its traits (e.g. age, breeding status) and social context (e.g. group size).

2.2.2 | Pattern-oriented modelling (POM)

For each study period, we ran the model with the same set of 135 parameterizations, that is, biologically sound combinations of values for 28 parameters (12 fixed and 16 non-fixed), including stage-specific overall mortality rates, breeding rates, individual movement decisions and other individual- or group-level parameters (Data S1 and S2; Figures S7 and S8). This allowed us to evaluate, for wolves in the Iberian Peninsula, the full multidimensional space of parameters known for the species, and also to ensure a consistent assessment across study periods. Details on the creation of parameterizations are in Supplementary Methods. We ran 100 simulations per parameterization and study period.

For each study period, we retained the parameterizations (out of the 135) that replicated published data on the number and distribution of groups at the end of the study period. Specifically, for each study period, we selected the parameterization that yielded the highest number of plausible simulations as well as those producing up to 15% fewer plausible simulations than this maximum. The procedure to classify a simulation as plausible is detailed in Figure S9. The detection of groups in the field typically relied on scat surveys, howling stations and direct observations, but also included interviews and camera trapping (Table S1). To account for uncertainty associated with imperfect detection and heterogeneous survey methods, we considered simulations within ±5% of the observed number of groups as plausible (Figure S9).

The parameterizations retained per period (2, 2 and 3, respectively) replicated published data on the number and distribution of groups with high accuracy and did not extrapolate beyond biologically realistic values (Figure 1). The performance of rejected parameterizations is illustrated in Figure S10. This approach of using multiple patterns observed in the real system to reduce model uncertainty in a bottom-up model is called Pattern-Oriented Modeling (Grimm et al., 2005). It is a powerful strategy to test theories for

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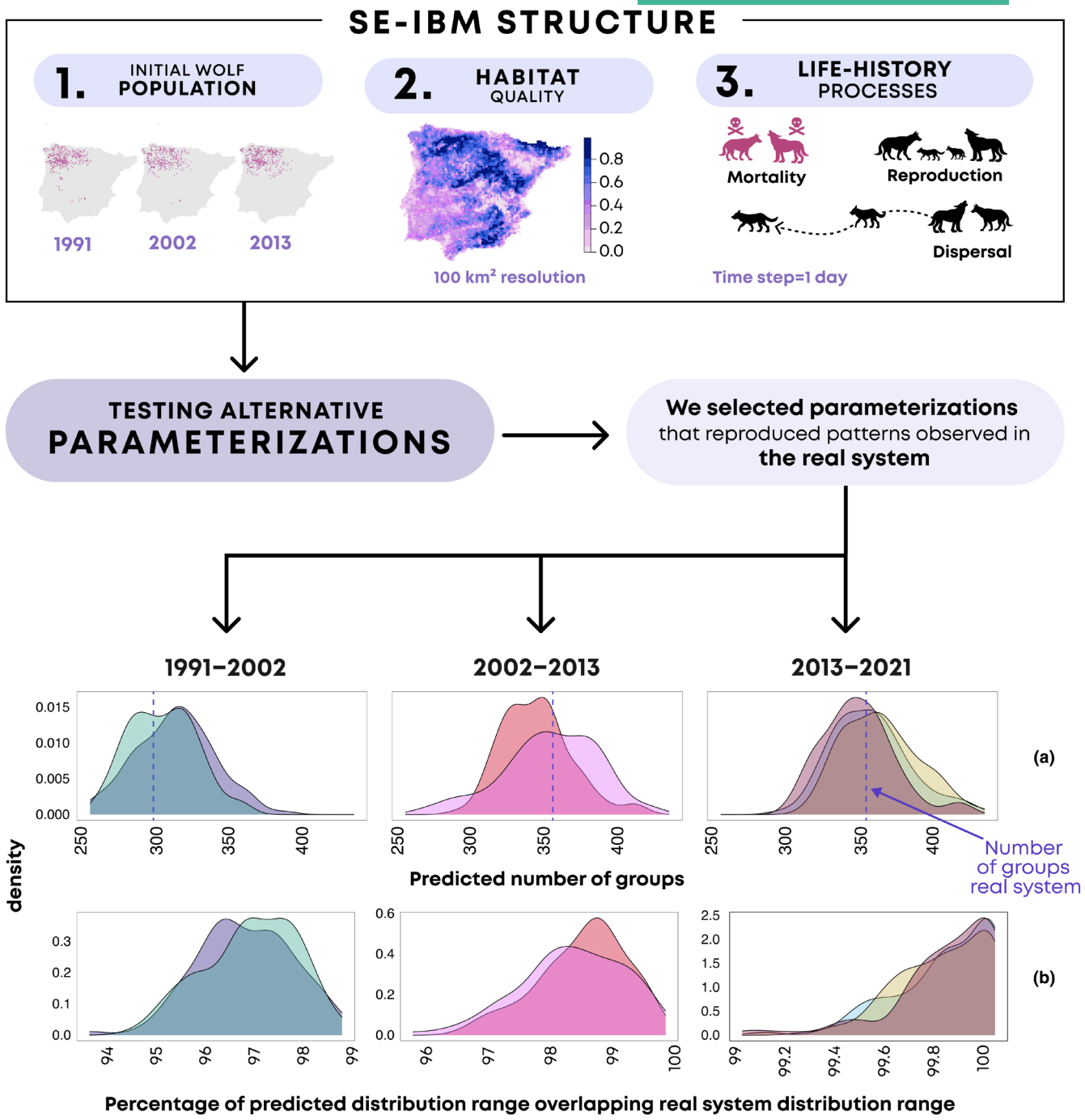

