A population viability analysis (PVA) for White-Tailed Eagle (*Haliaeetus albicilla*) reintroduction in Cumbria: an evaluation of release strategies and the impacts of population loss factors

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Contents

List of Tables/Figures

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White-Tailed Eagles (WTEs; *Haliaeetus albicilla*) have been extinct in the UK and Ireland for over 100 years, following intense raptor persecution. Conservation efforts since the 1970s have focused on reintroduction of the species, with populations re-established in Scotland, Ireland and the Isle of Wight. Cumbria has been identified as a possible location for further WTE reintroductions, with strong potential for ecosystem and economic benefits. Successful reintroductions rely on a viable breeding population becoming established. This study used the population viability analysis (PVA) software VORTEX, to estimate the long-term population dynamics and viability of a reintroduced population of WTEs in Cumbria over 100 years. Models examined population trajectories following different scenarios of reintroduction through supplementation, and assessed the impacts of factors causing additional population loss through dispersal, collisions with wind turbines and power lines, persecution and disease. Persecution has the most severe, negative impact on the viability of a reintroduced population of WTEs, with extinction probabilities >20% under all levels of persecution. This highlights the importance of building collaborative relationships with farmers and landowners throughout all phases of the project. When population loss factors are occurring together, the population is increasingly threatened with extinction. Reintroducing a population of 56 birds over five years has potential to be viable when modelled alongside low levels of combined population loss, with a final population size of 110 individuals and an extinction probability of 13.9% after 100 years. Prior to implementing this release strategy, further modelling should be carried out to determine the increase on 56 individuals required to improve confidence in population viability, reducing extinction probability below 10%. Implementing a second phase of releases may also improve population viability in Cumbria and should therefore be considered in project management.

1. Introduction

Biodiversity loss in the UK is significantly higher than global averages according to the UK's State of Nature Report (Hayhow et al. 2019). Over centuries, the UK has lost a number of charismatic and ecologically important species, including the wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), beaver (*Castor fiber*) and White-Tailed Eagle (*Haliaeetus albicilla*), all driven to extinction primarily by persecution (Arts et al. 2012). With many of these lost species being ecological keystones, having a disproportionately large effect within ecosystems, their loss has altered the balance of ecosystems across the UK indefinitely (Hale & Koprowski 2018).

Recognising the ecological importance of these lost species, conservation leaders within the UK and Ireland are using reintroduction as a management tool for recovering species to their former range (Seddon et al. 2007; Evans et al. 2009; O'Rourke 2014). A key element of rewilding (the large-scale restoration of nature until it can take care of itself (Rewilding Britain 2023)), reintroduction plays a vital role in enhancing biodiversity and restoring ecosystems on a wider scale (O'Rourke 2014). Successful reintroduction projects have taken place across the UK and Ireland, involving a range of species, from beavers to White-Tailed Eagles (WTEs).

WTEs were once widespread throughout the UK and Ireland, with an estimated 800-1400 pairs 1500 years ago (Mee et al. 2016). By 1918 they had become extinct across the UK and Ireland, following years of intense raptor persecution (Evans et al. 2009; Mayhew et al. 2016), brought about by the advent of the loading shotgun, the use of poisons, and nest/egg destruction, with the aim of eliminating predators from the landscape (Mee et al. 2016). Since the 1970s, successful reintroduction projects have seen populations re-established in Scotland (Green et al. 1996; Arts et al. 2012; Sansom et al. 2016), Ireland (O'Rourke 2014; Mee et al. 2016), and the Isle of Wight (Dennis et al. 2019). The first WTE reintroduction program was established in Scotland by the Nature Conservancy Council (now NatureScot) in 1975, with 225 birds being released between 1975 and 2012, over three phases (Sansom et al. 2016). In Scotland, there are currently around 150 breeding pairs (RSPB 2023). Reintroductions began in Ireland in 2007, with the release of 100 birds until 2011 (Mee et al. 2016).

WTEs show a strong preference for particular foraging and nesting habitats, selecting nest sites generally <4km from water (coastal or freshwater), near woodlands, and in flatter, lowland areas (Radovic & Mikuska 2009; Sansom et al. 2016; Carver et al. 2022). The majority of foraging takes place within a 5-10km radius from the nest site, and being opportunistic hunters and scavengers, WTEs will exploit seasonally abundant food sources (Carver et al. 2022). Fish, waterbirds and small-medium sized mammals make up the majority of their diet (Sandor et al. 2015; Carver et al. 2022), with the proportions of each varying seasonally and spatially across the landscape (Ekblad et al. 2016; Dennis et al. 2019). WTE mean natal dispersal distances (distance between natal (or release) site and first breeding site) are 42km for males and 59km for females (Whitfield et al. 2009), and maximum juvenile dispersal distance (distance travelled by juveniles from natal (or release) site before choosing a nesting site) ranges between 18-200km (Whitfield et al. 2009b).

Recent efforts have focused on identifying further locations to support the re-establishment of WTEs across their former range in the UK and Ireland, expanding the national metapopulation and facilitating dispersal and geneflow between sub-populations (Carver et al. 2022). One such location identified for reintroduction is Cumbria; a large (6,768km^2) and sparsely populated county (Mayhew et al. 2016), with ample suitable habitat for WTEs both inland and along the coastline (Carver et al. 2022). Despite occasional sightings of young WTEs in Cumbria, natural re-colonisation of the species to the county would take many years, due to the species delayed sexual maturity, limited dispersal potential and natal philopatric tendencies (Whitfield et al. 2009; Mayhew et al. 2016; Carver et al. 2022). Public perceptions of WTE reintroduction are generally positive in Cumbria, with over 80% of respondents in one study being in favour of the project (Mayhew et al. 2016). Furthermore, such reintroduction aligns with the requirement and moral duty of the UK government to enhance biodiversity and restore native species to the landscape, supported by legislation and policy: Habitats and Species Directive (Council Directive 92/43 EEC 1992), and the Bern Convention (Council Directive 82/72/EEC 1979; Williams 2021).

As an apex predator, WTEs have the potential to impact the entire ecosystem in Cumbria, creating top-down effects on species at lower trophic levels (Lyly et al. 2015; Hale & Koprowski 2018). Ecosystem benefits could include the regulation of species such as Greylag Geese (*Anser anser*), Canada Geese (*Branta canadensis*) and Coot (*Fulica atra*), whose high populations may have a detrimental effect on ecosystems through interspecific competition for food and nesting habitat with less dominant species (Dennis et al. 2019). Benefits may also arise through nature-based tourism boosting the local economy (Mayhew et al. 2016).

Given the resources and financial investments required, the success of reintroduction projects is crucial. At the population level, successful reintroductions rely on a viable population becoming established, characterised by positive growth rates, low extinction probabilities and a strong level of genetic diversity (Slotta-Bachmayr et al. 2004; Bach et al. 2010). This highlights the requirement for a thorough understanding of the population dynamics of a reintroduced population, prior to releasing individuals into a landscape. Population viability analysis (PVA) is a quantitative approach to studying population dynamics, used by the IUCN Conservation Planning Specialist Group (IUCN, CPSG 2023) to predict the likely future status of a population and assess the factors threatening viability, by incorporating data on life history parameters such as survival and fecundity rates (Lindenmayer et al. 1995; Lacy 2019; Chaudry & Oli 2020).

IUCN guidelines for reintroduction suggest factors that caused initial species extinction should not remain a threat within habitats where a new population will be released (IUCN/SSC 2013). Across Cumbria, man-made factors with the potential to cause additional mortality in WTEs are present, and realistic threats to the species must be accounted for. Large scale wind farms and energy facilities pose a threat through lethal collisions with turbine blades and power lines (Dahl et al. 2012; Heuck et al. 2019), there remain occasional reports of raptor persecution (Whitfield et al. 2004; Isomursu et al. 2018; RSPB 2022), and there is an increasing threat of avian flu across the UK (Krone et al. 2018; Lean et al. 2022). As the human population rises, these additional mortality factors are unlikely to be eradicated. Humans living in closer proximity to wildlife may potentially increase human-wildlife conflict (Whitfield et al. 2004), and an increased shift towards renewable energy sources may lead to the construction of more wind farms (Balotari-Chiebao et al. 2016). It is therefore important to evaluate the impacts of different severities of these factors on the viability of a reintroduced population in Cumbria, and examine which reintroduction release strategy is required to ensure a population is robust against the impacts of such factors (Sansom et al. 2016). The impacts of dispersal of birds out of Cumbria will also be considered.

The aim of this study was therefore to carry out a PVA for a proposed reintroduced population of WTEs in Cumbria, using the stochastic population simulation software VORTEX (Lacy 1993; Bach et al. 2010; Lacy 2019). PVA modelling was based on surrogate vital rate data, derived from WTE populations living in similar landscapes across Scotland, Ireland and mainland Europe (Evans et al. 2009; Radovic & Mikuska 2009b; Mee et al. 2016; Sansom et al. 2016). Such modelling will give insight into the likely trajectories of a WTE population in Cumbria following reintroduction, estimating population size, growth rates, probabilities of extinction and genetic diversity into the future (Lindenmayer et al. 1995; Evans et al. 2009; Chaudry & Oli 2020). Contributing to pre-feasibility studies of WTE reintroduction in Cumbria, modelling of various scenarios of release through supplementation, carrying capacity, dispersal and additional mortality through collisions, persecution and disease, will allow project managers to make informed decisions regarding release and mitigation strategies.

Specifically, this study aims to answer the following questions:

1. What is the likely trajectory of a population of reintroduced WTEs under different release strategy scenarios, with no additional mortality?
2. What are the impacts of additional mortality, caused by collisions with wind turbines/power lines, persecution and disease outbreaks, on WTE population growth rates and size, probabilities of extinction and genetic diversity?
3. What is the impact of dispersal of birds out of Cumbria on the viability of a reintroduced population?
4. What level of reintroduction through supplementation is required to ensure population viability is robust against combined factors causing population loss?
5. What must a post-release monitoring/management strategy include to ensure long term population viability?

