Assessing key demographic parameters and viability of a wolf population in a highly human-dominated landscape

Mónia Nakamura [a,b,c,d,*], Pedro Monterroso [a,c], Helena Rio-Maior [a,c,1], Raquel Godinho [a,b,c], Francisco Álvares [a,c], José Vicente López-Bao [e,2], Olivier Gimenez [d,2]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661, Vairão, Portugal
[b] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002, Porto, Portugal
[c] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661, Vairão, Portugal
[d] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[e] Biodiversity Research Institute (University of Oviedo – CSIC – Principado de Asturias), Oviedo University, Mieres, Spain

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ABSTRACT

The persistence of large carnivores in human-dominated landscapes is particularly sensitive to the impact of humans on key demographic parameters, such as survival, which is strongly influenced by legal and illegal killing. However, estimating demographic parameters is challenging, requiring remarkable logistical and economic efforts. We developed a Bayesian integrated population model for wolves persisting in a human-dominated landscape at the edge of their European range. We incorporated multiple long-term datasets (2007–2019) of population counts, fecundity, molecular individual identification, and dead recoveries of GPS-collared wolves. With the IPM, we estimated population size and structure, growth rate, survival and emigration rates, the latter two being largely unknown parameters for wolves persisting in these landscapes. We estimated a growth rate of 1.04 (95%BCI: 1.03–1.05). Estimated survival rates were 0.72 (95%BCI: 0.66–0.77) for adults and 0.53 (95%BCI: 0.30–0.71) for pups, and the emigration rate was 0.13 (95%BCI: 0.06–0.21). The low emigration rates estimated may contribute to explaining the cryptic population structure documented in the Iberian wolf population. By forecasting population growth over a ten-year period (2020–2029) under different fecundity and survival rate scenarios, we identified adult survival as a key factor influencing wolf persistence in human-dominated landscapes. Conflicts around wolf depredation on livestock, which may boost retaliatory killing and public pressure to reduce wolf populations, together with other anthropogenic mortality causes and the impacts of infrastructure development, can reduce wolf survival rates to an unknown extent and, therefore, jeopardize wolf recovery.

1. Introduction

Large carnivore conservation is challenging in human-dominated landscapes, as sharing the landscape with these species often leads to conflicts of different nature (Carter and Linnell, 2016; Lamb et al., 2020), mainly because of their predatory behaviour (Lute et al., 2018). Different viewpoints on how to share the landscape with these species collide and interact with social, cultural, political and institutional factors (Chapron and López-Bao, 2020; Lute et al., 2018), further complicating conservation. Sharing landscapes can influence demographic

parameters, such as survival, and ultimately determine the persistence of large carnivores in human-dominated landscapes (Benson et al., 2023; Lamb et al., 2020). This persistence is strongly modulated by the impact of humans on food availability, habitat, and the ecology and demography of species (Cassidy et al., 2023; López-Bao et al., 2019). In this context, identifying key demographic parameters or vital rates that most constrain their persistence is a cornerstone to appropriately developing effective large carnivore conservation strategies (Lamb et al., 2020).

Obtaining robust demographic estimates for elusive species is challenging since detecting family groups, reproductive events, mortality,

and dispersers is difficult. Large carnivores are usually nocturnal, wide-ranging, and occur at low densities, which further complicates detection and observation. Furthermore, their primary causes of mortality are anthropogenic, such as poaching, road kills or hunting (e.g., Benson et al., 2023; Liberg et al., 2020), and a large proportion of some of them are cryptic, making it even harder to obtain robust survival estimates (Liberg et al., 2012; Treves et al., 2021).

Wolves (*Canis lupus*) are one of the most adaptable and persistent species in human-dominated landscapes (e.g., Chapron et al., 2014; Di Bernardi et al., 2025). For example, in Europe, after a decrease in the intensity of persecution, several wolf populations have rapidly increased, with growth rates of up to 1.36 in the case of Germany (Reinhardt et al., 2019) or 1.27 in France (Marescot et al., 2011). Wolves are found in all mainland Member States of the European Union, with a total population estimate of 21,500 individuals (Boitani et al., 2022). Yet, this recovery is uneven: while some populations have shown a remarkably positive trend in the last decades, other populations have been relatively stationary, with lower growth rates, or even extinct (López-Bao et al., 2018) due to a variety of causes, including poaching or landscape fragmentation (Bischof et al., 2020; Boitani et al., 2022; Caniglia et al., 2012).

Population growth is determined by the interplay between fecundity, immigration, emigration, and survival. Among these, adult survival is particularly influential for long-lived species like wolves (Heppell et al., 2000), and likely represents a key parameter limiting population growth and connectivity in fragmented landscapes due to conflicts related to sharing the landscape with humans (Cooley et al., 2009). However, most estimates available on survival rates refer to wolf populations in North America in non-human-dominated landscapes, primarily derived from capture-recapture (CR) models based on non-invasive genetic sampling (e.g., survival rates of 0.74, Adams et al., 2011; and 0.71, Marucco et al., 2012) or from collared wolves (e.g., survival rates of 0.73, Hebblewhite and Whittington, 2020; and 0.82, Treves et al., 2017). Survival estimates from France between 1995 and 2003 (0.84; Marescot et al., 2012) and the Alps between 1999 and 2006 (0.82; Marucco et al., 2009) offer some insight based on CR models. Further studies distinguish survival rates at 0.66–0.75 for weakly detectable individuals and 0.75–0.90 for highly detectable individuals in Italy and France, respectively (Caniglia et al., 2012; Cubaynes et al., 2010). However, equivalent estimates are scarcely available for European wolf populations, and even less at the limit of species range, considering individual heterogeneity in detection or in populations with a cryptic structure, such as the wolf population in the Iberian Peninsula, characterized by a high genetic structure and low effective dispersal (Silva et al., 2018).

Assessing and identifying key demographic parameters is particularly relevant for wolves in the Iberian Peninsula. This wolf population is the largest remaining in Western Europe and yet genetically and geographically isolated, potentially representing a unique population from genetic, behavioural and ecological perspectives (Lobo et al., 2025; Silva et al., 2018). Considering the cryptic population structure of the Iberian wolf population, ensuring its long-term viability requires a better understanding of survival and dispersal rates among identified genetic clusters. To the best of our knowledge, in the Iberian Peninsula, only two studies addressed wolf survival. Blanco and Cortés (2007) estimated a 0.82 (95% CI: 0.71–0.94) survival rate, based on 14 collared wolves between 1997 and 2004 in central Spain, with 44% of mortality events attributed to poaching (deaths associated with poisoning or illegal shooting); and Campos (2018) estimated a 0.62 (95% CI: 0.486–0.799) survival rate, based on 32 collared wolves between 1991 and 2017 in Portugal, with poaching as the leading cause of mortality. This variability whithin the same wolf population suggests remarkable spatial heterogeneity in survival within and across populations occurring in human-dominated landscapes and underscores the urgency of obtaining robust region-specific demographic estimates (Milleret et al., 2025; Morales-González et al., 2025). In this regard, conflicts between wolves and humans, which mostly result from livestock depredation,

and related compensation issues in management compensation schemes (Lute et al., 2018) may drive such spatial heterogeneity in demographic parameters like survival. For instance, in Portugal, where our study is conducted, changes in legislation for compensation of wolf damages to livestock, with stricter conditions and reduced payment of animal value (according to the Portuguese legislation Decree-Law n°. 54/2016), coupled with bureaucratic and delayed procedures for compensation, likely decreased the tolerance towards wolves and increased retaliatory killing that can have a significant negative impact on the wolf survival. Our study includes the first two years (2018–2019) after this legal change for damage compensation, which could evidence its impact on demographic parameters.

Integrated Population Models (IPMs) have been progressively developed to inform conservation strategies (e.g., Abadi et al., 2017; Bled et al., 2017; Horne et al., 2019; Milleret, 2016; Paquet et al., 2021; Petracca et al., 2024; Sells et al., 2022b). By formally describing the ecological processes, IPMs combine multiple data sources (e.g., population counts, fecundity estimates) into a single unified analytical framework that yield more accurate and precise estimates of demographic parameters, including unknown parameters (Arnold et al., 2018; Besbeas et al., 2010; Schaub and Abadi, 2011). IPMs can be therefore be useful for identifying population-limiting factors (Arnold et al., 2018).

Focusing on wolves persisting in a human-dominated landscape at edge of its European distribution, we leverage the long-term wolf monitoring data available (2007–2019) in northern Portugal (Alto Minho, 2200 km^2), at the range edge of the Northwestern Iberian wolf population (Chapron et al., 2014), to investigate wolf population dynamics in a highly human-dominated and fragmented landscape. We developed an IPM to estimate key population parameters – including population size and structure, growth rate, survival and emigration rates – and to identify limiting parameters affecting the persistence of wolves in these human-dominated landscapes. We run population projections for a ten-year period (2020–2029) under different scenarios to identify critical parameters and thresholds for such persistence. In this study, we investigate wolf population trends since 2007, estimate key demographic parameters, and assess how the variation in such parameters influences the probability of near-extinction and extinction by 2029. Improving conservation actions and management strategies based on robust demographic parameter estimates (particularly survival and dispersal rates) is needed, particularly in the European human-dominated landscapes with limited connectivity and at the limit of species range. To our knowledge, this is one of the few studies for the grey wolf, and the first study for the Iberian wolf, resorting to long-term data and merging into an IPM, to estimate several utterly unknown wolf demographic estimates in human-dominated landscapes. Furthermore, although IPMs have already been developed for wolves in North America (e.g., Horne et al., 2019; Petracca et al., 2024), this powerful tool remains largely unused in the contexts of European human-dominated landscapes (see also Paquet et al., 2021).