FIGURE 1 POM steps followed to select the parameterizations of the SE-IBM that reproduced the real system. We first build the SE-IBM structure, which included the initial wolf population (in 1991, 2002 and 2013—depending on the period of analysis, that is, 1991–2002, 2002–2013 and 2013–2021, respectively), the map of habitat quality for wolf occurrence (Grilo et al., 2019), and the life-history processes related to mortality, reproduction and dispersal that determined the fate of each individual each day. We then ran 135 alternative biologically sound parameterizations (i.e. combinations of stage-specific mortality rates, breeding rates, individual movement decisions and other individual or group-level parameters). We finally retained the parameterizations that reproduced the real system, that is, published data on the number and distribution of groups. We defined 'group' as at least two individuals settled in a territory. Each density plot, represented with one colour, indicates the distribution of the 100 simulations from a single retained parameterization (2, 2, and 3 parameterizations were retained in the first, second and third periods, respectively). Panels show (a) the number of groups in the last year of simulation and (b) the mean annual percentage of the area predicted to be occupied by wolf territories that fell within the species' distribution range in the Iberian Peninsula (Kaczensky et al., 2021). The number of groups predicted were close to published estimates for the real system (Table S1), and near 100% of the groups predicted were inside the known distribution range of the species (Kaczensky et al., 2021), thus indicating high accuracy of the parameterizations retained. Further details are found in Supplementary Methods.

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agent behavior in complex systems, leading to unprecedented model robustness (Nathan et al., 2022).

2.2.3 | Derivation of metrics

From the retained parameterizations, we then derived eight metrics per simulation to describe the dynamics of the population: mean log annual population growth (r), mean group size in last simulated year (March 10th), stage-specific daily per capita mortality rates, mean proportion of groups with pups (July 15, i.e. pups are 2 months old), net (straight-line) distance and duration of dispersal events, mean proportion of dispersers (March 10) and proportion of dispersal events ending with mortality. For reporting purposes, daily mortality rates were converted to annual rates using $1 - (1 - m_{daily})^{365}$, where m_{daily} is the daily mortality rate. We discarded the three initial years of simulations to avoid the influence of the initial conditions of the model (Figure S11). Details on how we obtained the metrics and their biological relevance are in Supplementary Methods, Data S3 and Tables S3 and S4. We compiled previous estimates of these or similar metrics available in the literature for wolves in the Iberian Peninsula to identify similarities with our model outputs (i.e. namely secondary and independent predictions), which are indicators that the model is structurally realistic and robust (Grimm et al., 2005).

2.3 | Projecting mortality-driven changes in population demographics and range dynamics

We studied the effects of a potential reduction of mortality on the dynamics of the population (including effects on the population demographic metrics described above and range dynamics) from 2021 to 2050. We used the SE-IBM, with the three parameterizations that were plausible for 2021, to project population dynamics on the basis of two scenarios of mortality rates, that is, no changes in mortality rates and a reduction by 10% (100 simulations per parameterization and scenario). We built the initial population for 2021 following the same procedure as for previous study periods. To explore differential effects of mortality of residents and dispersing individuals, we assessed two additional scenarios: a reduction by 10% only for dispersers and a reduction by 10% only for residents (Table S5). The available evidence on human pressures presented above suggests that there is substantial scope for reducing anthropogenic mortality in the study area. We therefore assumed that a 10% reduction in overall mortality was possible. Our reductions affected all individuals except senescent (>6 years old), pups before den emergence and incorporation into the population (<2 months old) and very young dispersers (<8 months old; which may occur following group dissolution). These age classes experience high natural mortality (Morales-González, Ruiz-Villar, Quevedo, et al., 2025), and reducing their mortality could lead to unrealistic model outputs.

3 | RESULTS

3.1 | Dynamics of the wolf population in the Iberian Peninsula during 1991–2021

Visual inspection of population metrics across the study periods 1991-2002, 2002-2013, and 2013-2021 showed broad overlap (Figure S12), indicating largely stable dynamics. Only minor variations were observed. For instance, population growth tended to be slightly negative in the first period, slightly positive in the second and stable in the third. Other metrics, such as reproductive success, showed temporal variation only under specific parameter samples. We detail below the results for the last study period, 2013–2021 (Figure 2). Unless otherwise indicated, we report the mean value of all simulations of the retained parameterizations and 95% range (2.5th–97.5th percentiles).