2. Methods

This study used the population viability analysis (PVA) software VORTEX (Version 10.6; Lacy 1993; Lacy & Pollak 2023) to model the population dynamics of a hypothetical reintroduced population of WTEs in Cumbria over 100 years. VORTEX models population demographics, incorporating deterministic and stochastic factors to estimate population growth rate and size, probability of extinction and genetic diversity into the future. This software was chosen as it is open access, has been extensively tested for use in PVA across a variety of species (Lindenmayer et al. 1995; Lacy 2019), and is commonly used to plan species reintroductions (Bustamante 1998; IUCN, CPSG 2023).

2.1 Baseline data collection

A thorough literature review was carried out to obtain baseline data on the parameters required to populate a PVA in VORTEX, with values confirmed by WTE project experts across the UK and Ireland. This included vital rate data on survival and recruitment rates in WTEs (Table 1), obtained from studies of other WTE populations across Scotland (Evans et al. 2009; Sansom et al. 2016), Ireland (Mee et al. 2016) and mainland Europe (Radovic & Mikuska 2009b; Kruger et al. 2010). Subsequently, the data used in this study are surrogate data, available following long-term monitoring in these locations. For this modelling, the definition of extinction is ‘one sex remains’ (Radovic & Mikuska 2009b), inbreeding depression was set as the default 6.29 (O’Grady et al. 2006), there is no effect of density dependent reproduction (Sansom et al. 2016), and all simulations were run with 1000 iterations (Slotta-Bachmayr et al. 2004; Evans et al. 2009; Lee et al. 2020).

Table 1. Summary of the VORTEX input parameters used to build a baseline PVA model for WTE reintroduction in Cumbria, with sources identified for each parameter assumption/estimate. EV: Environmental Variation.

Parameter	Assumption/Estimate	Source
Breeding system	Long-term monogamy	Evans et al. 2009; Radovic & Mikuska 2009b
Age at first reproduction	5 years	Evans et al. 2009; Radovic & Mikuska 2009b; Kruger et al. 2010
Maximum age of reproduction	30 years	Evans et al. 2009
Maximum lifespan	36 years	Kruger et al. 2010
Maximum number of broods per year	1	BTO 2023
Maximum number of young per brood	3	Mee et al. 2016; RSPB 2023
Sex ratio at birth (males:females)	50:50	Evans et al. 2009; Radovic & Mikuska 2009b
% Females breeding (±SD)	82 (12.26)	Radovic & Mikuska 2009b; Sansom et al. 2016
% Males in breeding pool (±SD)	82 (12.26)	Sansom et al. 2016
Fledglings per brood (±SD)	1.48 (0.28)	Evans et al. 2009; Sansom et al. 2016; Mee et al. 2016
Annual % natural mortality rates (±SE) for males and females	0-1 years – 26.4 (7.7) 1-2 years – 27.4 (9.1) 2-3 years – 21 (9.1) 3-4 years – 7.8 (5.8) 4-5 years – 5.8 (2.2) 5+ years – 5.8 (2.2)	Evans et al. 2009 (calculated from released survival rates)
Initial population size (sex ratio)	8 individuals (50:50)	Dennis et al. 2019
Carrying capacity (±SD due to EV)	214 (21) – K2	Sansom et al. 2016; Carver et al. 2022
Supplementation	Scenario S4	Dennis et al. 2019
Genetics	Default values	O'Grady et al. 2006; Lacy & Pollak 2023

General baseline parameters

WTEs display a long-term polygynous mating system (Evans et al. 2009; Radovic & Mikuska 2009b), with adult birds pairing for life and often returning to the same nest site each year (Whitfield et al. 2009). The maximum lifespan was set at 36 years (Kruger et al. 2010), and the default genetics model was used (Lacy et al. 2020). In the baseline model, carrying capacity (K) was set at 214 (±21) (see below; Sansom et al. 2016; Carver et al. 2022). To model anticipated first release of birds in Cumbria, the initial population size is eight individuals (age 0-1; 50:50 sex ratio). The baseline reintroduction (supplementation) scenario followed the guidance of WTE project experts (Dennis et al. 2019), and includes releasing 12 birds (age 0-1; 50:50 sex ratio) every year for four additional years, following the initial release of eight birds, totalling 56 birds. No dispersal was included in the baseline model.

Baseline reproduction parameters

WTEs reach sexual maturity at five years, and can breed up to the age of 30 (Evans et al. 2009). They have a maximum of one brood per year (BTO 2023), and lay a maximum of three eggs per brood (Mee et al. 2016), with a 50:50 sex ratio at birth (Evans et al. 2009; Radovic & Mikuska 2009b). These data are difficult to obtain accurately in the field, due to the sensitivities surrounding nest disturbance (BTO 2023). The percentage of males and females in the breeding pool was modelled as 82%$\pm$12.26 (Radovic & Mikuska 2009b; Sansom et al. 2016). The average number of fledglings per brood was modelled as 1.48$\pm$0.28, the median of published values in Evans et al. (2009), Mee et al. (2016) and Sansom et al. (2016).

Baseline mortality rates

Baseline mortality rates were obtained using survival rates across each age group for released populations in Evans et al. (2009), assumed to be the same for males and females. Such survival rates informed the calculation of mortality rates (Table 1) through 1-(survival rate). These background mortality rates will include natural mortality from disease and starvation, as well as undetected illegal killing and collisions (Sansom et al. 2016), allowing known additional mortality to be included in further models.

2.2 Calculating carrying capacity

Carrying capacity (K) describes the upper limit for the size of the simulated population within the given habitat, enabling VORTEX to recognize when the population has exceeded K, after which it implements probabilistic truncation across all ages to reduce the population size back below K (Lacy et al. 2020).

Carrying capacity estimates for Cumbria were calculated using habitat suitability maps produced for the pre-feasibility report, a report aimed at informing the next steps for a full feasibility study of WTE reintroduction in Cumbria (Carver et al. 2022). Within QGIS (QGIS 2022), habitat suitability maps were rescaled to 0-1 (low-high suitability). As per the methods in Sansom et al. (2016; Appendix 2), the areas (km^2) of suitable habitat at each of 19 suitability thresholds between 0 and 1 were calculated, and then multiplied by the breeding densities (pairs/km^2) at the corresponding habitat suitability level on the Isle of Mull, estimating the total number of pairs in each habitat threshold (Table 2). It is assumed that the density of WTEs in Cumbria could only increase to levels the same as or slightly higher than the current highest breeding density recorded in Scotland, on the Isle of Mull (Sansom et al. 2016).

Three estimations of carrying capacity were made (Bach et al. 2010), defining 'suitable habitat' under different thresholds. Sansom et al. (2016) define suitable habitat at the threshold of 0.5 in Scotland, whereas Carver et al. (2022) use a threshold of 0.7 in Cumbria, with carrying capacity estimations of 121 breeding pairs, and 78 breeding pairs respectively (Table 2). A third estimation was made using a combination of these thresholds, whereby habitats with a suitability score between 0.5 and 0.7 were deemed sub-optimal, applying a multiplier of 0.5 on K, and habitats with a score $\geq$0.7 were deemed optimal, applying a multiplier of one on K. This method provided a carrying capacity estimation of 107 breeding pairs (Table 2), used in the baseline model.

Table 2. Calculations of carrying capacity (K) estimates for Cumbria, based on habitat suitability modelling and WTE population densities (pairs/km^2) on the Isle of Mull. Total breeding pair estimates were multiplied by two to obtain carrying capacity of total individuals. Estimations of K ($\pm$SD) used in the modelling are shown in bold.

Variable	**Habitat suitability threshold**			
	$\geq$0.50	$\geq$0.70	0.5-0.7	0.5-0.7+
Area of suitable habitat (km^2) in Cumbria	3914	2043	1871	3914
Density on Isle of Mull (pairs/km^2)	0.031	0.038	0.031	-
Carrying capacity (total pairs)	121	78	29 (58/2)	107 (29+78)
Carrying capacity (total individuals $\pm$SD)	**242 (24)**	**156 (16)**	58	**214 (21)**

As the density of WTEs on the Isle of Mull was recorded as pairs/km^2, to obtain carrying capacity as number of individuals, breeding pair estimates were multiplied by two. Although this does not account for non-breeding individuals, it can be assumed that if the habitats are fully occupied by breeding adults, juveniles will be forced to disperse, or juvenile mortality will be high. Standard deviation of K was incorporated as 10% of K itself (Radovic & Mikuska 2009b).

2.3 Modelling scenarios of reintroduction (S)

Variations on the baseline figure of reintroducing 56 juvenile birds over a five year period (Whitfield et al. 2009b; Dennis et al. 2019), were modelled in VORTEX (Table 3). An initial reintroduction of eight individuals will ensure all translocation, husbandry, release and monitoring are effective prior to the subsequent releases (Dennis et al. 2019).

Release (supplementation) scenarios were varied by changing the number of individuals released, the timescale covering releases, and the interval between releases. All but one scenario modelled the release of first year birds (Mee et al. 2016), with this age being the most successful for reintroduction (Dennis et al. 2019). One scenario (S5) modelled the release of 3-4 year old birds, to test subsequent population level impacts. Scenarios releasing a total number of birds ranging from 24-116 individuals were modelled (Table 3). Scenarios were modelled in VORTEX as a sensitivity analysis, holding all parameters at baseline values (Table 1; Slottta-Bachmayr et al. 2004) and changing the release (supplementation) strategy in isolation, examining the impacts on growth rates (Stoch-r), probability of extinction (PE), final population size (N-all) and genetic diversity (GD).