2. Material & methods

2.1. Long-term wolf population monitoring in Alto Minho

We conducted the study in Alto Minho region (northwest Portugal; Fig. 1), where wolves persist in a highly human-dominated landscape with a human population density of 107.7 inhabitants/km^2; (PORDATA, 2014), dispersed human settlements, and high paved road densities (1.60 km/km^2; INE, 2014); similar to most of the wolf range in north-western Iberia (e.g., Dennehy et al., 2021; Sazatornil et al., 2016; Torres et al., 2015) (for further description of the study area, see Appendix A1 in Supplementary Material). Wolves here form a distinct genetic cluster within the northwestern Iberian wolf population, with limited evidence of exchanging individuals with other neighbouring areas (Silva et al., 2018).
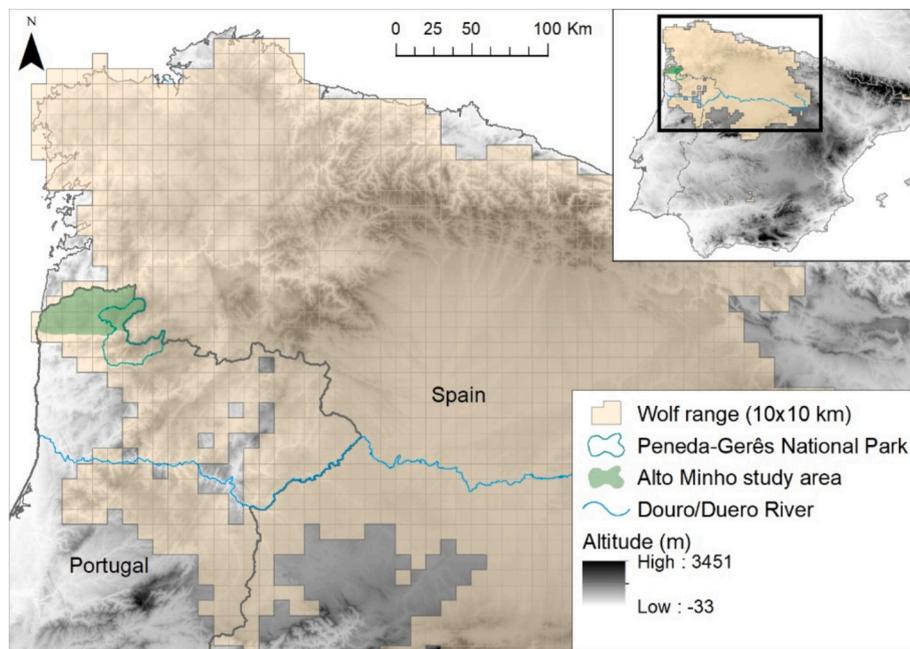
Fig. 1. Location of the study area (Alto Minho) in NW Portugal and wolf range in the Iberian Peninsula (adapted from Kaczensky, 2018).

Wolves were monitored annually between 2007 and 2019 to estimate the number of packs and reproduction events (e.g., Nakamura et al., 2021; Pacheco et al., 2024). Monitoring was based mainly on transects for wolf signs (scats and urine) covered on foot or by car (<10 km/h), simulated howling, observations, camera trapping, and individual molecular identification of non-invasive samples during the wolf pup-rearing season (from late June to early November). Additionally, several wolves were captured, GPS-collared, and genetically identified. For a detailed description of the procedures for field methodologies, see Appendix A1 in Supplementary Material). We submitted the samples to molecular analysis for species and individual identification, which included blood, scats, urine, saliva, and hair samples (for a detailed description of the molecular procedures, see Appendix A2 of the Supplementary Material).

Overall, we detected 4525 putative wolf signs (348 ± 139 signs per year; mean ± SD; range: 112–518), of which 31% were collected for genetic analysis (1355 scat, 20 urine, 14 saliva, and 15 hair samples). Species identification was successful in 85% of these non-invasive samples. We achieved 709 individual genotypes among analyzed wolf samples (i.e. number of scats with individual identification) during the study period, corresponding to 223 different wolves identified between 2007 and 2019. Eighteen of the 223 wolves identified were removed from the CR analysis due to lack of detections over time. Our dataset of capture-recapture history for wolves included 205 individuals, of which 144 were detected once, 30 twice, and the remnant 31 were detected up to 7 times during the 13 years of sampling. GPS-collared wolves that died ($n = 8$) were retrieved and used as information on dead-recoveries for survival estimation.

The occurrence of a pack was determined when at least two wolves were detected (Mech and Boitani, 2003) or whenever a breeding event (e.g., presence of pups) was confirmed. The number of adults and pups in packs was obtained by observations, howling detections, camera trapping events, and captures for GPS-collaring. For molecularly identified individuals from non-invasive samples, we used pack assignment criteria applied in previous studies, in which an individual was assigned to a pack if detected once in the pack's homesite (within a 1 km buffer around a den site or a rendezvous site) or detected at least twice a year inside a pack territory (Nakamura et al., 2021; Stenglein et al., 2011). Detailed descriptions of field molecular and pack assignment criteria are

described in (Nakamura et al., 2021) and (Rio-Maior et al., 2019, 2018). For a detailed description of the procedures regarding the obtention of the annual population counts, see Appendix A1 in Supplementary Material. We considered individuals <1 year old as a pup and > 1 year old as a subadult/adult (hereafter named as 'adult'; we merged adults and subadults due to the difficulty of distinguishing them remotely).

2.2. Integrated population model

To estimate population size and key demographic parameters, we developed our IPM in a hierarchical Bayesian framework, joining different data sources and accounting for the observation processes. The IPM included both sexes, accounted by the wolf social structure and annual biological cycle, and incorporated three components into a post-breeding stage-structured population matrix model: i) population size, ii) fecundity, and iii) capture-recapture models (hereafter CR). We estimated annual population size (Ntot), annual number of adults (Nad) and pups (Npup), survival of adults (Sad) and pups (Spup), the proportion of female breeders among adults (Prop_fb), and fecundity (F) (Fig. 2). By integrating a multistate CR model, we also estimated additional parameters of fidelity (Fd), dead recovery (rr) and detection (pp) probabilities (Lebreton et al., 1999). (For a detailed description of the IPM components and implementation, see Appendix A3 of the Supplementary Material).

2.3. Population viability analysis

We forecasted the trajectory of the population over a ten-year period (2020–2029) following the empirical dataset using the baseline parameters estimated from the IPM (control). To better understand the trend and structure of this population, we predicted the annual population size, annual growth rate, and the number of adults and pups for the forecast period. Additionally, to evaluate to what extent variations in fecundity and adult and pup survival impact the population trajectory and its extinction probability, we projected the trajectory for the same period under twelve different scenarios, by varying each of the following variables at a time: increased and decreased fecundity, adult survival or pup survival by 10% and 20%. We also evaluated how these variations in fecundity and survival affect the number of adults and pups during the
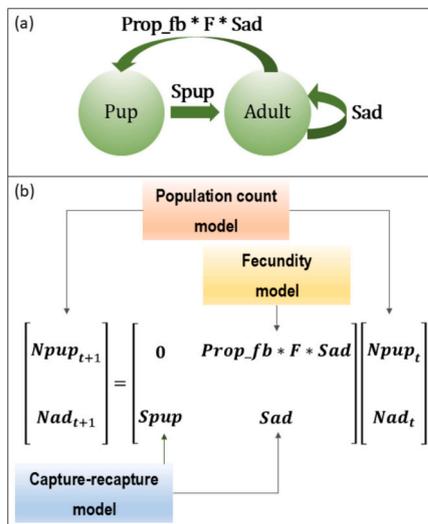
Fig. 2. (a) Diagram for building the age structured population matrix; (b) integrated population model components in a matrix model representation (for visual representation purposes only, since the matrix model is not implemented). (Prop_fb – proportion of female breeders among adults, F – fecundity, Spup – pup survival; Sad – adult survival; Nad – number of adults; Npup – number of pups).

forecast period. To assess which vital rates have a stronger effect on demography, we performed a sensitivity analysis of the population growth rate (Caswell, 2019) by fixing its parameters to the estimates obtained from the IPM. For all scenarios, we determined the cumulative probability of extinction (Ntot = 0; i.e. the probability of the population size becoming zero) and quasi-extinction with a threshold of Ntot = 5 individuals (i.e. the wolf population is unlikely to recover when the population is fewer than 5 wolves) for the forecasted period. We imposed this minimum population size as quasi-extinction, considering available studies on wolf population viability analysis with a population size threshold (e.g., USFWS, 2023), our study area size, and the average annual proportion of female breeders among adults obtained for our study area (0.17; see below) – in the absence of pups, the probability of existing at least one female breeder among the population is lower than one, when a maximum of five adults are present in the population.

3. Results

Overall, between 2007 and 2019, we performed 6371 km of transects (average effort: 796 km/year), and 1574 howling surveys complemented with 313 observation surveys. We carried out 1559 camera trapping nights and 3501 live trapping nights for GPS-collaring (see details on the effort of field methodological procedures in Table A1 in Appendix A1 of Supplementary Material).

Based on field and molecular information (i.e. considering the initial data, before running the IPM), the observed annual average population count between 2007 and 2019 was 34.8 ± 13.3 wolves (range: 13–61), with an average naïve growth rate of 1.17 ± 0.40 (range: 0.63–1.85). The observed annual average number of adults and pups were 18.5 ± 7.2 (range: 6–31) and 12.4 ± 5.3 (range: 4–20), respectively. We detected an annual average of 4.8 ± 1.6 packs (range: 2–7), with confirmed reproduction in an average of 3.7 ± 1.4 (range:1–6) of them (i.e. annually, $77 \pm 18\%$ of the detected packs reproduced; range: 50–100%). The average annual proportion of female breeders among adults was 0.17 ± 0.06 (range: 0.09–0.29; result used as an informative prior for Prop_fb the IPM). We obtained an average fecundity of 3.9 ± 2.4 pups per pack ($n = 20$; range: 1–9; result used as an informative prior of F for the IPM) based on only direct observations. It is important to note that the average fecundity was 3.4 ± 1.8 ($n = 48$; range: 1–9) when

we considered information from different field methodologies (see Appendix A4 and Fig. A1 in Appendix A5 of Supplementary Material).