The mean log annual population growth was 0 (−0.029–0.018), supporting the observed patterns of population stability. The mean group size during mating was 3.64 (3.250–3.970) wolves/group. The population showed reduced breeding capacity as indicated by the low mean proportion (0.48; 0.455–0.518) of groups breeding (i.e. having at least one pup 2 months old) each year. Dispersers frequently found settlement opportunities nearby as shown by the low proportion (0.1; 0.062–0.157) of dispersal events ending with mortality, the low mean proportion (0.04; 0.029–0.051) of dispersers in the population during mating, and the short dispersal events. Dispersal distances and durations were right-skewed, making median values more informative than mean values. The net (straight-line) distance of dispersal events averaged 66.35 (0–291.5) km and the duration of dispersal events averaged 66.10 (1–384) days, with median values of 31.6 km and 19 days, respectively. The annual per capita mortality rate for residents 1–6 years old was 0.25 (0.238–0.278). Mortality rates for pups (<1 year old) and dispersers were higher, although uncertainty was also higher, that is, 0.54 (0.453–0.610) and 0.37 (0.279–0.493), respectively (Table S5). Several parameter estimates previously obtained at local sites within the Iberian Peninsula are broadly consistent with our model outputs (Data S4; Figure S12), particularly dispersal distances and group size. Other estimates differed both from our model outputs and among studies (e.g. proportion of dispersers, proportion of groups with pups), likely reflecting variation in local conditions and methodological approaches. The estimates we used for comparison were not used to parameterize the model.

3.2 | Projected mortality-driven changes in population demographics and range dynamics

As expected, the dynamics of wolves in the Iberian Peninsula during 2021–2050 did not vary compared to the previous decades (i.e. 1991–2021) when mortality rates remained constant (Figures 2 and 3). However, a reduction in overall mortality rates by 10% improved the demography of the population and allowed range

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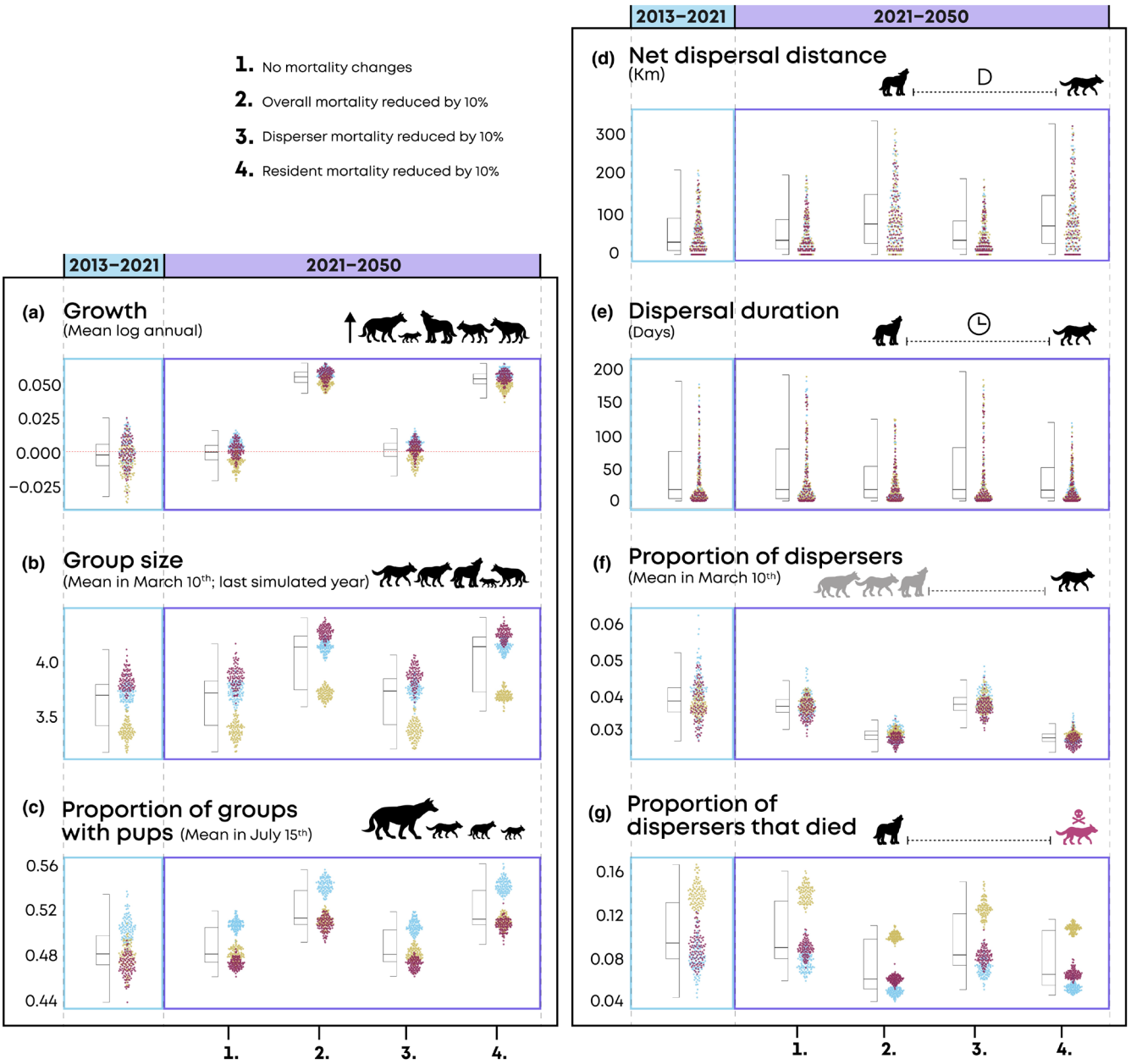