Table 3. Summary of the supplementation (S), carrying capacity (K), dispersal (D), collision mortality (M), persecution (H) and disease (C) scenarios and their VORTEX input parameters, used in the sensitivity analysis. Supplementation scenarios follow initial release of eight birds.

Scenario		Description	Parameters
Reintroduction (Supplementation)	S1	24 birds total – 4 every year over 4 years	First year: 2 Last year: 5 Interval: 1 year
	S2	32 birds total – 6 every year over 4 years	First year: 2 Last year: 5 Interval: 1
	S3	48 birds total – 10 every year over 4 years	First year: 2 Last year: 5 Interval: 1
	S4 (BASELINE)	56 birds total – 12 every year over 4 years	First year: 2 Last year: 5 Interval: 1
	S5	56 birds total – 12 every year over 4 years (sub-adults released)	First year: 2 Last year: 5 Interval: 1 Age: 3-4
	S6	58 birds total – 10 every other year over 9 years	First year: 2 Last year: 10 Interval: 2
	S7	62 birds total – 6 every year over 9 years	First year: 2 Last year: 10 Interval: 1
	S8	68 birds total – 12 every other year over 9 years	First year: 2 Last year 10 Interval: 2
	S9	98 birds total – 10 every year over 9 years	First year: 2 Last year: 10 Interval: 1
	S10	116 birds total – 12 every year over 9 years	First year: 2 Last year: 10 Interval: 1
Carrying capacity (K+SD)	K1	156 individuals (16)	SD is +10% of K, due to environmental variation
	K2 (BASELINE)	214 individuals (21)	
	K3	242 individuals (24)	
Dispersal (D)	D1	1 bird disperses out	Youngest age: 1 Oldest age: 2 Both sexes disperse Survival of dispersers: 100%
	D2	2 birds disperse out	
	D3	3 birds disperse out	
Collisions with wind turbines/power lines (Mortality)	M1	0.5% additional mortality	Additional mortality across all age groups
	M2	1% additional mortality	
	M3	2% additional mortality	
	M4	5% additional mortality	
	M5	10% additional mortality	
Persecution (Harvest)	H1	1 individual killed	First year: 1 Last year: 100 Interval: 1 year Age group: random
	H2	2 individuals killed	
	H3	3 individuals killed	
Disease (Catastrophe)	C1	1% frequency	Severity: 50% reduction in reproduction and survival
	C2	3% frequency	

2.4 Modelling population loss

Following a review of scientific and grey literature to identity the main threats to and causes of WTE population loss, further scenarios were modelled in VORTEX (Table 3) with the aim of reflecting population loss (offtake) caused by dispersal, collisions with wind turbines and power lines, illegal persecution, and catastrophic disease outbreaks (Whitfield et al. 2009; Dahl et al. 2012; Isomursu et al. 2018; Fujimoto et al. 2022). These factors were quantified and made Cumbria-specific where possible. Each factor was modelled in VORTEX independently as a sensitivity analysis, holding all other parameters to baseline values (Table 1), to assess impacts on growth rates (Stoch-r), probability of extinction (PE), final population size (N-all) and genetic diversity (GD).

Dispersal out of Cumbria (D)

It is likely that the majority of released birds will remain within Cumbria, as most WTEs select breeding sites within ~50km of their release site (Whitfield et al. 2009). Despite this, juvenile birds can travel distances up to 200km (Whitfield et al. 2009b). The direct distance from Cumbria to the nearest established WTE populations in Fife and Tayside, Scotland, is ~200km, making it possible for wandering juveniles to reach other established populations, where they may potentially find a mate or nest site and fail to return to their release area (Whitfield et al. 2009b).

It is therefore important to model the population level impacts of dispersal of individuals out of Cumbria. With a lack of published information regarding dispersal rates of WTEs between sub-populations within the UK, this study models dispersal as a fixed number of individuals leaving the Cumbrian population each year, aligning with published estimates from Ireland. In Ireland, of the 100 birds released over the five year period, four males and two females dispersed to Scotland (Mee et al. 2016), averaging 1.2 birds each year of the project. Based on this figure, scenarios of a fixed number of 1, 2 and 3 birds dispersing out of Cumbria each year were modelled (Table 3). To account for the likely scenario of more birds dispersing out of the Cumbrian population as the total population size increases towards carrying capacity, in further modelling, dispersal was modelled as a percentage of the total population (1, 2 and 3%) leaving Cumbria each year, making population loss by dispersal proportional to the overall population size.

Collisions with wind turbines and power lines (M)

Across Europe, as the demand for renewable energy rises, lethal collisions of birds with wind turbines and power lines are becoming increasingly common (Dahl et al. 2012; Heuck et al. 2019). Large soaring raptors appear to be most vulnerable, with turbine related deaths potentially increasing mortality rates to concerning levels (Dahl et al. 2012; Balotari-Chiebao et al. 2015; Schippers et al. 2019).

In Finland, from 2000-2014, 21 birds were killed by power line electrocution or wind turbine blade collisions (Isomursu et al. 2018). In Ireland, from 2011-2014, four birds were killed by collisions (Mee et al. 2016). Collision risk modelling carried out by May et al. (2010) suggest that at the Smøla wind farm in Norway, an average of 7.8 WTEs are killed by collisions each year, equating to 0.11 WTEs per turbine per year. It is likely that the total number of lethal collisions will increase as the population size increases, and therefore, collision mortality was modelled as additional percentage increase in mortality rates (Sansom et al. 2016). Based on figures in Sansom et al. (2016) and Schippers et al. (2019), 0.5, 1, 2, 5 and 10% additional mortality was modelled (Table 3). With a lack of evidence of age and sex-biased collision rates, each increase in mortality was added on to the baseline mortality rates across each age group and sex (Sansom et al. 2016; Schippers et al. 2019).

Persecution (H)

Given that WTEs were persecuted to extinction in the past, it is important to measure the impacts of persistent illegal killing on WTE population viability in Cumbria (Whitfield et al. 2004; Mayhew et al. 2016). From 2007 to 2021, the RSPB reported an average of 2.13 raptors (of all species) being killed each year in Cumbria (RSPB 2022), and in Ireland, from 2007-2016, an average of 1.78 WTEs were shot or poisoned each year (Mee et al. 2016). Based on these figures, scenarios of a fixed number of 1, 2 and 3 birds being removed from the Cumbrian population each year by harvest were modelled in VORTEX, starting at year one, and occurring every year, with the age and sex of the bird chosen at random (Table 3). It is possible that persecution of WTEs may not occur until the population has reached a certain size. Therefore, in further models, harvest was restricted to only take place once the population had reached a 10% threshold of carrying capacity, ~20 individuals.

Disease-based catastrophes (C)

Catastrophes can be defined as episodic events which occasionally depress survival or reproduction (Bach et al. 2010). With avian flu (HPAIV) becoming an increasing threat to bird populations around the world (Krone et al. 2018; Fujimoto et al. 2022; Lean et al. 2022), this study models outbreaks of avian flu in WTEs as catastrophic events in VORTEX. The likelihood of occurrence of a catastrophic disease outbreak was calculated based on the probability of a severe die-off for a population being approximately 14% per generation (Reed et al. 2003). WTE generation length was calculated using the IUCN generation length calculator (IUCN 2023), estimated at 15 years, in line with the published estimate in Bird et al. (2020). A 15 year generation time, alongside 14% likelihood per generation, gave a 1% likelihood of a catastrophic event happening in any given year (one event every 100 years). This study modelled the impacts of 1 and 3% likelihood of a catastrophe occurring, with each resulting in a 50% reduction in both reproduction and survival (Table 3; Reed et al. 2003).

2.5 Modelling combined population loss with different reintroduction scenarios

In order to advise on the most appropriate management (supplementation) strategy for WTE reintroduction, low (S2), medium (S4) and high (S9) levels of supplementation were modelled alongside low, medium and high levels of combined population loss (Table 4). This will allow an evaluation of the level of supplementation required to ensure a population is robust against a combination of factors causing population loss at different severities. Each of the three levels of supplementation were modelled alongside low, medium and high levels of dispersal, collision mortality and persecution (Table 4). All scenarios were modelled with a carrying capacity of 214 (K2) and a 1% likelihood of a disease-based catastrophe (C1).

Initially, the population loss scenarios matched those modelled in the sensitivity analysis (Table 3; Table 4; models 1-9). In additional models 1a-9a, the offtake scenarios were changed to model dispersal as 1, 2 and 3% of the population dispersing out of Cumbria, and limiting harvest to only take place once the population size has reached 10% of K, at ~20 individuals. In models 1a-9a, the supplementation, collision mortality and disease scenarios were held the same as in models 1-9.

Table 4. Summary of the scenarios used in models of combined population loss (dispersal, collision mortality, persecution and disease), alongside different levels of supplementation. Scenarios used in models 1-9 are modelled as in the sensitivity analysis.

Model	Scenarios used in model
1 – High supplementation, Low loss	S9 D1 M1 H1 C1
2 – Medium supplementation, Low loss	S4 D1 M1 H1 C1
3 – Low supplementation, Low loss	S2 D1 M1 H1 C1
4 – High supplementation, Medium loss	S9 D2 M2 H2 C1
5 – Medium supplementation, Medium loss	S4 D2 M2 H2 C1
6 – Low supplementation, Medium loss	S2 D2 M2 H2 C1
7 – High supplementation, High loss	S9 D3 M3 H3 C1
8 – Medium supplementation, High loss	S4 D3 M3 H3 C1
9 – Low supplementation, High loss	S2 D3 M3 H3 C1

2.6 Criteria for population viability

There are no set limits on what defines a viable population, and with every population having some risk of extinction, there is no absolute viability (Lacy 2019). An acceptable level of risk must therefore be identified in order to define population viability, which often relates to extinction probabilities and genetic diversity (Lacy 2019). This study based population viability on the criteria set out by Bach et al. (2010), where a population is demographically viable when it has a <10% probability of extinction, and genetically viable when it has a <10% decrease in genetic diversity, over a 100 year period.

