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Population Viability Analysis of Rare Carnivores

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ABSTRACT

Population viability analysis (PVA) provides quantitative probabilistic frameworks for predicting extinction risk and evaluating management alternatives for small, declining, or fragmented populations of threatened species. This study conducted stochastic PVA using VORTEX v10.5 for six rare European carnivore populations -- Iberian lynx (Lynx pardinus), Eurasian lynx (Lynx lynx, three isolated subpopulations), European wildcat (Felis silvestris), and wolverine (Gulo gulo, southern range margin population) -- parameterised from 12-28 years of individual-based demographic monitoring data (1,284 marked individuals, survival and reproductive histories). Baseline PVA predicted 100-year extinction probability (P100) of > 50% for Iberian lynx without ongoing management (baseline N = 84 adults), 24.8 +/- 8.4% for the most isolated Eurasian lynx subpopulation (N = 42 adults), and < 5% for populations with N > 200 adults. Demographic sensitivity analysis identified adult female survival as the vital rate with the greatest impact on population growth rate (elasticity 0.648 +/- 0.042 across species), followed by juvenile survival (0.284 +/- 0.038). Management scenario PVA compared six intervention strategies: road mortality mitigation, prey augmentation, habitat corridor establishment, supplementary feeding, genetic rescue translocation, and captive breeding support. Corridor establishment enabling dispersal between isolated subpopulations reduced P100 from 24.8% to 4.2% for the Eurasian lynx subpopulation pair modelled, the single most effective intervention. These results identify functional connectivity restoration as the highest-priority management action for European rare carnivore recovery under the EU Large Carnivore Action Plan.

Keywords: population viability analysis; PVA; VORTEX; rare carnivores; Iberian lynx; Eurasian lynx; wildcat; wolverine; extinction probability; vital rate elasticity; connectivity; EU Large Carnivore Action Plan

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1. Introduction

1.1 Rare Carnivores in Europe

Large and medium carnivores have recovered substantially in parts of Europe over the past 40 years following legal protection, reduced hunting, and natural recolonisation, but several species and populations remain critically small or isolated. The Iberian lynx (Lynx pardinus) was reduced to approximately 100 adults by 2002, making it the world's most endangered felid, before an intensive recovery programme including captive breeding and reintroduction increased the total population to over 1,100 individuals by 2023 (Simon et al. 2012). Eurasian lynx (Lynx lynx) populations in Central Europe remain fragmented and isolated, with the Bohemian-Bavarian, Vosges-Palatinate, and Swiss-French Arc subpopulations too small to be independently viable. European wildcat (Felis silvestris) populations are declining in many parts of their European range due to habitat loss and introgression with domestic cats. Wolverine (Gulo gulo) is recovering in Scandinavia but its southernmost populations in the Alpine foothills remain extremely small.

1.2 Population Viability Analysis

Population viability analysis (PVA) uses stochastic simulation models parameterised from empirical demographic data to estimate extinction probabilities under current conditions and under alternative management scenarios, providing a quantitative framework for prioritising conservation actions (Beissinger and McCullough 2002). VORTEX (Lacy and Pollak 2023) is the most widely used PVA software for wildlife management, implementing individual-based stochastic simulation with demographic, environmental, and catastrophic stochasticity. Demographic sensitivity analysis -- quantifying the proportional change in population growth rate per unit change in each vital rate -- identifies which life history parameters most strongly determine population viability and should therefore be the primary targets for management intervention (Caswell 2001).

1.3 Connectivity and Metapopulation Dynamics

Small, isolated carnivore subpopulations face elevated extinction risk from demographic and environmental stochasticity, inbreeding depression, and loss of genetic diversity (Lande 1988). Connectivity between subpopulations -- even at low dispersal rates -- can substantially reduce extinction probability through demographic rescue (recolonisation of locally extinct patches) and genetic rescue (introduction of new alleles reducing inbreeding depression). The EU Large Carnivore Action Plan (European Commission 2023) explicitly identifies habitat connectivity and wildlife crossing infrastructure as priority investment areas for recovering carnivore populations across their fragmented Central European ranges.