From our IPM, we estimated an average annual growth rate and population size of 1.04 (95% Bayesian Credible Interval (95%BCI): 1.03–1.05; range: 0.88–1.29) and 35.6 ± 9.3 (range: 23–53), respectively (Fig. 3A and B); with an annual average of 21.6 ± 5.5 (range: 15–32) adults and 13.6 ± 4.2 (range: 8–23) pups in the population (Fig. 3C). The annual rate of increase for the number of adults was 1.07 ± 0.11 and for the number of pups (1.07 ± 0.27). Average survival rate for adults was estimated in 0.72 (95%BCI: 0.66–0.77) and 0.53 (95% BCI: 0.30–0.71) for pups. The lowest annual adult survival rates were obtained between 2008 and 2009 (0.68) and 2009–2010 (0.65) (Fig. 3D). The fidelity rate of adults to the study area was estimated to be 0.87 (95%BCI: 0.79–0.94), and apparent survival to be at 0.63 (95%BCI: 0.52–0.72). The probability of individual detection was 0.44, and that of dead recovery was 0.06 (see details on parameter estimates in Table 1 and the model output with all estimates in Table A2 in Appendix A5 of Supplementary Material).

Our population viability analysis revealed that, if adult survival rate is maintained at 0.72, the estimated average annual population size for the forecasted period (2020–2029) would be 60.7 ± 8.4 wolves Fig. 4A, with an average of 36.9 ± 5.1 adults and 22.5 ± 3.0 pups (Table 2 and Fig. 4B). By 2029, the extinction probability (Ntot = 0) of wolves in Alto Minho would be 0.001, and the quasi-extinction probability (Ntot = 5) would be 0.013 (Table 2 and Fig. 5). Conversely, if the adult survival rate decreases by 10%, the growth rate will decrease to 0.96, with the extinction and quasi-extinction probabilities increase to 0.01 and 0.07, respectively (Table 2). If the adult survival rate decreases by 20%, the growth rate will decrease to 0.89, and the extinction and quasi-extinction probabilities increase to 0.06 and 0.22, respectively (Table 2; see additional details in Fig. A2 and Fig. A3 in Appendix A5 of Supplementary Material). Varying pup survival rate and fecundity by 10% or 20% for the forecast period had little effect on the demographic parameters analyzed – i.e. low sensitivity, with up to 1% and 8% of variation on growth rate, respectively – and, consequently, on the extinction probabilities (Table 2; Fig. A4 and Fig. A5 in Appendix A5 of Supplementary Material).

4. Discussion

In this study, we estimated key demographic parameters for a wolf population persisting in a highly human-dominated landscape with a cryptic population structure, and performed a population viability analysis based on an IPM. The population viability analysis showed how much the variation in adult survival impacts wolf persistence. Accordingly, we predict that a potential decrease in adult survival by 10% until 2029 would result in a negative trend (0.97 growth rate) in wolf numbers. Remarkably, our estimates suggest that a quasi-extinction likelihood of 22% would be achieved in only 10 years if adult survival decreases by 20%. Given that conflicts with humans often result in the illegal killing of wolves to an unknown extent (e.g., Liberg et al., 2012), efforts should focus on reducing anthropogenic mortality, particularly illegal killing, to increase adult survival and dispersal rates, thereby improving the overall population viability.

Between 2007 and 2019, wolves in Alto Minho recovered and recolonized previously occupied areas (Nakamura et al., 2021), with two to seven packs detected annually. The IPM estimated an overall growth rate of 1.04 (95%BCI: 1.03–1.05), similar to values reported for stable wolf populations in Europe or in an initial phase of expansion (e. g., 1.04, Marucco et al., 2009; 1.02, Nowak et al., 2008), but much lower than growth rates observed at clear expansion fronts of wolf populations in human-dominated landscapes (1.36, Fechter and Storch, 2014; 1.27, Marescot et al., 2011). Notably, the growth rate obtained here using only field and molecular data was higher (1.17) and closely aligned with previous estimates from 2007 to 2016 (1.16; Nakamura et al., 2021). The differences observed between the initial population counts and IPM
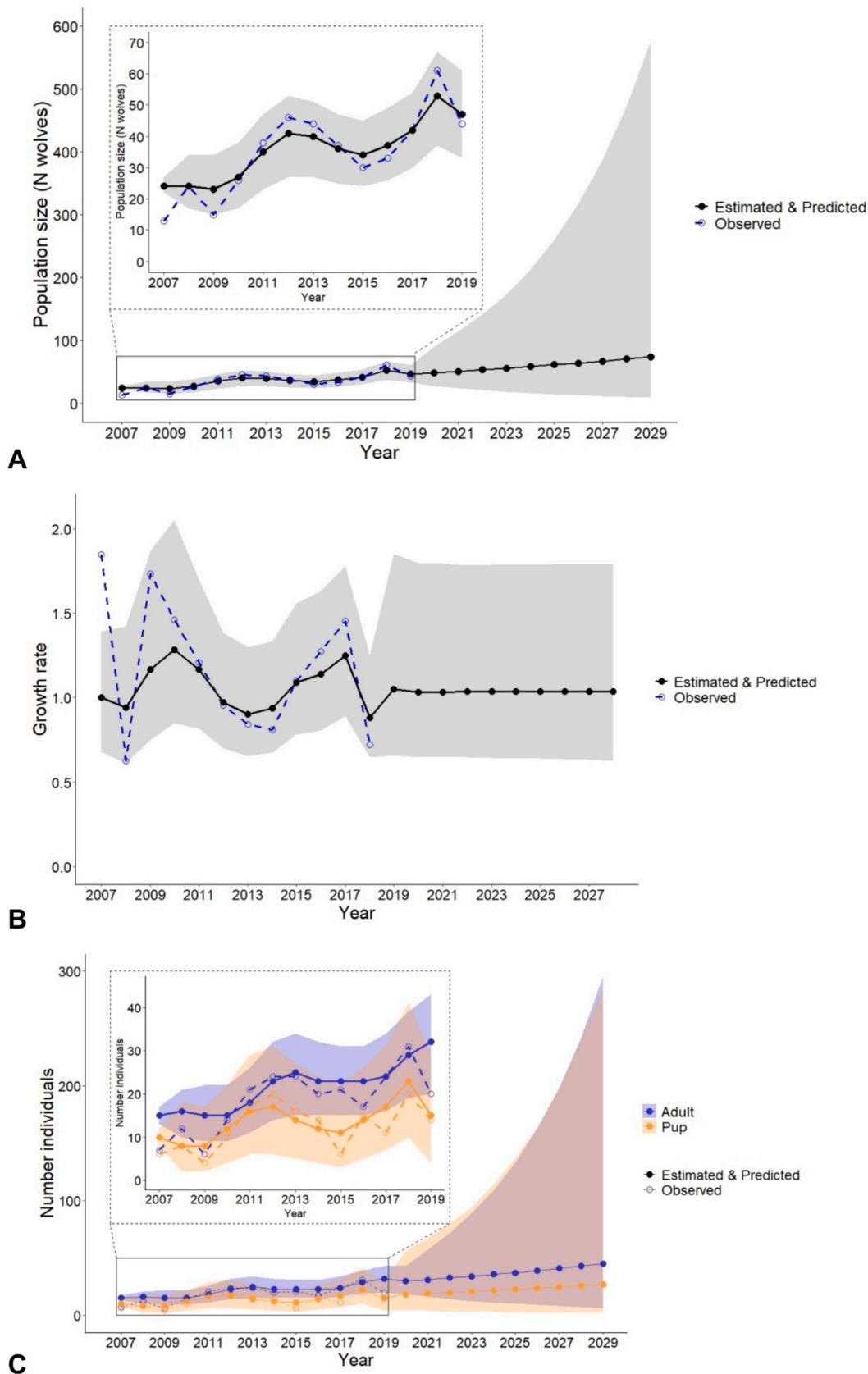
Fig. 3. Annual observed values and parameter median estimates and projections obtained by the integrated population model for the sampling period (2007–2019) and the forecast period (2020–2029): A) population size, with inset for the sampling period; B) growth rate; C) number of adults and pups, with inset for the sampling period; and D) annual adult survival rate with overall average values of adult apparent survival rate (black dashed line) and of pup survival (orange line); shadow areas represent 95% Bayesian credible intervals.
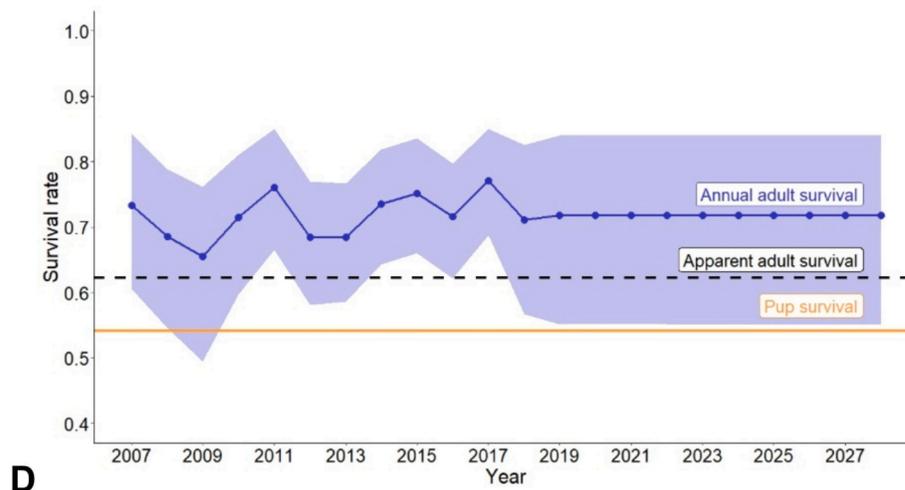
Fig. 3. (*continued*).

Table 1

Parameter estimates obtained by the integrated population model; posterior mean of median estimates (Mean), standard deviation (SD), and 95% Bayesian credible interval (95%BCI).