3. Results

3.1 Baseline model

Under the baseline model (Table 1), with no additional population loss through dispersal or additional mortality (collisions, persecution, disease), and 56 birds reintroduced over a five year period, the population is characterised by positive growth rates (0.079

±0.153), a zero probability of extinction over 100 years, a final population size close to carrying capacity at 192.07 (±17.53) individuals, and high genetic diversity (0.929 ±0.017) (S4, Table 5; Figure 1). According to Bach et al. (2010) viability criteria, this population maintains its viability.

3.2 Independent modelling and sensitivity analysis

Reintroduction (S)

Under all scenarios of supplementation (S1-S10), the population appears to remain viable, with low extinction probabilities and positive growth rates across all release strategies (Table 5; Figure 2). However, the standard deviation values for Stoch-r suggest positive growth rates were not guaranteed across all iterations. As the total number of birds reintroduced increases, growth rates increase, reducing the time it takes for the population to reach final N-all (Figure 1a). Probability of extinction ranged from 0 to 0.033 (Table 5; Figure 2b). The release scenarios that produced some level of extinction probability are those releasing 24 or 32 birds (S1 and S2). Final population sizes range from 178.87 (±46.80) to 194.46 (±16.95) individuals, increasing as the total number of birds reintroduced increases (Table 5; Figure 1a). Genetic diversity remains high, ranging from 0.869 (±0.064) to 0.946 (±0.010). There does not appear to be a substantial difference in results between scenarios releasing birds every year, versus those releasing birds every other year. See Appendix A for genetic diversity graphs from independent modelling.

Carrying capacity (K)

Modelling different levels of carrying capacity had no impact on population viability (Table 5). As carrying capacity increases, growth rates and genetic diversity increase slightly, whilst probability of extinction remains at zero (Table 5; Figure 2a; Figure 2b). The only substantial impact was on final population size, where the population increases towards but not beyond its respective carrying capacity under each scenario (Figure 1b).

Dispersal out of Cumbria (D)

Losing one bird every year to dispersal (D1) would maintain population viability, with a positive growth rate of 0.070 (±0.162), an extinction probability of 0.012, a final population size of 188.59 (±29.40) individuals and genetic diversity of 0.921 (±0.026; Table 5; Figure 1c; Figure 2). Again, the standard deviation values for Stoch-r indicate the potential for negative growth rates across iterations. Losing two or more birds to dispersal each year causes the population to lose viability, with decreases in growth rates and genetic diversity, extinction probabilities >0.200 (Figure 2b), and final population size dropping to 50.9 (±83.35) when three birds disperse out of Cumbria every year (D3, Figure 1c). The standard deviation for final N-all in scenario D3 is larger than the final N-all value, highlighting the potential for population extinction.

Table 5. Results of the sensitivity analysis, modelling the independent effects of each scenario on a reintroduced WTE population over 100 years, using a PVA in VORTEX. Stoch-r (+SD): stochastic growth rates and standard deviation; PE: mean probability of extinction; N-all (+SD): mean final population size and standard deviation; GD (+SD): genetic diversity and standard deviation. Values have been rounded to 3 d.p. where applicable.

Scenario		Stoch-r (+SD)	PE	N-all (+SD)	GD (+SD)
Reintroduction (S)	S1	0.059 (0.125)	0.033	178.87 (46.80)	0.869 (0.064)
	S2	0.067 (0.130)	0.004	189.91 (26.90)	0.894 (0.044)
	S3	0.076 (0.143)	0	192.17 (18.09)	0.922 (0.021)
	S4 (BASELINE)	0.079 (0.153)	0	192.07 (17.53)	0.929 (0.017)
	S5	0.091 (0.155)	0	194.07 (17.75)	0.943 (0.010)
	S6	0.078 (0.159)	0	193.48 (16.70)	0.930 (0.015)
	S7	0.080 (0.126)	0	193.40 (17.90)	0.932 (0.014)
	S8	0.081 (0.169)	0	192.56 (18.35)	0.935 (0.013)
	S9	0.086 (0.143)	0	193.64 (17.93)	0.944 (0.010)
	S10	0.088 (0.149)	0	194.46 (16.95)	0.946 (0.010)
Carrying capacity (K)	K1	0.077 (0.152)	0	139.06 (13.95)	0.918 (0.018)
	K2 (BASELINE)	0.079 (0.153)	0	192.07 (17.53)	0.929 (0.017)
	K3	0.080 (0.151)	0	218.92 (19.33)	0.933 (0.015)
Dispersal (D)	D1	0.070 (0.162)	0.012	188.59 (29.40)	0.921 (0.026)
	D2	0.045 (0.130)	0.236	141.28 (83.49)	0.905 (0.036)
	D3	0.008 (0.158)	0.715	50.90 (83.35)	0.898 (0.038)
Collisions mortality (M)	M1	0.072 (0.153)	0	191.97 (17.75)	0.926 (0.020)
	M2	0.066 (0.154)	0.001	188.13 (21.45)	0.921 (0.023)
	M3	0.052 (0.159)	0.005	178.38 (32.42)	0.908 (0.041)
	M4	0.001 (0.199)	0.530	22.82 (42.61)	0.771 (0.140)
	M5	-0.034 (0.309)	1	0 (0)	0 (0)
Persecution (H)	H1	0.054 (0.163)	0.200	150.26 (79.54)	0.915 (0.032)
	H2	0.028 (0.179)	0.438	95.81 (92.83)	0.895 (0.055)
	H3	-0.019 (0.250)	0.963	5.64 (31.73)	0.897 (0.057)
Disease (C)	C1	0.070 (0.172)	0.009	181.57 (34.59)	0.921 (0.028)
	C2	0.051 (0.207)	0.063	146.91 (65.90)	0.893 (0.078)

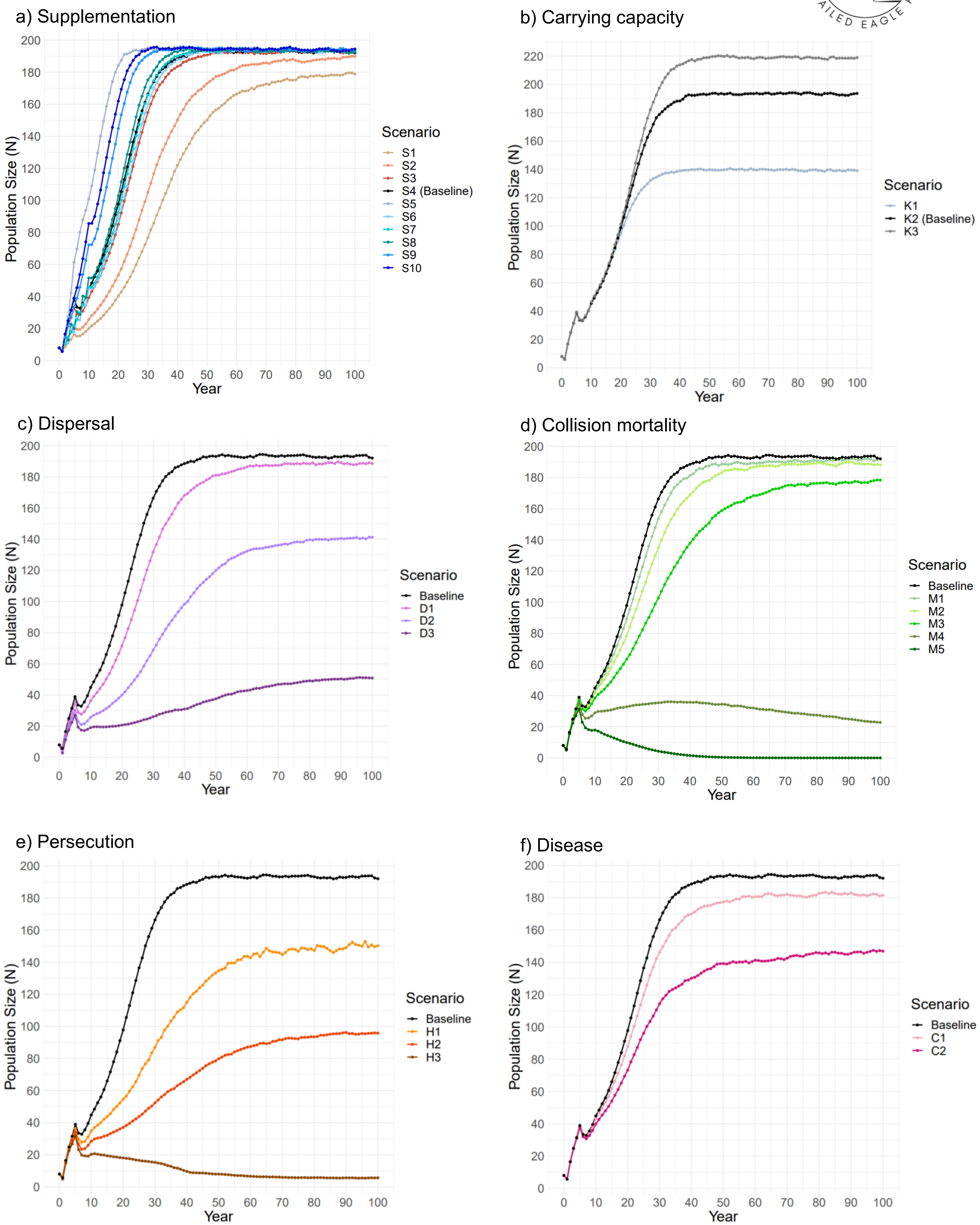


Figure 1. Population size (N) over 100 years under each scenario of a) supplementation, b) carrying capacity, c) dispersal, d) collision mortality, e) persecution and f) disease-based catastrophes, simulated in VORTEX, compared to the baseline model (black line). Within each graph, each coloured line represents a different severity of each scenario.