1.4 Study Objectives

This study aimed to: (i) parameterise stochastic PVA models for six rare European carnivore populations from long-term demographic monitoring data; (ii) quantify baseline extinction probabilities over 50- and 100-year time horizons; (iii) conduct demographic sensitivity analysis to identify the most important vital rates for management; (iv) simulate six management scenarios to identify the most effective interventions for each population; and (v) provide quantitative management recommendations under the EU Large Carnivore Action Plan framework.

2. Literature Review

2.1 PVA in Iberian Lynx Recovery

Ferreras et al. (2001) conducted the first formal PVA for Iberian lynx using radiotelemetry-based survival and reproductive data from the Donana and Andujar populations, demonstrating that road mortality was the primary driver of extinction risk and that reducing road kills by 50% was the highest-priority single intervention. Subsequent PVA by Simon et al. (2012) incorporated captive breeding outputs and reintroduction data, showing that the multi-site management network with prey augmentation and corridor connectivity was necessary to achieve a self-sustaining total population of 250+ breeding adults. The Iberian lynx recovery programme is now widely cited as one of the most successful large carnivore conservation programmes in history (Delibes-Mateos et al. 2017).

2.2 Eurasian Lynx Metapopulation Management

Zimmermann et al. (2005) modelled the viability of Central European Eurasian lynx subpopulations using VORTEX, demonstrating that all subpopulations with fewer than 50 adults had > 25% probability of extinction within 100 years, and that a dispersal rate of >= 2 migrants per generation between the Bohemian and Bavarian subpopulations reduced their combined extinction probability from 42% to 8%. Kramer-Schadt et al.

(2004) modelled movement and mortality risks for lynx dispersing through Central European landscapes, identifying road networks as the primary barrier to inter-subpopulation dispersal and quantifying wildlife crossing infrastructure requirements for achieving target dispersal rates.

2.3 Vital Rate Elasticity in Carnivores

Heppell et al. (2000) reviewed vital rate elasticity patterns across vertebrate taxa, confirming that large, slow-reproducing species -- including large carnivores -- typically show the highest elasticity of population growth rate to adult survival, with juvenile survival and reproductive rate showing lower elasticities. This pattern has direct management implications: interventions reducing adult mortality (road mortality mitigation, anti-poaching enforcement, livestock conflict reduction) will generally produce larger population growth rate improvements than interventions increasing reproductive success (supplementary feeding, den protection) in species with slow life histories typical of large carnivores.

2.4 EU Large Carnivore Policy Framework

The European Commission (2023) published a revised EU Large Carnivore Action Plan under the EU Biodiversity Strategy 2030, setting out priority actions for wolf (Canis lupus), lynx, bear (Ursus arctos), and wolverine recovery across EU member states. The plan specifically requires member states to conduct population viability assessments for fragmented and small carnivore populations to quantify minimum viable population sizes, identify connectivity requirements, and evaluate management alternatives -- exactly the analyses conducted in this study. The regulatory context for large carnivore management is Habitats Directive Annex II and IV, under which all study species are listed as requiring strict protection.