Parameter	Mean ± SD	95%BCI
Proportion female breeders (mean.Prop_fb)	0.17 ± 0.02	[0.12; 0.22]
Fecundity (mean.F)	4.00 ± 1.47	[1.94; 7.65]
Pup Survival (mean.Spup)	0.53 ± 0.12	[0.30; 0.71]
Adult Survival (Sad)	0.72 ± 0.03	[0.66; 0.77]
Fidelity (Fd)	0.87 ± 0.04	[0.79; 0.94]
Dead recovery (rr)	0.06 ± 0.02	[0.03; 0.10]
Detection (pp)	0.44 ± 0.04	[0.35; 0.52]

estimates, show the importance of the implementation of such models. The population size and growth rate estimates obtained by the IPM are likely more robust and accurate than the initial ones, since it integrates several datasets into the sub-models and it considers detection probabilities and several demographic parameters. Such differences, particularly on population growth rates, can have strong implications when it comes to implementing conservation and management actions.

We observed some fluctuations in population size over time, though these seem to be less accentuated than previously thought (Nakamura et al., 2021). These fluctuations may be related to the annual variations observed in adult survival rates and the number of packs reproducing and pups. The annual variation in the number of pups was more pronounced than in the number of adults, which may suggest a demographic compensation mechanism when reproduction is less successful. Another compensatory mechanism known for wolf populations is the low dispersal rates of adults due to low social or intraspecific competition (Ballard et al., 1987; Sells et al., 2022a) or mortality rates. The particular characteristics of wolves in some areas of Iberia, such as high food availability in the form of extensive livestock as in our study area (Álvares et al., 2015), may decrease intraspecific competition, and consequently decrease the need to emigrate, which likely partially explains the cryptic genetic structure observed by Silva et al. (2018).

To simplify the IPM, the population model assumed a geographically closed population. However, by integrating a multistate CR model, it allowed to estimate fidelity rates to further assess apparent survival rate (0.63). This value was lower than in studies conducted in France (0.84, Marescot et al., 2012) and Italy (0.66–0.75, Caniglia et al., 2012). Such lower survival rate observed in Alto Minho could be related to high levels anthropogenic mortality (e.g., retaliatory killing linked to high depredation levels on livestock, since wolves feed mostly on extensively grazed livestock in this area, comprising more than 70% of the wolf diet;

Álvares et al., 2015). Although some of the first captures in our CR model may include pups – which typically have a lower survival rate than adults (Marucco et al., 2009) – the goodness-of-fit tests did not show lack of fit. Thus, the apparent adult survival is unlikely to be underestimated. Since we could not distinguish pups from adults from non-invasive samples for the first year of capture, it was not possible to proceed with a CR model with individual heterogeneity for age. Such a differentiation could distinguish part of the highly or weakly detectable individuals (Cubaynes et al., 2010). However, by including a prior for pup survival rate, we could estimate an average pup survival rate for this population (0.53). Previous studies show that wolf populations decline when the survival rate is below 0.65 or 0.68 (Chapron et al., 2003; Fuller, 1989; Marescot et al., 2012). Thus, according to the estimates of the adult survival rate (0.72) and the positive growth trend (1.04), our estimated apparent adult survival rate (0.63) could be slightly underestimated, possibly due to an underestimation of the fidelity rate, though, as previously mentioned, the goodness-of-fit tests did not show lack of fit. To better understand how growth rate is affected by other compensation mechanisms, additional studies with more detailed analysis are needed, such as age-structured CR models.

Changes in pup survival rate and fecundity had some effect on the population projections. Though, growth rates are more strongly affected by adult survival variations than pup survival or fecundity. Although, the influence of pup survival on growth rate should be interpreted with caution since this parameter was not estimated within the CR model due to data limitations, the IPM allowed to infer the sensitivity of the extinction risk to changes in adult or pup survival. By increasing adult survival by 10% during the forecasted period, the population would increase sustainably with a 1.11 growth rate, though it would not significantly affect the extinction risk of wolves in the study area. Nevertheless, it could increase the number of dispersers and the number of packs in the surroundings and potentially contribute to recolonizing new areas. However, in a scenario where the adult survival rate decreases by 10% (i.e. Sad = 0.65) between 2020 and 2029, the population declines at a rate of 0.97. In a more extreme scenario of a 20% decrease in adult survival (i.e. Sad = 0.57), the growth rate decreases to 0.89, with a 22% risk that the population will decline to only five individuals by 2029. Despite the low quasi-extinction probabilities in such scenarios, these results highlight that a decrease in adult survival can significantly impact this population in a short time. In fact, although wolves in Alto Minho have been increasing since 2007, the number of individuals suffered a steep decline between 1996 and 2007, possibly related to high levels of wolf persecution and decreased habitat connectivity (Nakamura et al., 2021). Our study shows the relevance of ensuring high adult survival rates to guarantee the persistence of wolves
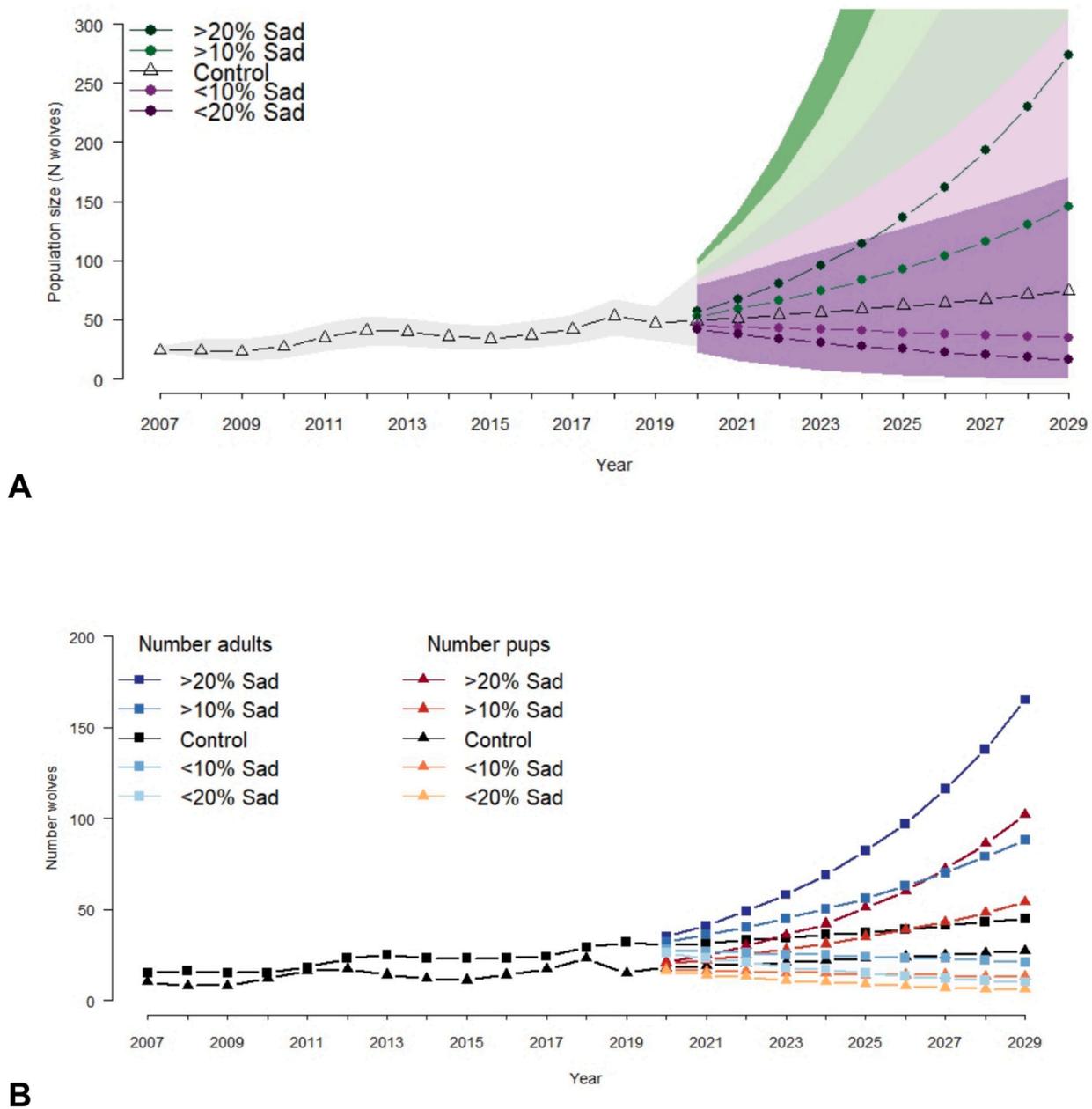
Fig. 4. Annual population size (A) and number of adults and pups (B) for the sampling (2007–2019) and forecast (2020–2029) periods, based on the developed integrated population model. Predictions for the forecast period obtained without (control) and with variation (<10%, <20%, >10% and > 20%) in adult survival rates (Sad); shadow areas represent 95% Bayesian credible intervals.

in human-dominated landscapes because such declines may occur even with small increases in adult mortality.

Survival rates lower than that obtained in our study (0.63) have been observed in North America, where the management and conservation strategies are very different from those in Portugal. In the USA, Ballard et al. (1997) estimated a 0.55 survival rate and a 0.88 growth rate, where hunting is the leading cause of mortality. In Canada, Hebblewhite and Whittington (2020) estimated a 0.44 survival rate for individuals in the surroundings of a protected area, as opposed to a 0.84 survival rate inside the protected area. Such studies show the impact that hunting can have on wolf populations and the role of protected areas in North America. In Portugal, although hunting is not allowed and it is still unclear to what extent protected areas affect the success of wolves, our IPM shows that the decrease in the survival of wolves in Alto Minho due to, for instance, increased poaching levels, in addition to natural mortality causes, would result in a negative growth rate that the population

would not sustain in the long term.