FIGURE 2 Growth, reproduction and dispersal for wolves in the Iberian Peninsula for 2013–2050 obtained from the SE-IBM. Box plots within each plot panel depict (a) mean log annual population growth, (b) mean group size in last simulated year (March 10; i.e. mating season), (c) mean proportion of groups with pups (July 15; i.e. pups are 2 months old), (d) net (straight-line) dispersal distance (km), (e) dispersal duration (days), (f) mean proportion of dispersers (March 10th), and (g) proportion of dispersers that died; for past (2013–2021) and future (2021–2050) study periods. The leftmost box plot depicts 2013–2021 study period. We assessed future metrics under four scenarios of mortality rates, that is, no changes in mortality, overall mortality reduced by 10%, disperser mortality reduced by 10% and resident mortality reduced by 10%. Three parameterizations (represented by different colours; out of 135) were retained to derive population dynamics during 2013–2021. These parameterizations were also used to project future population dynamics. Given the large number of dispersal events, points for distance and duration correspond to a random sample of 100 observations (excluding outliers) per parameter sample, study period and mortality scenario, while boxplots are computed using the full dataset. Input annual mortality rates per period and mortality scenario are found in Table S5. The red dashed line indicates no growth.

expansion (Figures 2 and 3; Table S5). Importantly, these changes in the dynamics of the population were largely driven by reductions in resident mortality (Figures 2 and 3), which supports that high levels of mortality of residents have limited range expansion in the Iberian Peninsula for the last 30 years. Reducing only disperser mortality yielded dynamics similar to those under constant mortality (Figures 2 and 3), indicating that changes in disperser survival alone do not substantially affect population outcomes. The annual per capita mortality rate of residents 1–6 years old and pups after the reduction in mortality was 0.233 (0.216–0.255) and 0.505

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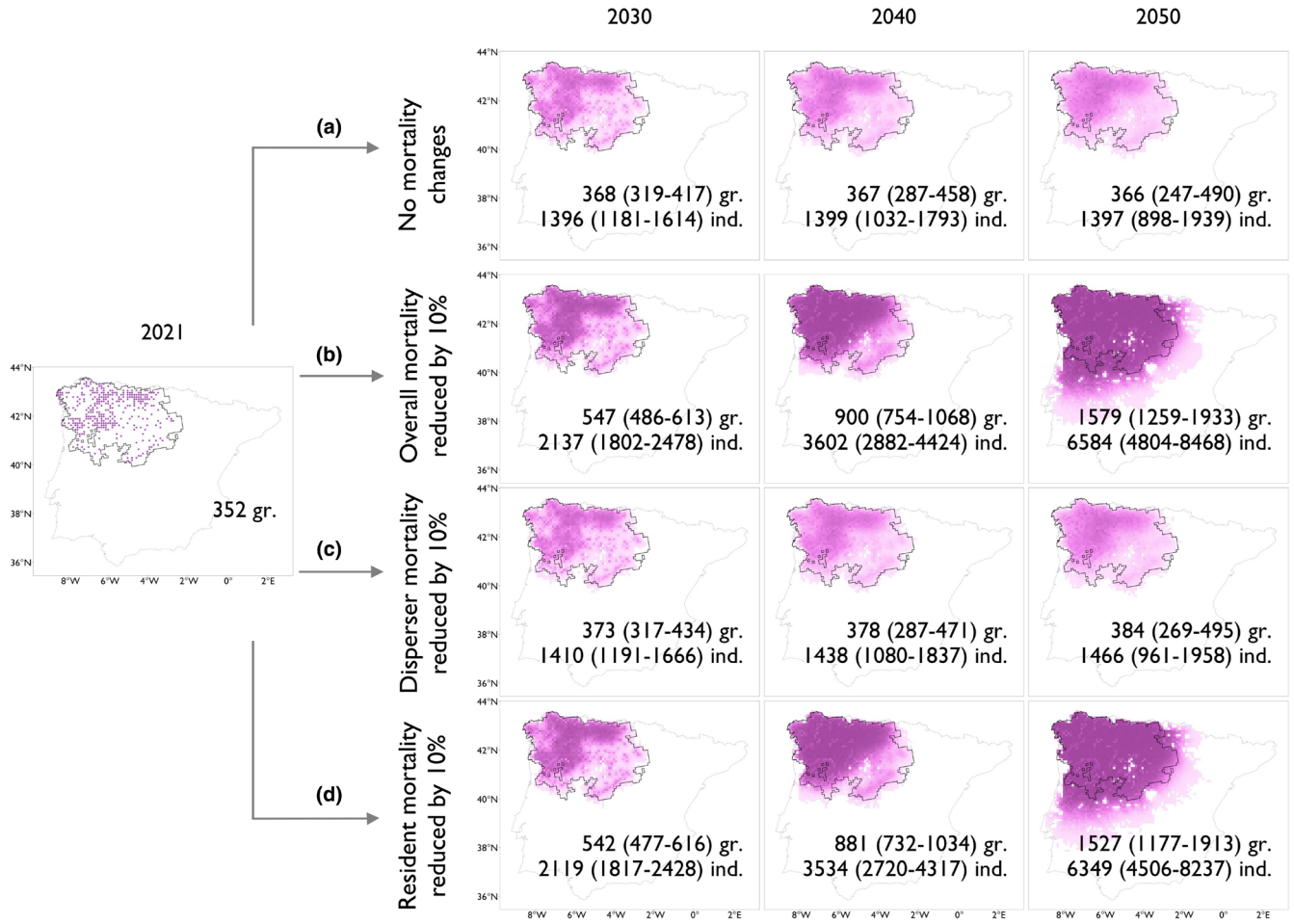