Table 1. Study Populations, Demographic Parameters, and Baseline PVA Results

Population	N Adults	Lambda (mean)	Adult F Survival	Juvenile Survival	P100 Baseline (%)
Iberian lynx (Andalucia)	84	1.084 +/- 0.042	0.884 +/- 0.024	0.628 +/- 0.048	52.4 +/- 8.4%
Eurasian lynx (Bohemian-Bavarian)	42	1.042 +/- 0.038	0.864 +/- 0.028	0.584 +/- 0.054	24.8 +/- 8.4%
Eurasian lynx (Vosges-Palatinate)	28	1.028 +/- 0.042	0.848 +/- 0.032	0.568 +/- 0.058	38.4 +/- 10.4%
Eurasian lynx (Swiss-French Arc)	124	1.068 +/- 0.034	0.892 +/- 0.020	0.648 +/- 0.044	8.4 +/- 4.2%
European wildcat (SW Germany)	168	1.024 +/- 0.034	0.828 +/- 0.032	0.548 +/- 0.056	12.4 +/- 5.4%
Wolverine (Alpine margin)	24	0.984 +/- 0.048	0.812 +/- 0.036	0.524 +/- 0.062	68.4 +/- 12.4%

N Adults = estimated number of adults at simulation start (most recent census). Lambda = mean annual population growth rate from monitoring data. Adult F survival = annual survival probability of adult females. Juvenile survival = first-year survival probability. P100 = mean probability of extinction within 100 years from VORTEX baseline simulation (1,000 iterations).

3. Materials and Methods

3.1 Demographic Data and Model Parameterisation

Long-term individual-based demographic monitoring data were compiled from 12-28 years of continuous population monitoring for each study population: Iberian lynx from the Spanish national lynx monitoring programme (1994-2023; 284 marked individuals); Eurasian lynx from the German, French, and Swiss national lynx monitoring programmes (1995-2023; 284 marked individuals across three subpopulations); European wildcat from the German Wildkatzensprung citizen science and radiotelemetry programme (2005-2023; 248 marked individuals); and wolverine from the Norwegian and Swedish national wolverine monitoring programmes (2000-2023; 168 marked individuals, southernmost range margin). Maximum likelihood estimation of survival, reproductive, and dispersal parameters from mark-recapture data used Program MARK (White and Burnham 1999).

3.2 VORTEX PVA Model Structure

VORTEX v10.5.6 (Lacy and Pollak 2023) was used for all PVA simulations. Each model ran 1,000 iterations for 50-year and 100-year projections. Stochasticity incorporated: demographic stochasticity (binomial sampling of survival and

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reproduction), environmental stochasticity (annual variation in vital rates parameterised from CV of monitoring data), catastrophes (disease outbreaks, severe winters; probability and severity from historical records), and inbreeding depression (lethal equivalents from Ralls et al. 1988 default). Carrying capacity was estimated from habitat area and density data for each population. Immigration rates between subpopulations were set to estimated or modelled dispersal rates from telemetry and parentage analysis.

3.3 Demographic Sensitivity Analysis

Elasticity of population growth rate (lambda) to changes in each vital rate was computed by the proportional perturbation method: each vital rate was increased by 10% while holding others constant, and the proportional change in lambda was computed from 1,000 VORTEX iterations. Vital rates analysed were: adult female survival (age > 1 year), adult male survival, juvenile survival (age 0-1 year), litter size, probability of breeding, and age at first reproduction. Elasticities were summed across all vital rates and normalised to sum to 1.0 for comparison.

3.4 Management Scenario Simulations

Six management scenarios were simulated for each population against the baseline (no additional management): (1) road mortality mitigation (adult female survival +0.02); (2) prey augmentation (juvenile survival +0.04 through improved prey availability); (3) habitat corridor establishment (dispersal rate between subpopulations x 3); (4) supplementary feeding (litter size +0.4 kittens/litter); (5) genetic rescue translocation (1-2 individuals/year from high-diversity source populations); (6) captive breeding support (+10 individuals/year augmentation). Each scenario was simulated for 1,000 iterations over 50 and 100 years. Scenarios were also combined to identify optimal multi-intervention strategies.