The temporal variation in survival rates between 2007 and 2019 likely resulted from a combination of natural and anthropogenic mortality. A natural cause could be the prevalence of sarcoptic mange, an infectious and contagious disease caused by *Sarcoptes scabiei* mite (Bornstein et al., 2001). Though it has been suggested that this disease has a limited demographic effect on wolf populations (Oleaga et al., 2011), wolf mortality from sarcoptic mange has been occasionally recorded in the Iberian Peninsula (Domínguez et al., 2008). In Alto Minho, several wolves were observed with skin lesions compatible with sarcoptic mange and peaks in the seroprevalence and the non-invasive predicted prevalence of this disease were detected during 2006–2009 (Rousseau et al., 2021), which coincide with the years of the lowest estimated adult survival rates. Furthermore, the concomitance and interactions between the Canine Distemper Virus (Müller et al., 2011) and the mite causing sarcoptic mange (Oleaga et al., 2015) may make

Table 2

Average annual median estimates (mean ± SD; range) of population size, growth rate, and number of adults and pups for the forecast period (2020–2029) by maintaining (Control model) and varying each variable at a time: increasing (+20%, +10%) or decreasing (−20%, −10%) fecundity (F), adult survival (Sad), or pup survival (Spup) rates. Probability of extinction (population size = 0) and quasi-extinction (with a threshold of population size of 5 wolves) by 2029.

| Model	F (n pups per female breeder)	Sad (%) Real	Sad (%) Apparent	Spup (%)	Population size	Growth rate	N adult	N pup	Extinction (%)	Quasi-extinction (%)
+20% F	4.9	72	63	54	114.2 ± 49.1 (55–201)	1.14 ± 0.01 (1.13–1.17)	61.6 ± 26.3 (30–108)	49.5 ± 21.0 (24–87)	0.05	0.35
+10% F	4.3	72	63	54	81.3 ± 22.7 (52–119)	1.08 ± 0.01 (1.08–1.11)	46.7 ± 12.8 (30–68)	32.6 ± 9.0 (21–48)	0.08	0.62
+20% Sad	3.8	86	75	54	140.9 ± 72.9 (57–274)	1.18 ± 0.01 (1.18–1.21)	85 ± 43.5 (35–165)	52.5 ± 27.2 (21–102)	0.00	0.02
+10% Sad	3.8	79	69	54	92.4 ± 31.2 (53–146)	1.11 ± 0.01 (1.1–1.13)	55.9 ± 18.8 (32–88)	34.5 ± 11.4 (20–54)	0.02	0.16
+20% Spup	3.2	72	63	65	61.3 ± 8.7 (49–75)	1.04 ± 0.00 (1.04–1.04)	39.4 ± 5.5 (32–48)	20.3 ± 3.0 (16–25)	0.12	1.10
+10% Spup	3.5	72	63	60	61.3 ± 8.7 (49–75)	1.04 ± 0.00 (1.03–1.05)	38.4 ± 5.5 (31–47)	21.5 ± 3.0 (17–26)	0.13	1.18
Control	4.0	72	63	54	60.7 ± 8.4 (49–74)	1.04 ± 0.00 (1.03–1.05)	36.9 ± 5.1 (30–45)	22.5 ± 3.0 (18–27)	0.15	1.25
−10% Spup	4.2	72	63	49	60.4 ± 8.1 (49–73)	1.04 ± 0.01 (1.03–1.06)	35.3 ± 4.7 (29–43)	23.6 ± 3.2 (19–29)	0.18	1.29
−20% Spup	4.6	72	63	43	59.4 ± 7.5 (49–71)	1.04 ± 0.01 (1.03–1.06)	33.4 ± 4.1 (28–40)	24.6 ± 2.9 (21–29)	0.21	1.43
−10% Sad	3.8	65	56	54	40 ± 3.5 (35–45)	0.97 ± 0.00 (0.96–0.98)	24.4 ± 2.2 (21–28)	14.7 ± 1.3 (13–17)	1.17	6.69
−20% Sad	3.8	57	50	54	27.3 ± 8.7 (16–42)	0.89 ± 0.00 (0.89–0.89)	16.6 ± 5.4 (10–26)	10.0 ± 3.5 (6–16)	6.01	22.15
−10% F	3.3	72	63	54	47.3 ± 0.5 (47–48)	1.00 ± 0.00 (1–1)	30.0 ± 0.0 (30−30)	16.0 ± 0.0 (16–16)	0.27	2.37
−20% F	2.9	72	63	54	38.2 ± 4.3 (32–45)	0.96 ± 0.00 (0.96–0.97)	25.5 ± 3.03 (21−30)	11.8 ± 1.3 (10–14)	0.50	4.54
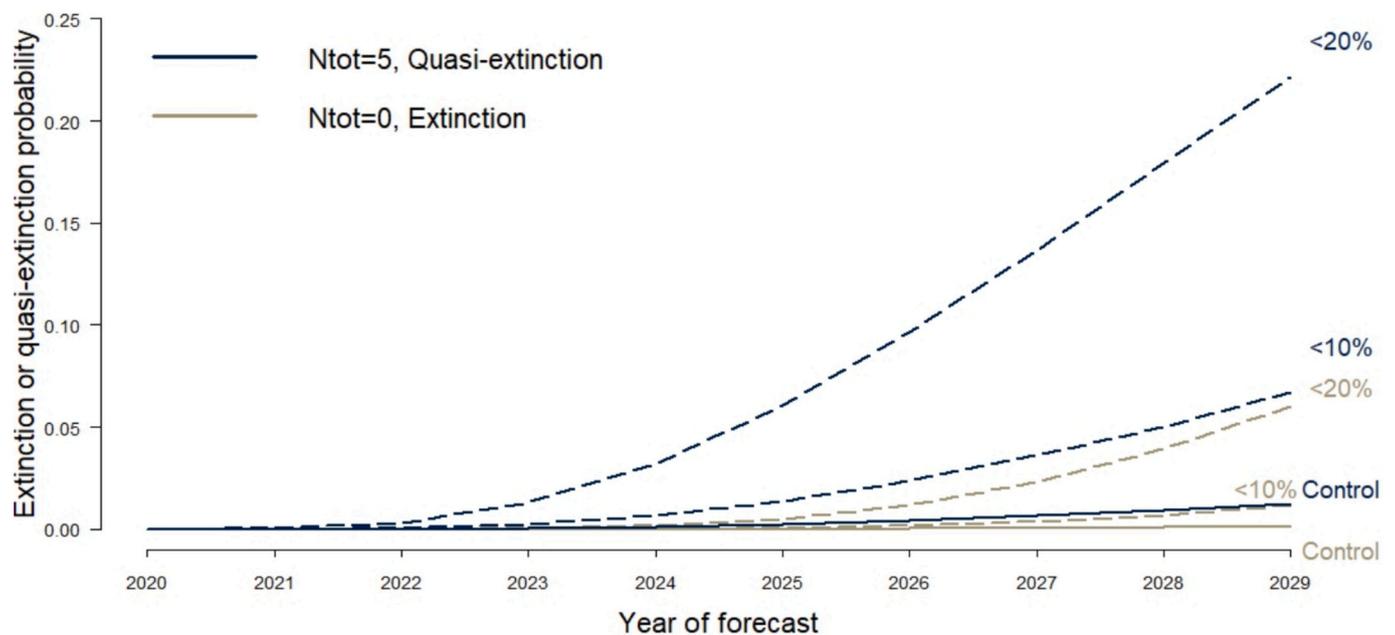
Fig. 5. Cumulative probability of extinction (Ntot = 0 individuals, blue lines) and of quasi-extinction (threshold of Ntot = 5 individuals, grey lines) for wolves in Alto Minho within 10 years for the forecast period (2020–2029). Probabilities obtained for the control model (i.e. adult survival rate at 72%; solid lines) and for the models with a decrease of adult survival by 20% and 10% (dashed lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

individuals more vulnerable. Nevertheless, conflicts with people due to the high frequency of livestock depredations by wolves (Pimenta et al., 2018) suggest that a high proportion of wolf mortalities may also be related to anthropogenic causes (Campos, 2018). In fact, poaching

caused the deaths of 47% of GPS-collared wolves tracked in the study area during 2007–2017 (Rio-Maior et al., 2018). To better understand the causes of wolf mortality and enhance the development of studies for wolf conservation, the Institute for Nature Conservation and Forests (ICNF) in Portugal implemented the 'Monitoring System of Dead Wolves' since 1999, in which all wolf carcasses are registered in a national database, and samples are collected for multiple purposes (Barroso and Pimenta, 2008). However, most dead wolves are opportunistically detected and do not reflect the actual rate of mortality causes, resulting in biased mortality causes towards more easily detectable deaths (e.g., road kills 0.35), with lower detections of poaching (shot 0.20, snared 0.12, or poisoned 0.03) or natural causes (e. g., infectious diseases 0.06) (Álvares et al., 2015). Therefore, poaching may be the main limiting factor of wolves in this area and other regions of the range of the northwestern Iberian wolf population.

We estimated that only 13% of the wolves emigrate from the study area. Such remarkably high estimated fidelity would partially explain the cryptic genetic structure observed in the Northwestern Iberian wolf population (Silva et al., 2018). Previously, it has been estimated a very low proportion of dispersal individuals among genetic clusters in this population (4%; Silva et al., 2018) and even among packs within the same genetic cluster (11%; Nakamura et al., 2021). Wolves in Alto Minho have delayed dispersal and tend towards philopatric behaviour (Pacheco et al., 2024), probably contributing to the low emigration rate. The observed low dispersal rate has also been related to higher landscape fragmentation and human-related mortality risk in wolves (Rio-Maior et al., 2019; Sells et al., 2022a), which can, in turn, decrease pack sizes and resource competition in established populations (Treves et al., 2017; Webb et al., 2011). Since food is not a limiting factor, as mentioned above, competition is expected to be lower, possibly delaying dispersal age (Ballard et al., 1987; Sells et al., 2022a). Furthermore, the mortality of pack members can increase the recruitment of new members into vacant positions (depending also on the status of the individual lost; Brainerd et al., 2008; Cassidy et al., 2023), reducing the need for inbreeding avoidance and dispersal since breeding opportunities arise within the pack (Ausband et al., 2017b; Pacheco et al., 2024; Packard, 2003).