FIGURE 3 Projected changes in the distribution of wolf groups (gr.) in the Iberian Peninsula for 2021–2050 obtained from the SE-IBM. The map on the left shows the distribution of wolf groups in 2021 according to available national and regional estimates (purple points; Table S1) and the three columns show the predicted distribution of wolf groups in 2030, 2040 and 2050 under four scenarios of mortality rates, that is, (a) no changes in mortality, (b) overall mortality reduced by 10%, (c) disperser mortality reduced by 10%, and (d) resident mortality reduced by 10%. The mean and 95% range (2.5th–97.5th percentiles) of the number of predicted groups (gr.) and individuals (ind.) are indicated for each map. The Iberian Peninsula (grey polygon) is gridded into 100 km^2 cells. Each cell holds the number of simulations that predicted the presence of a group (out of 300 simulations from the three retained parameterizations). Such number is represented in shades of purple (light = lower number; dark = higher number; white = 0 value). The black polygon represents the distribution range of the species by Kaczensky et al. (2021). Annual mortality rates for each scenario of mortality are found in Table S5.

(0.419–0.572), respectively (Table S5). For dispersers, it was 0.346 (0.254–0.458; Table S5).

With a reduction in resident mortality rates by 10% (Figure 2), the mean annual population growth turned positive, that is, 0.05 (0.042–0.061), corresponding to an average annual population increase of 5.1%. The mean group size during mating increased by 11% to 4.03 (3.649–4.329). The mean proportion of groups breeding each year increased by 8% to 0.52 (0.497–0.545). The average net distance of dispersal events increased by 55.4% to 103.09 km (0–362.2), while the median distance increased by 130% to 72.8 km. The duration of dispersal events barely varied. This meant that, as nearby territories were already occupied, dispersers found settlement opportunities by increasing the net distance travelled per day. The mean proportion of dispersers during mating slightly decreased to 0.03 (0.025–0.032), and the proportion of dispersers dying also decreased to 0.08 (0.050–0.114).

The presence and distribution of groups in the Iberian Peninsula greatly increased when overall or resident mortality rates were reduced by 10% (Figure 3). By 2030, the presence of groups increased through the current distribution range, particularly in the northern and western areas, which nowadays represent the main strongholds for wolves in the Iberian Peninsula. By 2040, the probability of finding a group was nearly one in all areas of the distribution range but the southeastern edges, and wolf expansion slightly began across areas where wolves are currently absent. By 2050, the wolf distribution range approximately doubled its size, avoiding large cities and highly modified and barren areas. The population increased from 1,350 (1,153–1,580) individuals in 2021 to 6,584 (4,804–8,468) by 2050 under reduced overall mortality, and to 6,349 (4,506–8,237) under reduced resident mortality.

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4 | DISCUSSION

Our study showed that high annual per capita mortality of resident wolves (mean values of 0.54 for pups and 0.25 for wolves aged 1–6 years in the Iberian Peninsula during 2013–2021) causes reductions in group size, reproductive success and dispersal distances, ultimately hindering population growth and range expansion (Figure 4). In the Iberian Peninsula, our model showed that decreasing resident mortality by 10%, even when holding disperser mortality constant (mean value of 0.37), can double the wolf distribution range in 30 years.

The mean annual mortality derived from our simulations for wolves aged 1–6 years was high compared to values below 0.19 reported for other European wolf populations during early recolonization phases, when human persecution was limited and populations were expanding (Cubaynes et al., 2010; Marucco et al., 2009; Planillo et al., 2024). Instead, mortality rates in our study were closer to those reported for populations under active lethal management (Morales-González, Ruiz-Villar, Quevedo, et al., 2025).