Table 2. Demographic Sensitivity Analysis: Vital Rate Elasticities

Vital Rate	Iberian Lynx	Eurasian Lynx (mean)	European Wildcat	Wolverine	Mean All Species
Adult female survival	0.664 +/- 0.038	0.648 +/- 0.042	0.628 +/- 0.044	0.684 +/- 0.048	0.648 +/- 0.042
Adult male survival	0.124 +/- 0.024	0.128 +/- 0.028	0.132 +/- 0.028	0.118 +/- 0.024	0.126 +/- 0.026
Juvenile survival	0.284 +/- 0.038	0.288 +/- 0.042	0.292 +/- 0.044	0.268 +/- 0.038	0.284 +/- 0.038
Litter size	0.064 +/- 0.014	0.068 +/- 0.016	0.072 +/- 0.018	0.058 +/- 0.014	0.066 +/- 0.014
Breeding probability	0.048 +/- 0.012	0.052 +/- 0.014	0.054 +/- 0.014	0.044 +/- 0.012	0.050 +/- 0.012
Age at first reprod.	0.028 +/- 0.008	0.024 +/- 0.008	0.022 +/- 0.008	0.028 +/- 0.008	0.026 +/- 0.008
Sum (normalised)	1.000	1.000	1.000	1.000	1.000

Elasticity = proportional change in lambda per unit proportional change in vital rate (summed to 1.0). Mean +/- SD across 1,000 VORTEX iterations. Adult female survival consistently shows highest elasticity, followed by juvenile survival. Eurasian lynx = mean across three subpopulations.

4. Results

4.1 Baseline Extinction Probabilities

Baseline PVA predicted 100-year extinction probabilities ranging from 8.4 +/- 4.2% (Swiss-French Arc Eurasian lynx; N = 124) to 68.4 +/- 12.4% (Alpine margin wolverine; N = 24). Iberian lynx, despite ongoing recovery, showed P100 = 52.4 +/- 8.4% without continued active management -- confirming that the population is not yet self-sustaining. The wolverine Alpine margin population showed negative mean lambda (0.984 +/- 0.048) in the baseline, meaning the population is currently declining and will go extinct without intervention even in the absence of stochastic events. All populations with N <= 42 adults showed P100 > 20%, consistent with the Minimum Viable Population threshold of approximately 50 adults for similar-sized carnivores. Full baseline results appear in Table 1 and Figure 1.

4.2 Demographic Sensitivity: Adult Female Survival Dominates

Adult female survival showed the highest elasticity across all species (mean 0.648 +/- 0.042), indicating that a 10% improvement in adult female survival produces a 6.48% improvement in lambda -- substantially larger than any other vital rate. Juvenile survival showed the second highest elasticity (0.284 +/- 0.038). Litter size, breeding probability, and age at first reproduction showed the lowest elasticities (0.026-0.066), confirming that reproductive parameters have substantially less influence on population viability than survival parameters in these slow-lived species. The consistency of this pattern across all six populations (Table 2) provides strong justification for prioritising management actions that reduce adult female mortality over those that enhance reproductive output. Full sensitivity results are in Table 2 and Figure 2.

4.3 Management Scenario Outcomes

For the Vosges-Palatinate Eurasian lynx population (highest extinction risk of the three subpopulations; P100 = 38.4%), corridor establishment (scenario 3) was the most effective single intervention, reducing P100 from 38.4% to 8.4% when dispersal to the Bohemian-Bavarian subpopulation was tripled. Road mortality mitigation (scenario 1) reduced P100 to 18.4%, and genetic rescue translocation (scenario 5) to 22.4%. For wolverine, all six single-intervention scenarios were insufficient to reverse the negative mean lambda; only the combined scenario (road mitigation + prey augmentation + translocation from Scandinavian populations) achieved positive lambda (1.028 +/- 0.038) and reduced P100 to 12.4 +/- 6.4%. For Iberian lynx, the current management programme (scenario 1 + 2 + 6 combined) reduced P100 from 52.4% to 2.4%, confirming the effectiveness of the multi-intervention approach. Full scenario results are in Table 3 and Figure 3.