The average litter size obtained by direct observations (3.9) was similar to estimates in other areas of the Northwestern Iberian wolf population (4.0, Fernández-Gil et al., 2020), although lower compared to other areas, such as the Cantabrian Mountains (5.15, Llaneza et al., 2023). However, the number of pups detected in packs can be highly variable depending on the effort or difficulty of observation among packs (e.g., Barrientos, 2000). For instance, Barrientos (2000) observed 4.7 pups per pack, and Fernández-Gil et al. (2020) observed 4.0 pups per pack in the same study area. Further studies are needed to assess differences in fecundity and pup survival within the wolf population across Iberia; although we cannot rule out the influence of different methodological approaches on these figures (e.g., Palacios et al., 2017; see also Llaneza et al., 2023), as shown for our study area (3.9 and 3.4 pups detected by direct observation and all field methods, respectively, in this work; and 3.7 ± 1.8 pups inferred from a genealogical analysis; Pacheco et al., 2024).

Fecundity could vary with the age of the breeding females (Ferreras-Colino et al., 2021; Mech et al., 2016; Stahler et al., 2013) and food availability (Boertje and Stephenson, 1992). Our estimates of fecundity (3.9) could also be influenced by low pup survival in early months, which can be affected, for example, by diseases, such as canine parvovirus, and the turnover of breeders (Ausband et al., 2017a; Brainerd et al., 2008; Stahler et al., 2013). Indeed, the estimated average fecundity of female breeders in Iberia based on the foetus and placental scar counts (5.5–6.0; Ferreras-Colino et al., 2021) was higher than the estimated fecundity in our study. Additionally, wolves in Alto Minho have shown a lower genetic diversity (Silva et al., 2018) and a frequent turnover of breeders (Pacheco et al., 2024), which could be affecting the reproductive success of packs. Furthermore, in areas where people are less tolerant of wolf presence, pups might be more susceptible to being killed or poached than adults, particularly when homesites are located in more human-accessible areas with higher disturbance (Sazatornil et al., 2016). Further studies are needed to study pup survival and understand the different causes of mortality affecting this cohort (e.g., Ballard et al., 1987; Fritts et al., 1981). Lastly, future studies accounting for individual heterogeneity, such as breeding status, sex or intrinsic differences in detection among methods, would likely improve the estimation of demographic parameters. In our study, we lacked information on GPS-collared wolves to include differences between the detection probabilities of individuals by non-invasive molecular methods and GPS-collaring wolves.

4.1. Conservation and management implications

Currently, wolf populations appear to have stagnated in several areas of Spain (eastern Castilla y León, the Basque Country and north of Castilla-La Mancha) and wolf range continues decreasing in Portugal (Blanco and Cortés, 2009; Di Bernardi et al., 2025; López-Bao et al., 2018; Nores and López-Bao, 2022; Pimenta et al., 2023), which might be a consequence of high levels of poaching associated with livestock depredation. Additionally, the legal changes for damage compensation may also have an impact on wolf survival. Until 2017, the Portuguese government fully compensated wolf damages to livestock when protection measures were implemented (namely, fences or livestock guarding). However, after 2018, the compensation was limited to 15 annual attacks per livestock owner and payment of animal value at 100% only for the first three declared animals and decreasing percentage down to 50% for the 15th attack (according to the Portuguese legislation Decree-Law n°. 54/2016). This change reduced the number of declared attacks, particularly in chronically affected farmers, which coupled with the bureaucratic and delayed procedures for compensation, likely decreased the tolerance towards wolves and increased retaliatory killing. In fact, we observed a decrease in adult survival between 2018 and 2019, which coincide with the first two years after the legal changes that reduced the compensation values for damages on livestock. Although the implications of such changes may only be reflected in demographic parameters in the longer term, we cannot rule out the possibility of an immediate impact on the wolf population. As such, a follow-up on the compensation schemes adopted in Portugal and in other human-dominated landscapes where livestock damages are frequent is urgently needed to assess the impact of implemented policies on wolf conservation and adapt accordingly.

In fragmented and human-dominated environments, survival is not only a limiting factor for population growth but also constrains dispersal and connectivity between subpopulations (Cooley et al., 2009). Thus, estimating and understanding spatial variability in survival and dispersal is crucial for assessing the viability and connectivity of wolf populations (e.g., Milleret et al., 2025). The proportion of emigration with successful dispersal (i.e. with establishment in other areas) is yet to be assessed in human-dominated landscapes. By estimating emigration and immigration rates among different areas, wolf conservation and management actions could be focused on areas with lower connectivity. Studies on wolf demography, and particularly adult survival rates – a key limiting factor of wolves – in other human-dominated areas of Europe are needed to detect demographic variations in space, particularly in conflict-prone areas, where wolves rely on livestock, in the expansion fronts, and where wolves seem to be more fragile and susceptible, such as in small and isolated wolf populations.

CRediT authorship contribution statement

Mónia Nakamura: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Pedro Monterroso:** Conceptualization, Formal analysis, Funding acquisition, Methodology,

Supervision, Writing – review & editing. **Helena Rio-Maior:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. **Raquel Godinho:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Francisco Álvares:** Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **José Vicente López-Bao:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. **Olivier Gimenez:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111784.

Data availability

The processed data file (.Rdata) and code of the integrated population model (.Rmd), are available on the Zenodo Digital Repository (https://doi.org/10.5281/zenodo.18853020). The processed data file includes the data objects of the annual population size (C), annual number of female breeders (y_female), first year of capture (fir_final), and the capture history with states (rCH) of the 205 individuals genetically identified.

References

Abadi, F., Barbraud, C., Gimenez, O., 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. Glob. Chang. Biol. 23, 1353–1359. https://doi.org/10.1111/gcb.13538.

Adams, J.R., Vucetich, L.M., Hedrick, P.W., Peterson, R.O., Vucetich, J.A., 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. Proc. R. Soc. B Biol. Sci. 278, 3336–3344. https://doi.org/10.1098/rspb.2011.0261.

Álvares, F., Barroso, I., Costa, G.F. da, Espírito-Santo, C., Fonseca, C., Godinho, R., Nakamura, M., Petrucci-Fonseca, F., Pimenta, V., Rio-Maior, H., Santos, N., Torres, R.T., 2015. Situação de referência para o Plano de Ação para a Conservação do Lobo-ibérico em Portugal. Lisbon, Portugal.

Arnold, T.W., Clark, R.G., Koons, D.N., Schaub, M., 2018. Integrated population models facilitate ecological understanding and improved management decisions. J. Wildl. Manag. 82, 266–274. https://doi.org/10.1002/jwmg.21404.

Ausband, D.E., Mitchell, M.S., Stansbury, C.R., Stenglein, J.L., Waits, L.P., 2017a. Harvest and group effects on pup survival in a cooperative breeder. Proc. R. Soc. B Biol. Sci. 284, 20170580. https://doi.org/10.1098/rspb.2017.0580.

Ausband, D.E., Mitchell, M.S., Waits, L.P., 2017b. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. J. Anim. Ecol. 86, 1094–1101. https://doi.org/10.1111/1365-2656.12707.

Ballard, W.B., Whitman, J.S., Gardner .C., L, 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98, 3–54.

Ballard, W.B., Ayres, L.A., Krausman, P.R., Reed, D.J., Fancy, S.G., 1997. Ecology of wolves in relation to a migratory Caribou Herd in Northwest Alaska. J. Wildl. Manag. 61, 1–47. https://doi.org/10.2307/3830776.

Barrientos, L.M., 2000. Tamaño y composición de diferentes grupos de lobos en castilla y león. Galemys 12, 249–256.

Barroso, I., Pimenta, V., 2008. Sistema de Monitorização de Lobos Mortos: Relatório de Actividades 1999–2008. ICNF, Lisboa.

Benson, J.F., Dougherty, K.D., Beier, P., Boyce, W.M., Cristescu, B., Gammons, D.J., Garcelon, D.K., Higley, J.M., Martins, Q.E., Nisi, A.C., Riley, S.P.D., Sikich, J.A., Stephenson, T.R., Vickers, T.W., Wengert, G.M., Wilmers, C.C., Wittmer, H.U., Dellinger, J.A., 2023. The ecology of human-caused mortality for a protected large carnivore. Proc. Natl. Acad. Sci. 120, 2017. https://doi.org/10.1073/pnas.2220030120.

Besbeas, A.P., Freeman, S.N., Morgan, B.J.T., Catchpole, E.A., Besbeas, P., 2010. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. Society 58, 540–547. https://doi.org/10.1111/j.0006-341X.2002.00540.x.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., Ordiz, A., de Valpine, P., Turek, D., Royle, J.A., Gimenez, O., Flagstad, Ø., Åkesson, M., Svensson, L., Brøseth, H., Kindberg, J., 2020. Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. Proc. Natl. Acad. Sci. 117, 30531–30538. https://doi.org/10.1073/pnas.2011383117.

Blanco, J.C., Cortés, Y., 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. J. Zool. 273, 114–124. https://doi.org/10.1111/j.1469-7998.2007.00305.x.

Blanco, J.C., Cortés, Y., 2009. Ecological and social constraints of wolf recovery in Spain. In: Musiani, M., Boitani, L., Paquet, P.C. (Eds.), A New Era for Wolves and People: Wolf Recovery, Human Attitudes, and Policy. University of Calgary Press, Calgary, pp. 41–66.

Bled, F., Belant, J.L., Van Daele, L.J., Svoboda, N., Gustine, D., Hilderbrand, G., Barnes, V.G., 2017. Using multiple data types and integrated population models to improve our knowledge of apex predator population dynamics. Ecol. Evol. 7, 9531–9543. https://doi.org/10.1002/ece3.3469.

Boertje, R.D., Stephenson, R.O., 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Can. J. Zool. 70, 2441–2443. https://doi.org/10.1139/z92-328.

Boitani, L., Kaczensky, P., Alvares, F., Andrén, H., Balys, V., Blanco, J.C., Chapron, G., Chiriac, S., Cirovic, D., Drouet-Houguet, N., Groff, C., Huber, D., Iliopoulos, Y., Ionescu, O., Kojola, I., Krofel, M., Kutal, M., Linnell, J., Majic, A., Mannil, P., Marucco, F., Melovski, D., Mengüllüoğlu, D., Mergeay, J., Nowak, S., Ozolins, J., Perovic, A., Rauer, G., Reinhardt, I., Rigg, R., Salvatori, V., Sanaja, B., Schley, L., Shkvyria, M., Sunde, P., Tirronen, K., Trajce, A., Trbojevic, I., Trouwborst, A., Arx, M. von, Wolfl, M., Zlatanova, D., Patkó, L., 2022. Assessment of the Conservation Status of the Wolf (*Canis lupus*) in Europe.