Our results confirm previous studies (Bassing et al., 2020; Sells et al., 2022; Tallian et al., 2023) showing that high mortality of residents reduces group size. Additional impacts can include an increased frequency of groups with missing breeders, shorter pair bond duration (Milleret et al., 2017) and fewer auxiliary nonbreeders in groups (Brainerd et al., 2008; Tallian et al., 2023). Because breeders constitute a large fraction of individuals in our population, mortality is expected to frequently involve them. Moreover, in small groups averaging 2.36 individuals, the loss of breeders often leads to group dissolution and dispersal of all members (Brainerd et al., 2008; Cassidy et al., 2023). Collectively, these mortality-induced social disruptions can hinder reproduction, including denning and recruitment rates (Borg et al., 2015; Brainerd et al., 2008; Cassidy et al., 2023), and may explain the low breeding capacity we obtained for groups in the Iberian Peninsula. This is also in line with studies showing that small groups generally show lower reproductive output (Ausband & Mitchell, 2021). Even when breeder replacement occurs, reproductive success can remain reduced (Ausband, 2025), and compared to populations close to carrying capacity, replacement in the Iberian

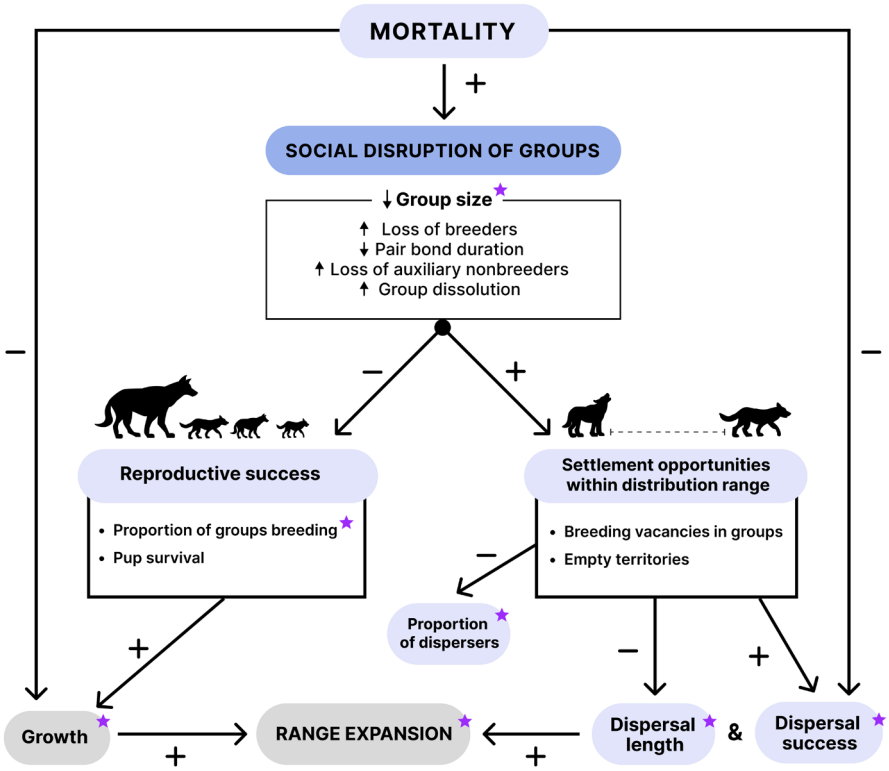

FIGURE 4 Demographic effects of mortality. The functions of demographic processes included in the model allow reliable inference of the cascading effects of mortality. Ovals represent parameters that are directly or indirectly affected by changes in mortality. Arrows indicate the direction of the relationship between parameters (A → B). Symbols '+' and '−' indicate whether B changes in the same ('+') or opposite ('−') direction as A (e.g. if reproductive success decreases, '+' indicates that growth also decreases). Black boxes indicate proxies for the parameters in the ovals, which are interpreted following the same directional signs. The parameters with small arrows represent scenarios of social disruption of groups, which can occur alongside a reduction in group size. Conversely, if social disruption decreased, the arrows would point in the opposite direction. The proportion of dispersers may also be affected by other parameters not shown in the figure. The star symbols depict model outputs evaluated when reducing mortality levels. Resident mortality can determine range dynamics through cascading effects on group social structure, reproduction and dispersal. In the model, high levels of resident mortality are associated with groups losing breeders and small groups that dissolve. Accordingly, we obtain that the reproductive success of the population decreases and dispersers frequently find settlement opportunities nearby. In turn, these circumstances contribute to limit range expansion.

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Peninsula is expected to be slower, increasing the time to subsequent reproduction because fewer reproductively viable individuals are available within groups and among dispersers (Borg et al., 2015; Brainerd et al., 2008). Our results align with general findings across social species showing that individual losses in small groups can disproportionately reduce group functioning (Maldonado-Chaparro et al., 2021). In turn, high resident mortality combined with low reproduction can explain the lack of population growth of wolves in the Iberian Peninsula.