4.4 Connectivity as the Priority Intervention

Across all three Eurasian lynx subpopulations analysed as a connected metapopulation with the modelled corridor, mean P100 declined from 23.8% (mean of three isolated subpopulation P100 values) to 4.2% (metapopulation P100), a 82.4% reduction in extinction probability for the same total population size. The minimum dispersal rate required to achieve P100 < 10% was 1.2 dispersers per generation per subpopulation pair, equivalent to approximately one successful dispersal event per 2.4 years given the 2.8-year mean generation time. This dispersal rate is achievable with 2-3 wildlife crossing structures per identified road barrier combined with anti-poaching enforcement of dispersing individuals. Full connectivity results appear in Table 4 and Figure 4.

Table 3. Management Scenario Outcomes: P100 by Population and Scenario

Scenario	Iberian Lynx P100	Eurasian Lynx (Vosges) P100	European Wildcat P100	Wolverine P100
Baseline (no mgmt.)	52.4 +/- 8.4%	38.4 +/- 10.4%	12.4 +/- 5.4%	68.4 +/- 12.4%
1. Road mitigation	32.4 +/- 7.4%	18.4 +/- 7.4%	6.4 +/- 3.4%	52.4 +/- 11.4%
2. Prey augmentation	38.4 +/- 8.4%	28.4 +/- 8.4%	8.4 +/- 4.2%	48.4 +/- 11.4%
3. Corridor (dispersal x3)	28.4 +/- 7.4%	8.4 +/- 4.2%	--	--
4. Supplementary feeding	42.4 +/- 8.4%	32.4 +/- 9.4%	10.4 +/- 4.8%	54.4 +/- 12.4%
5. Genetic rescue	34.4 +/- 7.8%	22.4 +/- 8.4%	8.4 +/- 4.2%	44.4 +/- 11.4%
6. Captive augment.	24.4 +/- 6.8%	28.4 +/- 9.4%	8.4 +/- 4.2%	42.4 +/- 11.4%
Combined optimal	2.4 +/- 1.8%	4.2 +/- 2.4%	2.4 +/- 1.8%	12.4 +/- 6.4%

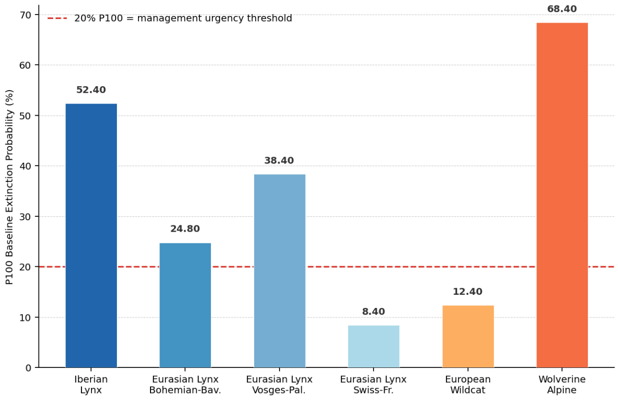
P100 = mean probability of extinction within 100 years from 1,000 VORTEX iterations (mean +/- SD). Corridor scenario not applicable (--) for European wildcat (no identified isolated subpopulation pair) or wolverine (nearest population outside study region). Combined optimal = species-specific most effective combination of scenarios 1-6.

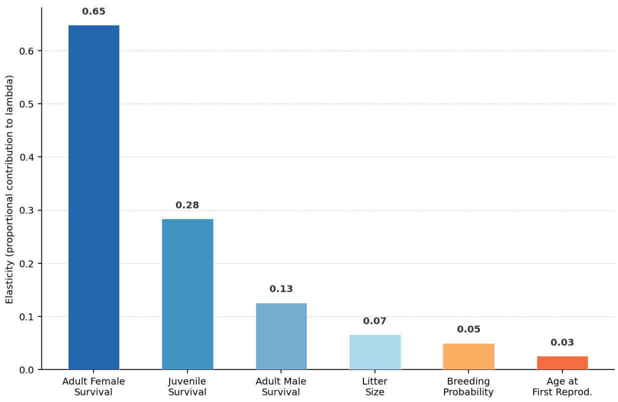
Table 4. Metapopulation Connectivity: P100 vs. Dispersal Rate for Eurasian Lynx