Bornstein, S., Mörner, T., Samuel, W.M., 2001. Sarcoptes scabiei and Sarcoptic Mange. In: Parasitic Diseases of Wild Mammals. Wiley, pp. 107–119. https://doi.org/10.1002/9780470377000.ch5.

Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., Jimenez, M.D., Jozwiak, E.A., Liberg, O., others, 2008. The effects of breeder loss on wolves. J. Wildl. Manag. 72, 89–98. https://doi.org/10.2193/2006-305.

Campos, R., 2018. Survival and Population Dynamics of the Iberian Wolf in Portugal. MSc Thesis. Universidade do Porto.

Caniglia, R., Fabbri, E., Cubaynes, S., Gimenez, O., Lebreton, J.-D.D., Randi, E., 2012. An improved procedure to estimate wolf abundance using non-invasive genetic sampling and capture–recapture mixture models. Conserv. Genet. 13, 53–64. https://doi.org/10.1007/s10592-011-0266-1.

Carter, N.H., Linnell, J.D.C., 2016. Co-adaptation is key to coexisting with large carnivores. Trends Ecol. Evol. 31, 575–578. https://doi.org/10.1016/j.tree.2016.05.006.

Cassidy, K.A., Borg, B.L., Klauder, K.J., Sorum, M.S., Thomas-Kuzilik, R., Dewey, S.R., Stephenson, J.A., Stahler, D.R., Gable, T.D., Bump, J.K., Homkes, A.T., Windels, S.K.,

Smith, D.W., 2023. Human-caused mortality triggers pack instability in gray wolves. Front. Ecol. Environ. https://doi.org/10.1002/fee.2597.

Caswell, H., 2019. Sensitivity Analysis: Matrix Methods in Demography and Ecology. Springer Nature.

Chapron, G., López-Bao, J.V., 2020. The place of nature in conservation conflicts. Conserv. Biol. 34, 795–802. https://doi.org/10.1111/cobi.13485.

Chapron, G., Legendre, S., Ferrière, R., Clobert, J., Haight, R.G., 2003. Conservation and control strategies for the wolf (Canis lupus) in western Europe based on demographic models. C. R. Biol. 326, 575–587. https://doi.org/10.1016/S1631-0691(03)00148-3.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balciauskas, L., Balys, V., Bed, P., Bego, F., Blanco, J.C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjager, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremi, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Maji, A., Mannil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunovi, M., Persson, J., Poto nik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbin ek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Va a, M., Veeroja, R., Wabakken, P., Wolfl, M., Wolfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science (80-.). 346, 1517–1519. https://doi.org/10.1126/science.1257553.

Cooley, H.S., Wielgus, R.B., Koehler, G.M., Robinson, H.S., Maletzke, B.T., 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90, 2913–2921. https://doi.org/10.1890/08-1805.1.

Cubaynes, S., Pradel, R., Choquet, R., Duchamp, C., Gaillard, J.-M., Lebreton, J.-D., Marboutin, E., Miquel, C., Reboulet, A.-M., Poillot, C., Taberlet, P., Gimenez, O., 2010. Importance of accounting for detection heterogeneity when estimating abundance: the case of french wolves. Conserv. Biol. 24, 621–626. https://doi.org/10.1111/j.1523-1739.2009.01431.x.

Dennehy, E., Llaneza, L., López-Bao, J.V., 2021. Contrasting wolf responses to different paved roads and traffic volume levels. Biodivers. Conserv. 30, 3133–3150. https://doi.org/10.1007/s10531-021-02239-y.

Di Bernardi, C., Chapron, G., Kaczensky, P., Álvares, F., Andrén, H., Balys, V., Blanco, J.C., Chiriac, S., Duško, Ć., 2025. Continuing Recovery of Wolves in Europe, pp. 1–18. https://doi.org/10.1371/journal.pstr.0000158.

Domínguez, G., Espí, A., Prieto, J.M., Torre, J.A.De, 2008. Sarcoptic mange in Iberian wolves (Canis lupus signatus) in northern Spain. Vet. Rec. 162 (23), 754–755. https://doi.org/10.1136/vr.162.23.754.

Fechter, D., Storch, I., 2014. How many wolves (Canis lupus) fit into Germany? The role of assumptions in predictive rule-based habitat models for habitat generalists. PLoS One 9. https://doi.org/10.1371/journal.pone.0101798.

Fernández-Gil, A., Quevedo, M., Barrientos, L.M., Nuño, A., Naves, J., de Gabriel, M., Ordiz, A., Revilla, E., 2020. Pack size in humanized landscapes: the Iberian wolf population. Wildl. Biol. 2020. https://doi.org/10.2981/wlb.00594.

Ferreras-Colino, E., García-Garrigós, A., Gortázar, C., Llaneza, L., 2021. Wolf (Canis lupus) litter size in Spain. Eur. J. Wildl. Res. 67, 31. https://doi.org/10.1007/s10344-021-01473-7.

Fritts, S.H., Mech, L.D., Roberts, K., 1981. Dynamics, movements and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. 80, 3–79.

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105, 1–41.

Hebblewhite, M., Whittington, J., 2020. Wolves without borders: transboundary survival of wolves in Banff National Park over three decades. Glob. Ecol. Conserv. 24, e01293. https://doi.org/10.1016/j.gecco.2020.e01293.

Heppell, S.S., Caswell, H., Crowder, L.B., 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81, 654–665. https://doi.org/10.1890/0012-9658(2000)081[0654:LHAEPP]2.0.CO;2.

Horne, J.S., Ausband, D.E., Hurley, M.A., Struthers, J., Berg, J.E., Groth, K., 2019. Integrated population model to improve knowledge and management of Idaho wolves. J. Wildl. Manag. 83, 32–42. https://doi.org/10.1002/jwmg.21554.

INE, . Instituto Nacional de Estatística - Statistics Portugal. http://www.ine.pt/. Instituto Nacional de Estatística – Statistics Portugal.

Kaczensky, P., 2018. IUCN Red List Mapping for the regional assessment of the Wolf (Canis lupus) in Europe.

Lamb, C.T., Ford, A.T., McLellan, B.N., Proctor, M.F., Mowat, G., Ciarniello, L., Nielsen, S.E., Boutin, S., 2020. The ecology of human–carnivore coexistence. Proc. Natl. Acad. Sci. USA 117, 17876–17883. https://doi.org/10.1073/pnas.1922097117.

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.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H.H., Thompson Hobbs, N., Sand, H.H., 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B-Biological Sci. 279, 910–915. https://doi.org/10.1098/rspb.2011.1275.

Liberg, O., Suutarinen, J., Åkesson, M., Andrén, H., Wabakken, P., Wikenros, C., Sand, H., 2020. Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling. Biol. Conserv. 243, 108456. https://doi.org/10.1016/j.biocon.2020.108456.

Llaneza, L., Sazatornil, V., García, E.J., Palacios, V., López-Bao, J.V., 2023. Minimum average pack size in Iberian wolves. Eur. J. Wildl. Res. 69, 1–6. https://doi.org/10.1007/s10344-023-01695-x.

Lobo, D., Morales, H.E., Oosterhout, C. Van, López-bao, J.V., Silva, P., Llaneza, L., Pacheco, C., Castro, D., Hernández-alonso, G., Pacheco, G., Archer, J., Gilbert, M.T. P., Ferrand, N., Godinho, R., 2025. Ancient dog introgression into the Iberian wolf genome may have facilitated adaptation to human-dominated landscapes, pp. 432–445. https://doi.org/10.1101/gr.279093.124.Freely.

López-Bao, J.V., Fleurke, F., Chapron, G., Trouwborst, A., 2018. Legal obligations regarding populations on the verge of extinction in Europe: conservation, Restoration, Recolonization. Reintroduction. Biol. Conserv. 227, 319–325. https://doi.org/10.1016/j.biocon.2018.09.027.

López-Bao, J.V., Aronsson, M., Linnell, J.D.C., Odden, J., Persson, J., Andrén, H., 2019. Eurasian lynx fitness shows little variation across Scandinavian human-dominated landscapes. Sci. Rep. 9, 8903. https://doi.org/10.1038/s41598-019-45569-2.

Lute, M.L., Carter, N.H., López-Bao, J.V., Linnell, J.D.C., 2018. Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. Biol. Conserv. 218, 223–232. https://doi.org/10.1016/j.biocon.2017.12.035.

Marescot, L., Pradel, R., Duchamp, C., Cubaynes, S., Marboutin, E., Choquet, R., Miquel, C., Gimenez, O., 2011. Capture-recapture population growth rate as a robust tool against detection heterogeneity for population management. Ecol. Appl. 21, 2898–2907. https://doi.org/10.1890/10-2321.1.

Marescot, L., Gimenez, O., Duchamp, C., Marboutin, E., Chapron, G., 2012. Reducing matrix population models with application to social animal species. Ecol. Model. 232, 91–96. https://doi.org/10.1016/j.ecolmodel.2012.02.017.

Marucco, F., Pletscher, D.H., Boitani, L., Schwartz, M.K., Pilgrim, K.L., Lebreton, J.-D.D., 2009. Wolf survival and population trend using non-invasive capture-recapture techniques in the Western Alps. J. Appl. Ecol. 46, 1003–1010. https://doi.org/10.1111/j.1365-2664.2009.01696.x.

Marucco, F., Vucetich, L.M., Peterson, R.O., Adams, J.R., Vucetich, J.A., 2012. Evaluating the efficacy of non-invasive genetic methods and estimating wolf survival during a ten-year period. Conserv. Genet. 13, 1611–1622. https://doi.org/10.1007/s10592-012-0412-4.

Mech, L.D., Boitani, L., 2003. Wolves: Behavior, Ecology, and Conservation. The University of Chicago Press.

Mech, L.D., Barber-Meyer, S.M., Erb, J., 2016. Wolf (Canis lupus) generation time and proportion of current breeding females by age. PLoS One 11, 1–13. https://doi.org/10.1371/journal.pone.0156682.