Simultaneously, the continuous creation of empty territories and breeding vacancies in groups may prompt dispersers to occupy the nearby opportunities in preference to making longer dispersals, as reported in pumas *Puma concolor* (Newby et al., 2013) and suggested for wolves in northwest Portugal (Nakamura et al., 2021). In Portugal, groups located in higher quality areas may act as sources of dispersers supporting the persistence and recovery of nearby groups (Nakamura et al., 2021). Such processes can explain the low dispersal lengths and the lack of range expansion of wolves in the Iberian Peninsula. It has also been suggested that dispersing wolves select habitats similar to their natal site for territory establishment (Morales-González et al., 2022). This may occur across populations and contribute to explaining short dispersal distances when settlement opportunities are available via resident mortality. However, wolves have high adaptability to habitat, and it seems extremely unlikely that such a mechanism by its own limits growth and range expansion.

We found that the proportion of dispersers declined when the survival of residents increased. This seems counterintuitive since higher survival may promote more stable groups that function as sources of dispersers (Nakamura et al., 2021). However, this pattern is consistent with non-limiting habitat availability in the Iberian Peninsula (Grilo et al., 2019). While higher resident survival promoted group growth, dispersers had access to suitable habitat and established new groups. These processes directly increased the number of resident individuals, which can explain the reduction in the relative proportion of dispersers. In contrast, if habitat availability were limiting, dispersers might experience deyeled settlement, leading to an increase in their relative proportion (Grente et al., 2024). Similarly, the high mortality rate per capita of dispersers had minimal impacts on the dynamics of the Iberian population likely because most individuals settled quickly, minimizing their risk of death. However, high mortality rates inarguably compromise rare long-distance dispersals, which can be fundamental to connect distant populations (Bartoń et al., 2019).

The contribution of different causes of mortality to limiting wolf range expansion remains an open question. Our study focuses on overall mortality, although the demographic effects of human-caused and natural mortality may differ, and they can affect individuals at different life stages (Packer & Pusey, 1983). Human-induced mortality has been shown to limit population growth and recovery in other large social carnivores (e.g. African wild dogs, *Lycaon pictus* and lions, *Panthera leo*; Woodroffe & Ginsberg, 1998). In wolves, studies in Scandinavia suggest that intentional mortality may strongly limit population range expansion, whereas the contribution of traffic infrastructures appears minor (Recio et al., 2020). Similarly, intense persecution of wolves in Poland coincided with short dispersals and lack of growth and expansion (Nowak & Mysłajek, 2017). Data on cause-specific mortality rates across life stages, and knowledge of their interactions, would allow further explorations using our model.

On the other hand, some studies in local areas within large populations found low to neglected effects of human-caused mortality rates (Adams et al., 2008), breeder loss and group dissolution (Borg et al., 2015) on growth. However, the lack of effects on local growth are not surprising. For instance, the flux of individuals from/to adjacent areas which are also part of the population can easily result in stable local abundance, distribution of groups and local growth. This does not imply that wolves are resilient to mortality-driven impacts, as effects at the population level cannot be excluded (Creel et al., 2015; Morales-González et al., 2022).

When we reduced resident mortality, groups spread widely across the landscape except in large cities and highly modified or barren areas. This is consistent with wolves' high tolerance for moving through diverse landscapes and crossing barriers (Chapron et al., 2014). Incorporating finer-scale aspects of landscape connectivity, though challenging, can improve the spatial precision of expansion maps (Recio et al., 2020). Features such as major rivers, roads or highly urbanized areas can reduce connectivity and affect local persistence, even for a generally tolerant species (Morales-González et al., 2022; Nakamura et al., 2021).

Our work emphasizes that assessing the interlinked effects of resident and disperser mortality on dispersal patterns may be key to understanding range dynamics and current expansion of large carnivores in Europe and North America. Our results have important implications for policy. They contrast with the recent political decision to downlist the wolf from Annex IV ('strictly protected') to Annex V ('protected') of the Habitats Directive at the European level (European Union, 2025), which has been justified by a reported 35% increase in wolf numbers in Europe between 2016 and 2023 (Kaczensky et al., 2024). Our study highlights two critical aspects. First, not all European populations are increasing, like the Iberian population, underscoring the need for policy decisions to adopt a population-level perspective. Second, our simulations demonstrate that small changes in mortality can shift population trajectories; therefore, evaluating the demographic consequences of potential mortality scenarios resulting from downlisting is necessary to avoid compromising the long-term conservation status of the populations (Council Directive, 1992).

In the Iberian Peninsula, wolves were already listed under Annex V of the Habitats Directive across most of their distribution when the European-level change occurred. However, this change was followed by the removal of nationwide legal protection in Spain in 2025, after only 4 years of implementation (2021–2024). During this period of legal protection, reported group numbers in Spain increased only modestly from previous estimates (from 297 to 333 groups; MITECO, 2025). When viewed against the broad range predicted by the 2013–2021 parameterizations, this provides no clear evidence of a substantial improvement in population status. Because the current legislative framework is similar to that in place

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during 1991–2021, it may plausibly lead to similar mortality levels. In that case, group structure and dispersal processes are expected to remain negatively affected, limiting expansion into suitable habitats and hindering improvements in the conservation status. Moreover, recent work showed that small reductions in adult survival can increase the risk of local quasi-extinctions (Nakamura et al., 2026).