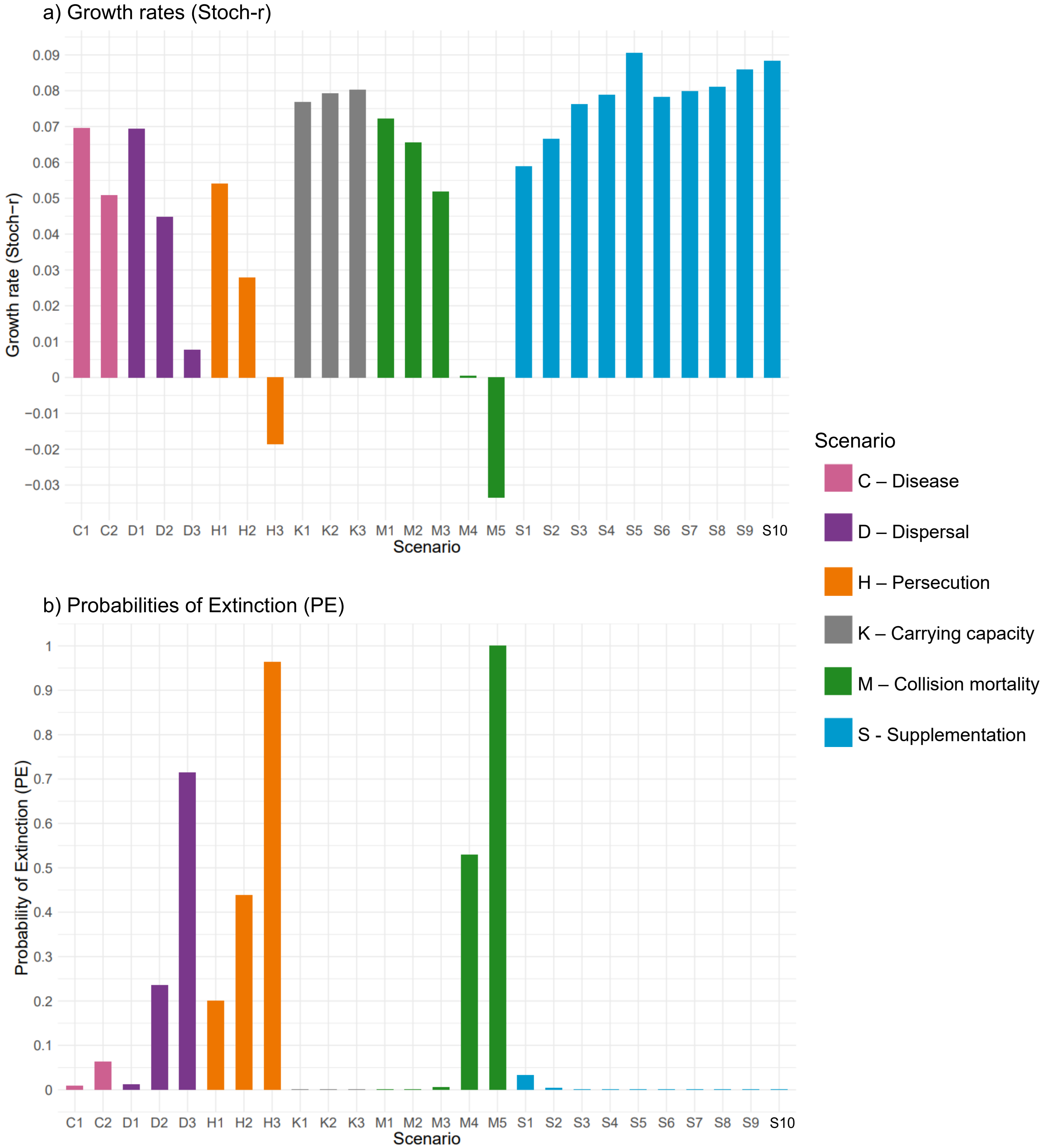


Figure 2. a) Stochastic population growth rates (Stoch-r) and b) probabilities of extinction (PE) under each individual scenario of supplementation, carrying capacity, dispersal, collision mortality, persecution and disease-based catastrophe, simulated in a VORTEX PVA (100 years, 1000 iterations).

Collisions with wind turbines and power lines (M)

The population remains viable when an additional 0.5, 1 or 2% mortality is modelled, with a maximum extinction probability of 0.005, positive growth rates, genetic diversity of at least 0.908 (±0.041) and population sizes of at least 178.38 (±32.42) individuals (Table 5; Figure 1d; Figure 2). However, when additional mortality is increased to 5 and 10%, the population loses viability with low and negative growth rates (Figure 2a), extinction probabilities of 0.530 and 1 (Figure 2b), and final population sizes dropping to 22.82 (±42.61) and 0 respectively (Figure 1d).

Persecution (H)

Under all scenarios of persecution (H1-H3), extinction probabilities are ≥0.200 (Table 5; Figure 2b), indicating that losing any number of individuals to persecution causes the population to lose viability (Bach et al. 2010). When one individual is persecuted every year (H1), despite the extinction probability (0.200) being above the viability threshold set by Bach et al. (2010), the population is characterised by a positive growth rate (0.054 ±0.163; Figure 2a), a final population size of 150.26 (±79.54) individuals, and genetic diversity of 0.915 (±0.032). Losing three individuals to persecution each year would be devastating for the population (Figure 1e), with a negative growth rate (-0.019 ±0.250), and an almost certain extinction probability of 0.963 (Figure 2).

Disease-based catastrophes (C)

In modelling catastrophic disease outbreaks, both the 1 and 3% likelihood scenarios left populations viable, with a maximum extinction probability of 0.063 (Table 5; Figure 2b). Both models are characterised by positive growth rates (Figure 2a), large final population sizes (Figure 1f), and genetic diversity of at least 0.893 (±0.078).

3.3 Modelling combined population loss with different reintroduction scenarios

Results from models 1-9 show that modelling population loss factors together (dispersal, collision mortality, persecution, disease), causes all populations to lose their viability, regardless of the level of supplementation (Table 6). The lowest probability of extinction is 0.335 (model 1), where high supplementation (98 birds released) is modelled alongside low population loss. In model 1, despite the extinction probability suggesting the population is unviable, the growth rate remains positive (0.035 ±0.174) and final population size is 110.18 (±87.65) individuals (Figure 3a; Figure 4). The standard deviation values for Stoch-r in model 1 indicate the potential for negative growth rates across iterations. Under model 2, (medium supplementation (56 birds released) and low loss), the population persists for 100 years with a final population size of 33.78 (±69.11) individuals, but the extinction probability is high at 0.781 (Figure 3a; Figure 4b). In models 3-9, all populations become unviable, characterised by almost certain extinction (Table 6; Figure 4b), negative growth rates (Figure 4a) and population sizes ranging from 9.17 (±38.26) to 0 (Table 6). See Appendix B for genetic diversity graphs of models 1-9 and Appendix C for population size trajectories following models 7-9.

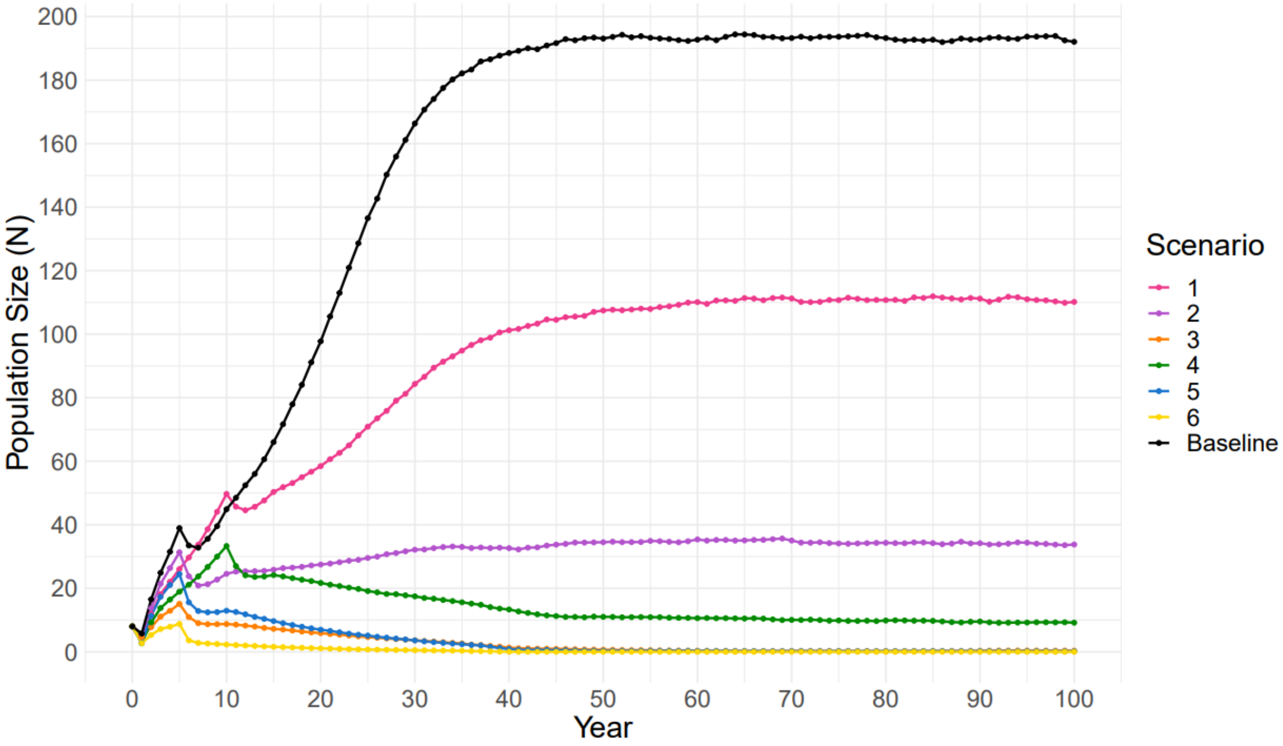
When modelling dispersal as a percentage of the overall population size, and limiting harvest to commence when the population reaches a certain size (models 1a-9a), population viability improves (Table 6). Models 1a-9a appear more optimistic, with all scenarios characterised by lower extinction probabilities (Figure 4b), positive growth rates in all but the 'high loss' scenarios (7a-9a; Figure 4a), and larger final population sizes (Table 6; Figure 3b). See Appendix B for genetic diversity graphs of models 1a-9a.