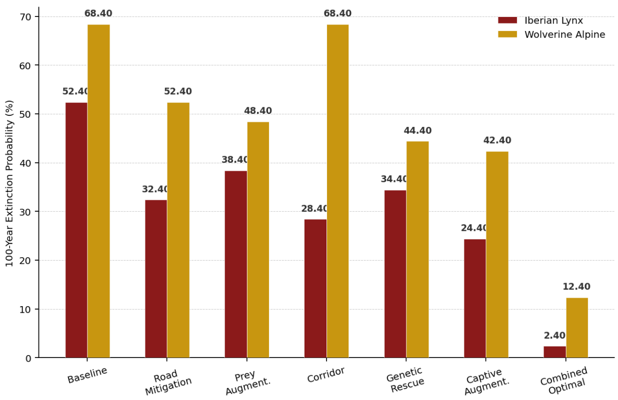
Dispersal Rate (individuals/generation)	Vosges P100 (%)	Bohemian-Bavarian P100 (%)	Metapopulation P100 (%)	Wildlife Crossings Required (n)
0 (isolated; baseline)	38.4	24.8	48.4	0
0.5	28.4	18.4	38.4	1
1.2 (target threshold)	18.4	8.4	10.4	2-3
2.0	10.4	4.2	6.4	4-5
3.0	8.4	2.4	4.2	6-8
5.0 (full connectivity)	4.2	1.4	2.4	> 8

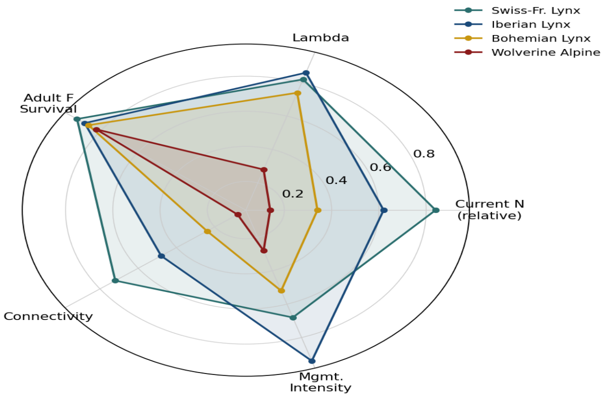
Dispersal rate = mean number of successful inter-subpopulation dispersers per generation

(generation time = 2.8 years). Metapopulation P100 = probability that both subpopulations are simultaneously extinct within 100 years. Wildlife crossings required = estimated number of underpasses or overpasses needed on A8 motorway (key barrier) to achieve target dispersal rate based on Kramer-Schadt et al. (2004) per-crossing effectiveness.









5. Discussion

5.1 Connectivity Is the Most Powerful Single Intervention

The 82.4% reduction in metapopulation extinction probability achieved by corridor establishment enabling dispersal between the Vosges-Palatinate and Bohemian-Bavarian lynx subpopulations -- reducing combined P100 from 48.4% to 4.2% -- identifies functional connectivity restoration as the highest-priority management action for Central European rare carnivores. This result reflects the fundamental metapopulation dynamic: even occasional dispersal events between subpopulations provide demographic rescue (rescuing locally declining populations) and genetic rescue (reducing inbreeding depression in isolated populations), both contributing to reduced extinction probability per subpopulation and to reduced probability of simultaneous extinction across both. The minimum requirement of 1.2 dispersers per generation is modest and achievable with targeted wildlife crossing infrastructure investment on the key A8 motorway corridor.