Our results indicate that reducing resident mortality of wolves in the Iberian Peninsula by 10% would favour a positive population trajectory. Achieving such reduction may be feasible through effective and sustained legal protection, including prohibiting hunting, limiting lethal control and strengthening enforcement to prevent illegal mortality, as these constitute the primary controllable sources of mortality (Morales-González, Ruiz-Villar, Quevedo, et al., 2025). Importantly, formal protection alone does not guarantee low mortality levels, as illustrated by populations classified as 'strictly protected' yet experiencing high mortality due to lethal control (e.g. France and Norway; Milleret, Duchamp, et al., 2025; Milleret, Dupont, et al., 2025). The current stable state of the Iberian population may also foreshadow dynamics in other recolonizing European populations. For example, following an initial phase of rapid expansion of wolves in France, recent high mortality levels (~0.38) may lead to demographic stabilization (Milleret, Duchamp, et al., 2025).

Finally, our study underscores the importance of modelling population demography in a detailed and process-explicit manner. Developing this framework required integrating heterogeneous monitoring data collected over decades and constraining plausible demographic combinations when direct empirical estimates were scarce. This highlights both the need for standardized, scientifically validated monitoring programmes capable of providing high-quality demographic data, and the value of mechanistic modelling to bridge monitoring gaps (e.g. in survival, reproduction and dispersal estimates), explore alternative management scenarios, and anticipate indirect demographic effects. As monitoring becomes more comprehensive, such models can be progressively refined. In this way, detailed demographic modelling enhances the interpretability of monitoring data and provides a robust foundation for adaptive and evidence-based conservation policy.

AUTHOR CONTRIBUTIONS

Ana Morales-González: Conceptualization, methodology, investigation, visualization, project administration, supervision, writing—original draft, and writing—review and editing. **Alberto Fernández-Gil**: Investigation, and writing—review and editing. **Mario Quevedo**: Investigation, and writing—review and editing. **Stephanie Kramer-Schadt**: Conceptualization, methodology, and writing—review and editing. **Maria Paniw**: Conceptualization, methodology, project administration, supervision, and writing—review and editing. **Eloy Revilla**: Conceptualization, methodology, funding acquisition, project administration, supervision, and writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9w0vt4bq9 (Morales-González et al., 2026).

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SUPPORTING INFORMATION

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

Supplementary Methods. Detailed description of the wolf SE-IBM, including model components, parameterizations, and the ODD protocol.

Figure S1. 'Population layers' (point vector layers) used to launch the wolf SE-IBM.

Figure S2. 'Territory layers' (raster layers) used to launch the wolf SE-IBM.

Figure S3. 'Habitat layer' (raster layer) of the wolf SE-IBM.

Figure S4. Structure of the wolf SE-IBM.

Figure S5. The life cycle of a wolf in the SE-IBM.

Figure S6. Structure of with-in-group demographic and dispersal sub-models of the wolf SE-IBM.

Figure S7. Probability of a maximum daily movement of 0, 1, 2, 3, 4, 5 and 6 cell steps for a disperser.

Figure S8. Probability of mortality associated with moving 0, 1, 2, 3, 4, 5 and 6 cell steps for a disperser between 8 months and 6 years-old.

Figure S9. Steps followed to identify plausible simulations of the wolf SE-IBM.

Figure S10. Comparison of the number and distribution of groups predicted by retained and rejected parameterizations for each past study period (1991–2002, 2002–2013, 2013–2021).

Figure S11. Assessment of initial-condition effects on the number of residents and dispersers predicted across years for seven random

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parameterizations per past study period (1991–2002, 2002–2013 and 2013–2021).

Figure S12. Growth, reproduction and dispersal of wolves in the Iberian Peninsula from 1991 to 2021, obtained from the wolf SE-IBM.

Table S1. References used to reconstruct snapshots of the number and distribution of wolf groups in the Iberian Peninsula in 1991, 2002, 2013 and 2021.

Table S2. Probability of travelling in each defined direction (i.e. 0°, 45°, 90°, 135°, 180°, 255°, 270° and 315°) for a disperser in a given day.

Table S3. Parameters extracted from each simulated year of each simulation of the wolf SE-IBM.

Table S4. Parameters extracted from each simulation of the wolf SE-IBM.

Table S5. Annual mortality rates per study period and future mortality scenarios for residents and dispersers.

Data S1. Parameterizations used to launch the wolf SE-IBM for the study periods 1991–2002, 2002–2013 and 2013–2021.

Data S2. Input demographic parameters used in the wolf SE-IBM.

Data S3. Biological relevance of the metrics that we used to describe the dynamics of wolves in the Iberian Peninsula.

Data S4. Published data on mortality, growth, reproduction and dispersal characteristics for wolves in the Iberian Peninsula.

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