Table 6. Results of the combined models 1-9 and 1a-9a, simulated over 100 years using a PVA in VORTEX. HS = High Supplementation, MS = Medium supplementation, LS = Low Supplementation, LL = Low Loss, ML = Medium Loss, HL= High Loss. Stoch-r (+SD): stochastic growth rates and standard deviation; PE: mean probability of extinction; N-all (+SD): mean final population size and standard deviation; GD (+SD): genetic diversity and standard deviation. Values have been rounded to 3 d.p. where applicable.

Model	Stoch-r (+SD)	PE	N-all (+SD)	GD (+SD)
1 – HS, LL	0.035 (0.174)	0.335	110.18 (87.65)	0.920 (0.031)
2 – MS, LL	0.003 (0.218)	0.781	33.78 (69.11)	0.891 (0.060)
3 – LS, LL	-0.033 (0.253)	0.998	0.35 (7.85)	0.886 (0.018)
4 – HS, ML	-0.025 (0.232)	0.933	9.17 (38.26)	0.896 (0.079)
5 – MS, ML	-0.056 (0.286)	0.999	0.17 (5.41)	0.921 (0.005)
6 – LS, ML	-0.087 (0.371)	1	0 (0)	0 (0)
7 – HS, HL	-0.057 (0.292)	1	0 (0)	0 (0)
8 – MS, HL	-0.098 (0.352)	1	0 (0)	0 (0)
9 – LS, HL	-0.132 (0.578)	1	0 (0)	0 (0)
1a – HS, LL	0.054 (0.168)	0.039	157.09 (61.86)	0.913 (0.071)
2a – MS, LL	0.034 (0.183)	0.139	110.38 (82.72)	0.847 (0.127)
3a – LS, LL	0.015 (0.174)	0.304	54.70 (73.65)	0.752 (0.164)
4a – HS, ML	0.036 (0.174)	0.078	120.97 (78.38)	0.876 (0.111)
5a – MS, ML	0.012 (0.198)	0.290	50.46 (72.83)	0.763 (0.156)
6a – LS, ML	0.002 (0.184)	0.459	15.56 (37.48)	0.654 (0.177)
7a – HS, HL	-0.005 (0.205)	0.654	5.07 (15.89)	0.645 (0.149)
8a – MS, HL	-0.009 (0.224)	0.757	2.30 (4.23)	0.583 (0.159)
9a – LS, HL	-0.008 (0.201)	0.768	2.11 (4.09)	0.554 (0.172)

Across all modelled scenarios, the population appears to be sensitive to a sharp decline in size during the period immediately after reintroduction at 5 or 10 years (Figure 1; Figure 3).

a) Models 1-6



b) Models 1a-9a

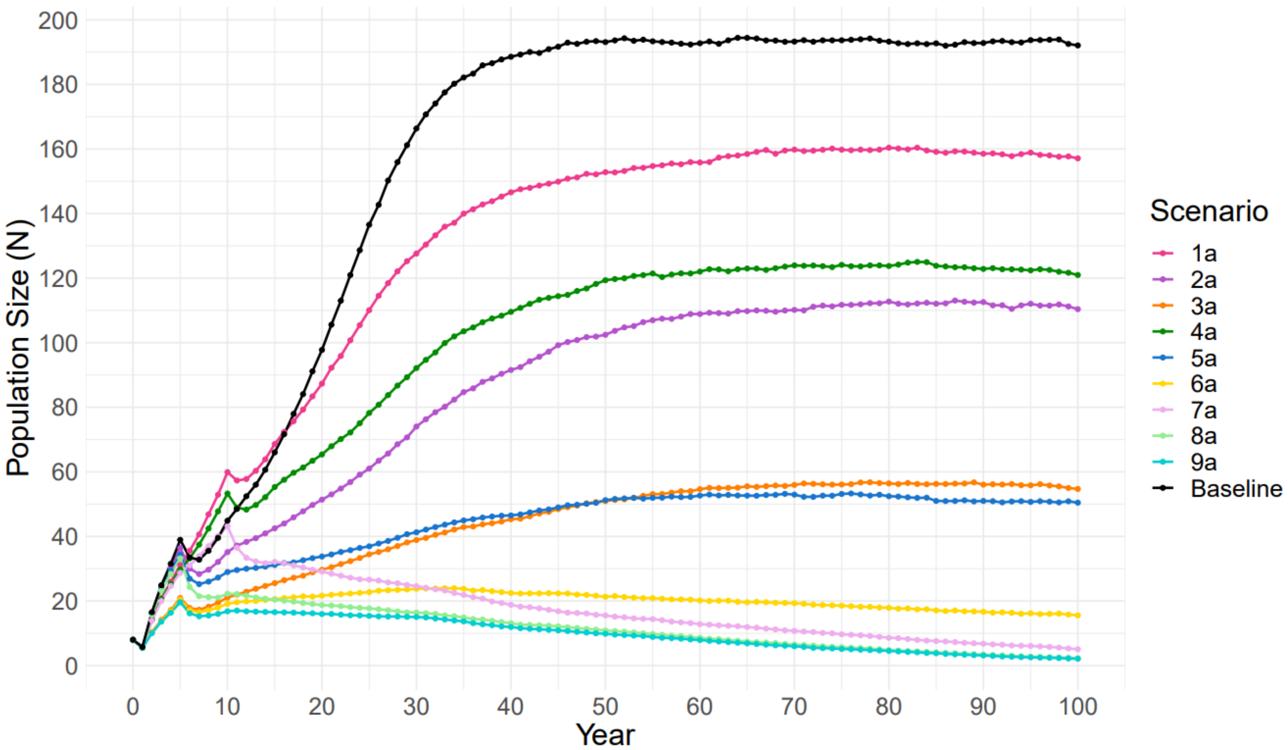


Figure 3. Population size (N) over 100 years under combined population loss models with different levels of supplementation, a) 1-6 and b) 1a-9a, simulated in a VORTEX PVA (100 years, 1000 iterations), compared to the baseline model (black line).

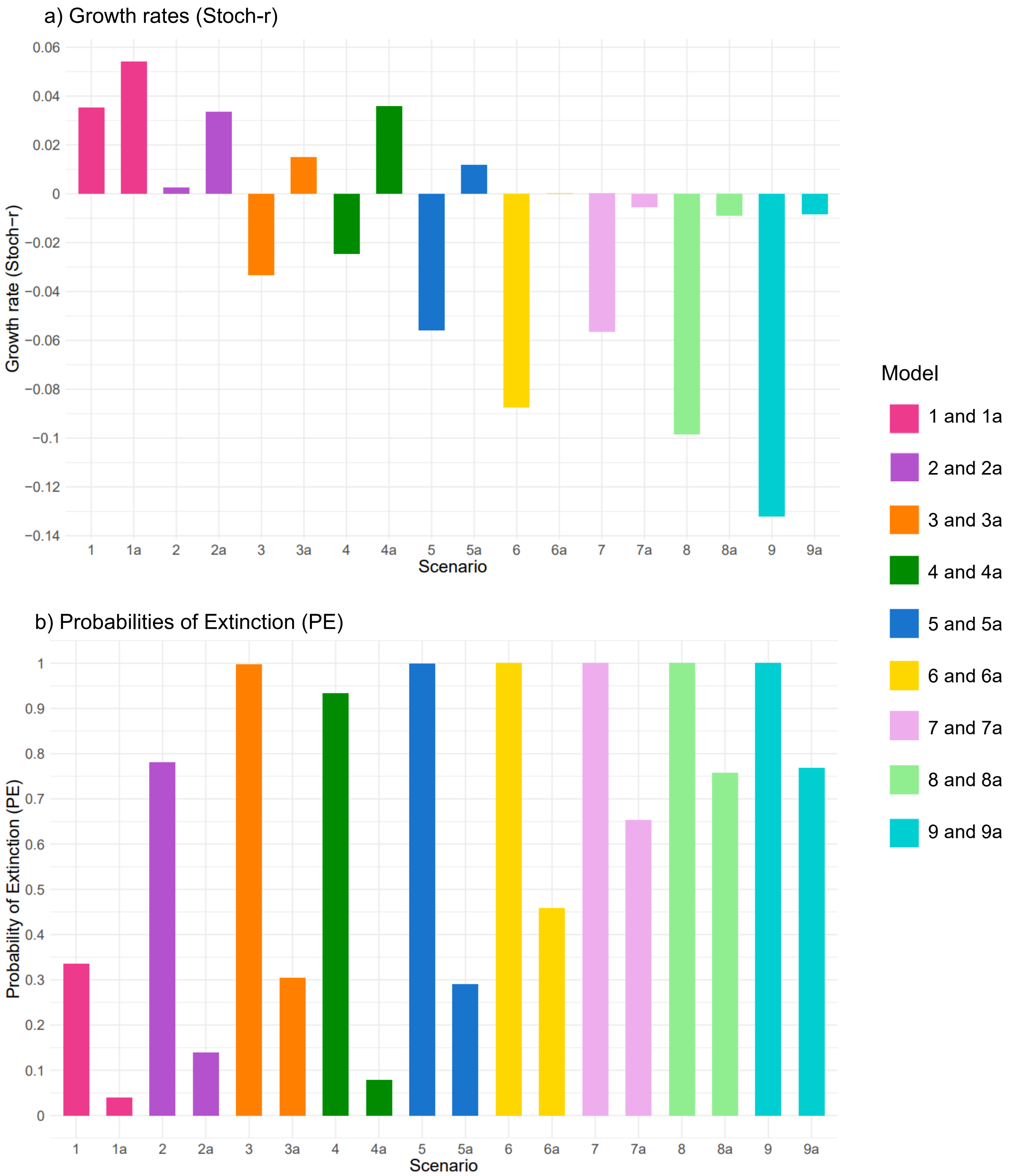


Figure 4. a) Stochastic growth rates (Stoch-r) and b) probabilities of extinction (PE) under combined population loss models with different levels of supplementation, a) 1-9 and b) 1a-9a, simulated in a VORTEX PVA (100 years, 1000 iterations).