Milleret, C., 2016. Spatial ecology of wolves in Scandinavia: from spatio-temporal dynamics of wolf pairs to wolf population dynamics. PhD Thesis. Hedmark Univ. Appl. Sci.

Milleret, C., Dupont, P., Dey, S., Brøseth, H., Kindberg, J., Turek, D., De Valpine, P., Åkesson, M., Wabakken, P., Zimmermann, B., Bischof, R., 2025. Map of death: spatially explicit mortality of the grey wolf. Proc. R. Soc. B Biol. Sci. 292. https://doi.org/10.1098/rspb.2025.0948.

Morales-González, A., Ruiz-Villar, H., Quevedo, M., Fernández-Gil, A., Paniw, M., Revilla, E., 2025. Patterns and determinants of mortality in grey wolves (Canis lupus). Mammal Rev. https://doi.org/10.1111/mam.70015.

Müller, A., Silva, E., Santos, N., Thompson, G., 2011. Domestic Dog Origin of Canine Distemper Virus in Free-ranging Wolves in Portugal as Revealed by Hemagglutinin Gene Characterization. J. Wildl. Dis. 47, 725–729. https://doi.org/10.7589/0090-3558-47.3.725.

Nakamura, M., Rio-Maior, H., Godinho, R., Petrucci-Fonseca, F., Álvares, F., 2021. Source-sink dynamics promote wolf persistence in human-modified landscapes: insights from long-term monitoring. Biol. Conserv. 256, 109075. https://doi.org/10.1016/j.biocon.2021.109075.

Nores, C., López-Bao, J.V., 2022. Historical data to inform the legal status of species in Europe: an example with wolves. Biol. Conserv. 272. https://doi.org/10.1016/j.biocon.2022.109639.

Nowak, S., Mysłajek, R.W., Jędrzejewska, B., 2008. Density and demography of wolf, Canis lupus population in the western-most part of the Polish Carpathian Mountains, 1996-2003. Folia Zool. 57, 392–402.

Oleaga, Á., Casais, R., Balseiro, A., Espí, A., Llaneza, L., Hartasánchez, A., Gortázar, C., 2011. New techniques for an old disease: sarcoptic mange in the Iberian wolf. Vet. Parasitol. 181, 255–266. https://doi.org/10.1016/j.vetpar.2011.04.036.

Oleaga, Á., Vicente, J., Ferroglio, E., Pegoraro de Macedo, M.R., Casais, R., del Cerro, A., Espí, A., García, E.J., Gortázar, C., 2015. Concomitance and interactions of pathogens in the Iberian wolf (Canis lupus). Res. Vet. Sci. 101, 22–27. https://doi.org/10.1016/j.rvsc.2015.05.010.

Pacheco, C., Rio-Maior, H., Nakamura, M., Álvares, F., Godinho, R., 2024. Relatedness-based mate choice and female philopatry: inbreeding trends of wolf packs in a human-dominated landscape. Heredity (Edinb.) 1–10. https://doi.org/10.1038/s41437-024-00676-3.

Packard, J.M., 2003. Wolf Behavior: Reproductive, Social, and Intelligent. In: Mech, L.D., Boitani, L. (Eds.), Wolf: Behavior, Ecology and Conservation, pp. 35–65. Chicago, IL.

Palacios, V., Font, E., García, E.J., Svensson, L., Llaneza, L., Frank, J., López-Bao, J.V., 2017. Reliability of human estimates of the presence of pups and the number of wolves vocalizing in chorus howls: implications for decision-making processes. Eur. J. Wildl. Res. 63, 1–8. https://doi.org/10.1007/s10344-017-1115-4.

Paquet, M., Knape, J., Arlt, D., Forslund, P., Pärt, T., Flagstad, Ø., Jones, C.G., Nicoll, M.A.C., Norris, K., Pemberton, J.M., Sand, H., Svensson, L., Tatayah, V., Wabakken, P., Wikenros, C., Åkesson, M., Low, M., 2021. Integrated population models poorly estimate the demographic contribution of immigration. Methods Ecol. Evol. 12, 1899–1910. https://doi.org/10.1111/2041-210X.13667.

Petracca, L.S., Gardner, B., Maletzke, B.T., Converse, S.J., 2024. Merging integrated population models and individual-based models to project population dynamics of recolonizing species. Biol. Conserv. 289, 110340. https://doi.org/10.1016/j.biocon.2023.110340.

Pimenta, V., Barroso, I., Boitani, L., Beja, P., 2018. Risks a la carte: modelling the occurrence and intensity of wolf predation on multiple livestock species. Biol. Conserv. 228, 331–342. https://doi.org/10.1016/j.biocon.2018.11.008.

Pimenta, V., Barroso, I., Álvares, F., Barros, T., Borges, C., Cadete, D., Carneiro, C., Casimiro, J., Ferrão da Costa, G., Ferreira, E., Fonseca, C., Gil, P., Godinho, R., Hipólito, D., José-Garcia, E., Llaneza, L., Marcos Perez, A., Monzón, A., Nakamura, M., Palacios, V., Paulino, C., Pereira, J., Pereira, A., Petrucci- Fonseca, F., Pinto, S., Rio-Maior, H., Roque, S., Sampaio, M., Serronha, A., Simões, F., Torres, R., 2023. Situação populacional do Lobo em Portugal: resultados do censo nacional de 2019/2021. ICNF, Lisboa, ICNF, Lisboa.

PORDATA, 2014. Bases de dados Portugal Contemporâneo. http://www.pordata.pt/Portugal.

Reinhardt, I., Kluth, G., Nowak, C., Szentiks, C.A., Krone, O., Ansorge, H., Müller, T., Mueller, T., 2019. Military training areas facilitate the recolonization of wolves in Germany. Conserv. Lett. 12. https://doi.org/10.1111/conl.12635.

Rio-Maior, H., Beja, P., Nakamura, M., Álvares, F., 2018. Use of space and homesite attendance by Iberian wolves during the breeding season. Mamm. Biol. 92, 1–10. https://doi.org/10.1016/j.mambio.2018.03.014.

Rio-Maior, H., Nakamura, M., Álvares, F., Beja, P., 2019. Designing the landscape of coexistence: integrating risk avoidance, habitat selection and functional connectivity to inform large carnivore conservation. Biol. Conserv. 235, 178–188. https://doi.org/10.1016/j.biocon.2019.04.021.

Rousseau, J., Nakamura, M., Rio-Maior, H., Álvares, F., Choquet, R., Madeira de Carvalho, L., Godinho, R., Santos, N., 2021. Non-invasive molecular survey of sarcoptic mange in wildlife: diagnostic performance in wolf faecal samples evaluated by multi-event capture-recapture models. Pathogens 10, 1–15. https://doi.org/10.3390/pathogens10020243.

Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., Borg, B.L., Cluff, D., Cortés, Y., García, E.J., Geffen, E., Habib, B., Iliopoulos, Y., Kaboli, M., Krofel, M., Llaneza, L., Marucco, F., Oakleaf, J.K., Person, D.K., Potočnik, H., Ražen, N., Rio-Maior, H., Sand, H., Unger, D., Wabakken, P., López-Bao, J.V., 2016. The role of human-related risk in breeding site selection by wolves. Biol. Conserv. 201, 103–110. https://doi.org/10.1016/j.biocon.2016.06.022.

Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 152, S227–S237. https://doi.org/10.1007/s10336-010-0632-7.

Sells, S.N., Mitchell, M.S., Podruzny, K.M., Ausband, D.E., Emlen, D.J., Gude, J.A., Smucker, T.D., Boyd, D.K., Loonam, K.E., 2022a. Competition, prey, and mortalities influence gray wolf group size. J. Wildl. Manag. 86, 1–17. https://doi.org/10.1002/jwmg.22193.

Sells, S.N., Podruzny, K.M., Nowak, J.J., Smucker, T.D., Parks, T.W., Boyd, D.K., Nelson, A.A., Lance, N.J., Inman, R.M., Gude, J.A., Bassing, S.B., Loonam, K.E., Mitchell, M.S., 2022b. Integrating basic and applied research to estimate carnivore abundance. Ecol. Appl. 32. https://doi.org/10.1002/eap.2714.

Silva, P., López-Bao, J.V., Llaneza, L., Álvares, F., Lopes, S., Blanco, J.C., Cortés, Y., García, E., Palacios, V., Rio-Maior, H., Ferrand, N., Godinho, R., 2018. Cryptic population structure reveals low dispersal in Iberian wolves. Sci. Rep. 8, 14108. https://doi.org/10.1038/s41598-018-32369-3.

Stahler, D.R., MacNulty, D.R., Wayne, R.K., VonHoldt, B., Smith, D.W., 2013. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. J. Anim. Ecol. 82, 222–234. https://doi.org/10.1111/j.1365-2656.2012.02039.x.

Stenglein, J.L., Waits, L.P., Ausband, D.E., Zager, P., Mack, C.M., 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. J. Mammal. 92, 784–795. https://doi.org/10.1644/10-MAMM-A-200.1.

Torres, R.T., Silva, N., Brotas, G., Fonseca, C., 2015. To Eat or Not To Eat? The Diet of the Endangered Iberian Wolf (*Canis lupus signatus*) in a Human- Dominated Landscape in Central Portugal. PLoS One 10, e0129379. https://doi.org/10.1371/journal.pone.0129379.

Treves, A., Langenberg, J.A., López-Bao, J.V., Rabenhorst, M.F., 2017. Gray wolf mortality patterns in Wisconsin from 1979 to 2012. J. Mammal. 98, 17–32. https://doi.org/10.1093/jmammal/gyw145.

Treves, A., Santiago-Ávila, F.J., Putrevu, K., 2021. Quantifying the effects of delisting wolves after the first state began lethal management. PeerJ 9, e11666. https://doi.org/10.7717/peerj.11666.

USFWS, 2023. U.S. Fish and Wildlife Service - Species status assessment for the gray wolf (*Canis lupus*) in the Western United States.

Webb, N.F., Allen, J.R., Merrill, E.H., 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Can. J. Zool. 89, 744–752. https://doi.org/10.1139/z11-043.