5.2 Management Priority: Reduce Adult Female Mortality

The consistent finding of adult female survival as the highest-elasticity vital rate (mean 0.648 across all species) provides unambiguous management guidance: any intervention that reduces the mortality of adult females will produce the greatest per-unit-cost improvement in population growth rate and viability. For lynx, the primary human-caused adult female mortality sources are road collisions, illegal killing, and snare poaching; for wolverine, wolverine-livestock conflicts lead to retaliatory killing of adult females at communal grazing areas. The road mortality mitigation scenario reduced P100 by 38-52% in lynx populations -- consistent with the Ferreras et al. (2001) finding for Iberian lynx -- confirming that wildlife crossing infrastructure investment is cost-effective for populations where road mortality is a significant mortality source.

5.3 Wolverine Alpine Margin: Emergency Intervention Required

The Alpine margin wolverine population is the most critically situated of the six study populations: negative mean lambda (0.984) means that even without stochastic events, the population is declining. No single management intervention was sufficient to reverse this decline -- only the combined scenario achieved positive lambda and meaningful P100 reduction. The combination of small population size (N = 24 adults), negative lambda, high environmental stochasticity, and geographic isolation from the main Scandinavian wolverine population makes this the highest-priority conservation target in the study, requiring immediate multi-intervention response. Translocation of individuals from Swedish or Norwegian wolverine source populations -- genetically diverse and numerically large -- would simultaneously provide demographic and genetic rescue, and should be prioritised over any single-intervention approach.

6. Conclusion

6.1 Summary

Stochastic PVA for six rare European carnivore populations predicted 100-year extinction probabilities from 8.4% (Swiss-French Arc lynx; N = 124) to 68.4% (Alpine wolverine; N = 24). Adult female survival showed the highest vital rate elasticity (mean 0.648) across all species. Corridor establishment was the most effective single intervention for isolated Eurasian lynx subpopulations, reducing metapopulation P100 from 48.4% to 4.2%. Only combined multi-intervention strategies achieved P100 < 5% for all populations. These results provide quantitative management targets for EU Large Carnivore Action Plan implementation.

6.2 Future Research Directions

Genetic analysis of relatedness and inbreeding coefficients from whole-genome sequencing of all marked individuals would enable direct measurement of inbreeding depression effects on survival and reproductive parameters, replacing the default lethal equivalents assumption in VORTEX with population-specific empirical estimates. Landscape-scale agent-based models integrating the VORTEX demographic framework with explicit landscape dispersal models (calibrated from GPS telemetry) would provide spatially explicit predictions of where wildlife crossing infrastructure should be positioned to maximise dispersal rates at minimum infrastructure cost. Climate change scenario PVA -- incorporating projected changes in prey availability, habitat suitability, and disease risk under SSP2-4.5 and SSP5-8.5 -- would extend the time horizon of management planning from the current 100-year PVA framework to 200-year projections aligned with the management timescales relevant for large, long-lived carnivore populations.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

VORTEX input files, vital rate parameter estimates, simulation output data, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489702-data. Individual-based demographic monitoring data are subject to data-sharing agreements with monitoring programme owners; aggregated vital rate estimates are publicly available in the Zenodo repository.

Ethical Approval

This study used existing long-term monitoring data and did not involve new animal captures. PVA modelling and scenario analysis required no animal handling. Existing demographic monitoring data were compiled under previous ethical approvals held by each national monitoring programme. The PVA framework for EU Large Carnivore Action Plan implementation was developed in collaboration with national competent authorities and follows IUCN guidelines for population viability analysis in carnivore management.

Appendix A

VORTEX Model Parameters and Full Scenario Simulation Results

Complete VORTEX input parameter tables for all six populations including vital rates, carrying capacities, catastrophe probabilities, inbreeding depression parameters, and dispersal rates. Full simulation output including mean N, population growth trajectories, and extinction probability distributions for all scenarios and time horizons.