3.4 Optimal supplementation and loss scenario

Based on these results, model 2a was chosen as the optimal combined loss scenario, with potential to generate a viable population, whilst also aligning with the most feasible reintroduction scenario. The standard deviation of population size in model 2a shows the potential for a large deviation from the predicted population size trajectory seen during the 100 year period (Figure 5).

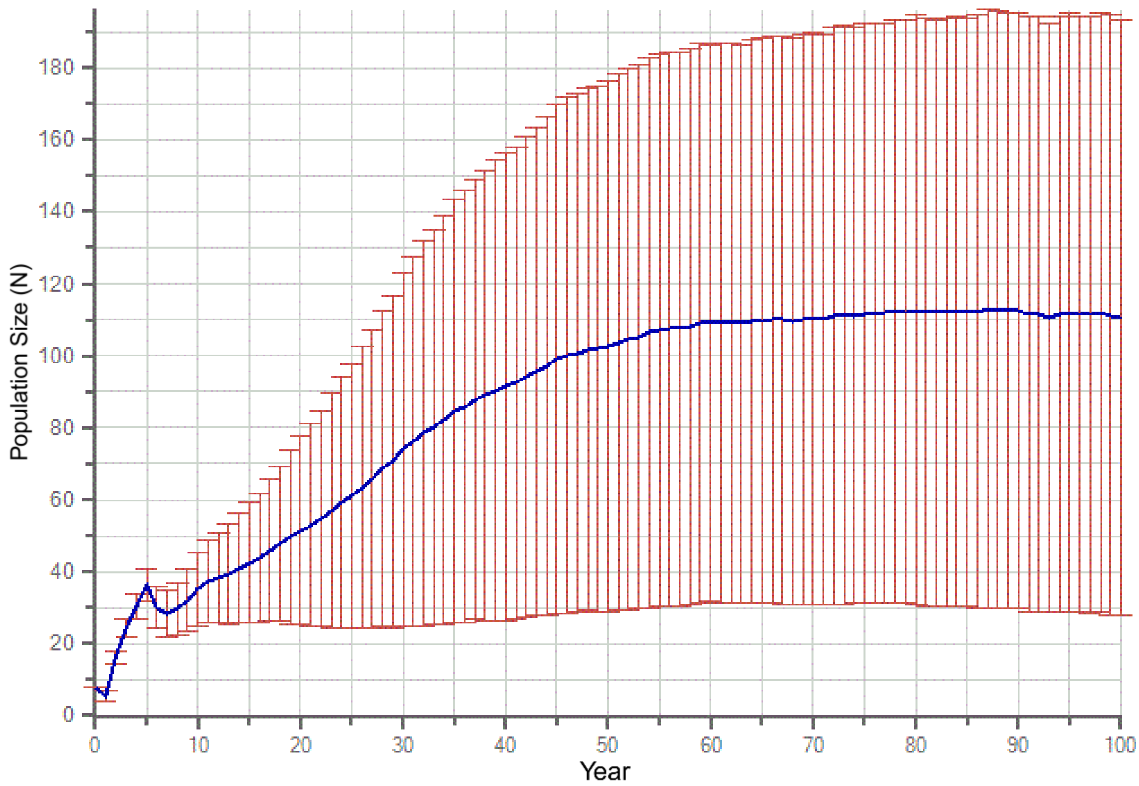


Figure 5. Population size (N) over 100 years under the optimal model 2a, simulated in a PVA in VORTEX. The blue line represents predicted population size (N), and the red line represents the standard deviation in population size.

4. Discussion

White-Tailed Eagles (WTEs) are an ecologically and culturally important species within the UK (O'Rouke 2014; Mayhew et al. 2016; Dennis et al. 2019). Their return to northern England would mark a turning point in conservation, delivering ecosystem benefits through top-down predator effects (Lyly et al. 2015), and cultural benefits through enriching experiences with nature (Mayhew et al. 2016). Establishing a viable breeding population is a primary conservation goal of reintroduction projects (Mee et al. 2016) and population modelling is a vital part of planning and pre-feasibility studies. The results of this study provide a comprehensive estimation of WTE population trajectories following different scenarios of reintroduction, and present the impacts of factors affecting population loss. This enables project managers to make informed decisions regarding release strategies and improves understanding of the impacts of dispersal, collisions with wind turbines and power lines, persecution and disease on population trends.

4.1 Analysis of results

According to the baseline model with 56 individuals released over five years, and no additional population loss (dispersal, collision mortality, persecution, disease), a reintroduced WTE population in Cumbria will be viable, growing to a population size of 192 individuals within 50 years (Figure 1). However, it is perhaps unlikely that a reintroduced population will not suffer additional loss, and therefore the results from subsequent models are more realistic. The growth rate of 7.9% in this baseline model is in line with modelled growth rates in the Scottish population, with 9.7% from 1997-2007 (Evans et al. 2009), and 8.6% from 2015-2025 (Sansom et al. 2016), providing a measure of reliability to this modelling (Aresu et al. 2021).

Independent modelling

Choosing a release strategy is an important decision for this reintroduction project. Dennis et al. (2019) claim that releasing 60 juvenile birds over five years will be sufficient to establish 6-8 breeding pairs. Although this figure was proposed for the Isle of Wight reintroduction based on modelling applicable to that location, it is a good baseline on which this modelling was formed, agreed alongside Cumbria project experts. Under all scenarios of reintroduction without additional population loss, populations maintain their viability, increasing towards carrying capacity at different rates. All final population sizes are >178 individuals, with scenarios S4 (56 birds) and S10 (116 birds) reaching similar final population sizes after 50 and 30 years respectively. The highest growth rate follows the scenario of releasing sub-adult birds, with final population size reached after around 25 years. Although Dennis et al. (2019) suggest it may be possible in later years of a reintroduction project to supplement the release of juvenile WTEs with sub-adult birds, focusing a whole reintroduction on this has the potential to be unsuccessful, with sub-adult birds having already learnt their home environment.

Carrying capacity estimations in this study should come with a strong caveat that they are based on highest WTE densities observed in Scotland (Sansom et al. 2016), and have the potential to vary over time following changes in habitat suitability caused by climate change and habitat loss. Following reintroduction, the population should be monitored to identify any signs of density-dependent effects, such as territorial disputes, that may influence carrying capacity (Kruger et al. 2010).

Raising the severity of factors causing additional population loss has an increasingly negative impact on population viability. Although dispersal of individuals out of Cumbria is a concern, decreasing genetic diversity and overall viability, a desired outcome of this reintroduction project is range expansion of WTE populations in the UK, and gene flow between Cumbria and nearby populations in Fife and Tayside for example (Carver et al. 2022). Dispersal of individuals between populations is an important driver of this, and although not modelled, it is important to recognise that dispersal of individuals into Cumbria from nearby populations has the potential to offset the impacts of losses modelled in this study.

Despite renewable energy sources playing a vital role in climate change mitigation, wind turbine density is a strong predictor of collision mortality in large raptors (Heuck et al. 2019). Evidence suggests that when WTE territories are located closer to wind turbines, the probability of a pair breeding successfully is lower, potentially a result of collision mortality (Balotari-Chiebao et al. 2016). In this study, additional mortality of >5% causes a population to become unviable, in line with published results suggesting that population viability can be sensitive to proportionally small increases in mortality (Schippers et al. 2019). Although additional mortality was modelled to occur across all age groups (Sansom et al. 2016), the most extensive movements by WTEs take place in the first two years after fledging (Whitfield et al. 2009b). These wide-ranging movements may subsequently put one and two year-old birds at higher risk of exposure to collisions.

According to the IUCN's guidelines for reintroduction, there should be evidence that the threats causing previous species extinction have been identified and sufficiently reduced or removed (IUCN/SSC 2013). Although less prevalent across the UK today, due to protective legislation, changes in cultural attitudes and reduction in game hunting (Whitfield et al. 2004), illegal persecution of raptors still occurs (Mee et al. 2016), and can take many forms, from nest destruction, to poisoning and shooting (Whitfield et al. 2004). It also appears evident that persecution is the most influential factor on population viability, with the largest decrease in final population size compared to the baseline (Figure 1e). It is not unusual for persecution to be a main threat to large raptor populations, with similar results arising from a PVA on Griffon Vultures (*Gyps fulvus*) in Italy (Aresu et al. 2021). Whitfield et al. (2004) also emphasise the severe impacts of persecution on golden eagles (*Aquila chrysaetos*) in Scotland, where 3-5% of breeding adults are illegally killed each year, being the primary cause of population vulnerability and decline.

Incidences of high pathogenicity avian influenza virus (HPAIV), with lethal consequences (Krone et al. 2018), are becoming increasingly common in the UK and WTEs are among the species affected (Lean et al. 2022). With other PVAs reporting catastrophic events to be the most influential factor on population viability (Bach et al. 2010), it is perhaps unexpected that disease-based catastrophic events did not have a more profound effect on population viability in this study. Avian flu can be difficult to predict spatially and temporally, meaning the actual frequency and severity of events may differ from those modelled in this study.

The viability criteria (Bach et al. 2010) used in this study are one example of how population viability can be defined. In reality, viability definitions are open to interpretation, and it must be considered that there may be other suitable limits for population viability.

Combined modelling

Regardless of how many individuals are reintroduced, all populations struggle to maintain viability when population loss factors (dispersal, collision mortality, persecution, disease) are acting together (models 1-9). When dispersal is modelled as a fixed number of individuals and persecution occurs immediately following reintroduction, under the low level of population loss, a high level of supplementation (model 1) would be required to provide the population with any chance of survival (Table 6), with an extinction probability of 33.5%.

It is perhaps more realistic to model dispersal as a percentage of the total population size, and limit persecution (harvest) to only occur once the population has reached a certain size. Under such offtake models (models 1a-9a), the population maintained viability for longer. Under the medium loss scenarios (models 4a-6a), high supplementation is required to ensure population viability is robust against factors causing population loss. Under the low loss scenarios (models 1a-3a), medium supplementation (model 2a) leaves the population with a healthy final population size of 110 individuals, but an extinction probability of 13.9%, just above the viability threshold of 10%. Subsequently, given that the reintroduction strategy involved in the medium supplementation scenario (56 birds over five years) is the most feasible (Dennis et al. 2019), model 2a became the optimal scenario, with potential for the population to be viable.

The sensitivity of the reintroduced population to combined population loss could be explained by the small population paradigm (Caughley 1994). If the population remains small in the years during and following reintroduction, it may be highly vulnerable to demographic and environmental stochasticity, potentially explaining the loss of viability when all additional population loss scenarios are at play together. This aligns with what was observed in the Scottish population following the first release of 82 individuals from 1975-1985 (Sansom et al. 2016), where subsequent modelling revealed a 60% probability of extinction within 100 years (Green et al. 1996; Evans et al. 2009). This was likely because the population remained small following the first release, which may be a result of the species delayed sexual maturity (Whitfield et al. 2009b).

4.2 Management and post-release strategy recommendations

From a management perspective, the success of a reintroduction programme relies on several factors such as the size of the release cohort, quality of the release area, release strategies and post-release monitoring (Mee et al. 2016). Long-term viability of a reintroduction programme also relies on minimising the losses of adult and sub-adult birds (Mee et al. 2016). Given that a reintroduced population of WTEs in Cumbria may be at increased risk from population loss factors due to the small population paradigm (Caughley 1994), management should carefully consider the most effective release strategy, as well as mitigation of population loss factors and population monitoring to safeguard long-term population viability.

Practical interventions

Given that the first reintroduction of 82 individuals in Scotland was followed by a high probability of extinction (60% within 100 years; Green et al. 1996), it is perhaps not surprising that releasing a total of 56 birds in Cumbria presents undesirable population viability. With the optimal model 2a presenting an extinction probability that is 3.9% over the viability threshold of 10%, the first practical recommendation is to explore question 4 further. Additional modelling of 2a should be carried out to determine exactly how many more birds than 56 should be released over a five year period to improve confidence in the viability of a population experiencing a combined low loss scenario. Reintroductions of a total of 58, 60, 62, 64 and 66 birds should be trialled under the low loss scenario, to test at what point extinction probability drops below 10%.

With populations struggling to maintain viability under the combined population loss scenarios, results from this study raise the possibility that a second phase of WTE releases may be required in Cumbria. It is likely that the initial small population size is causing the population to be susceptible to losing viability (Chaughley 1994), and the populations vulnerability to decline is evidenced by the sharp dip in population size immediately following reintroduction (Figure 1; Figure 3). This recommendation aligns with the reintroduction strategy in Scotland, where a thriving WTE population has been established following three phases of reintroductions (Evans et al. 2009; Sansom et al. 2016). The Scottish reintroduction saw 82 birds released between 1975 and 1985, 58 birds released between 1993 and 1998, and 85 birds released between 2007 and 2012 (Evans et al. 2009; Sansom et al. 2016). Second and third phases of release in the Scottish project were implemented following concerns surrounding the high probability of extinction (60%) within 100 years (Green et al. 1996). A second phase of releases in Cumbria would help mitigate the impacts of the small population paradigm by ensuring the population does not stay small for longer than necessary, improving the confidence in population viability as evidenced in Scotland. Further modelling could be carried out to determine the size of these subsequent release cohorts, and timescales over which they should occur to be most effective. It was suggested that releasing more birds in Scotland increased the species capacity to reoccupy its former breeding range in Britain more rapidly (Evans et al. 2009), a theory that could be applied to reintroductions in Cumbria.

Mitigation

This study suggests that harvest has the strongest negative impact on population viability and size, and it is therefore vital that persecution is discouraged and prevented. Although farmers concerns around lamb predation are understood, evidence suggests that when WTEs do predate live lambs, those lambs are often not viable (Carver et al. 2022), and in Ireland there have been no reports of lamb predation by reintroduced WTEs (Dennis et al. 2019). Persecution can be discouraged through working collaboratively with farmers, setting up compensation schemes to support farmers should they lose livestock to WTE predation, and issuing information leaflets to all farmers and landowners, as in Ireland, to raise awareness of the detrimental impacts of poisons on eagles, other wildlife and farm animals (Mee et al. 2016). In Scotland, a voluntary management scheme has been implemented, paying farmers living within 5km of an active WTE nest to partake in various management and monitoring measures, encouraging their cooperation (Sansom et al. 2016). Aresu et al. (2021) emphasise the importance of preventing poisoning events to conserve Griffon Vultures in Italy, suggesting tactics including economic sanctions, legal punishment and poison detection dogs. Further techniques to protect WTEs from persecution include education and outreach programmes to enthuse local people, encouraging them to report sightings and giving them a sense of involvement with the project, and an increased desire to protect the birds.

Mitigating the risks of collision mortality is also crucial. With WTEs covering large distances during their juvenile years (Whitfield et al. 2009b), potentially making one to two year-old birds more vulnerable to collisions, one key factor in reducing collision risk is the choice of release sites. Dennis et al. (2019) recommend release sites are at least 10km from the nearest wind turbines and away from overhead powerlines. However, this will not eradicate collision risk, with Mee et al. (2016) reporting multiple deaths caused by collisions with wind turbines despite turbines being 19-25km from release sites.

Monitoring

To build increasingly reliable PVA models, a reintroduced population should be monitored to obtain data on survival and recruitment rates relevant to the Cumbrian population. As in Evans et al. (2009), a reintroduced WTE population should be monitored annually, with efforts made to determine how many individuals have survived (survival rates), detect territorial pairs, and determine the outcomes of breeding attempts. All released birds should be individually marked with rings containing numbers and different colours to identify individuals and determine the year of release (Evans et al. 2009; Mee et al. 2016).

Population monitoring should also aim to evaluate and quantify the real risks of population loss associated with factors modelled in this study. To monitor dispersal of birds out of Cumbria, and estimate dispersal rates, wing-tags and GPS satellite transmitters can be fitted to the birds to identify individuals and track movements (Krone et al. 2009; Mee et al. 2016). The number of birds that can be fitted with GPS tracking devices will depend on funding available to the project. GPS tracking data from the Irish reintroduction project has allowed estimations of the average number of birds lost from the population through dispersal every year (Mee et al. 2016). Analysis of GPS tracking data in GIS software will also allow estimation of the proximities of flight paths to wind turbines and powerlines, with the aim of quantifying collision risk. Levels of persecution are difficult to quantify due to its illegal and covert nature (Whitfield et al. 2004). Where possible, with the help of GPS tracking, dead birds should be recovered to determine cause of death (Mee et al. 2016), and the project should collaborate with the RSPB to report raptor persecutions (RSPB 2022). Finally, reports of avian flu in Cumbria and surrounding areas should be monitored closely, and recovered WTE carcasses could be analysed for presence of avian flu (Lean et al. 2022).

4.3 Limitations of this study

Despite being used extensively in conservation management, PVA models have faced scrutiny regarding their accuracy (Reed et al. 1998; Lacy 2019). Firstly, PVAs are models requiring data on a large number of demographic and environmental variables (Lacy 2019). Such data should be comprehensive and accurate (Morrison et al. 2016), yet there is often a lack of complete biological data available for a given species (Lacy 2019). PVA models omit some variables, such as the impacts of interspecific interactions (Lacy 1993), and make assumptions about others, such as genetics, and hence come with a degree of uncertainty (Aresu et al. 2021) making some results misleading (Reed et al. 1998). PVA models in this study are limited, as surrogate data from other established WTE populations were used to populate VORTEX and model a hypothetical reintroduced population in Cumbria. Such surrogate data may not fully reflect the population dynamics that will be characteristic of the reintroduced population. Furthermore, input parameters related to population loss were based on best estimates from other WTE populations, potentially mis-representing the actual severities that a reintroduced population in Cumbria may face.

PVAs rarely aim to provide entirely accurate estimates of population trends. Instead they are useful in supporting project managers and policy makers in conservation decisions. This study can be regarded as an indicator of likely population trajectories and extinction probabilities of a reintroduced population of WTEs in Cumbria, and suggests that reintroducing >56 birds over five years has strong potential to be viable. Results should be used to inform further feasibility studies and project management, in conjunction with other research and modelling.

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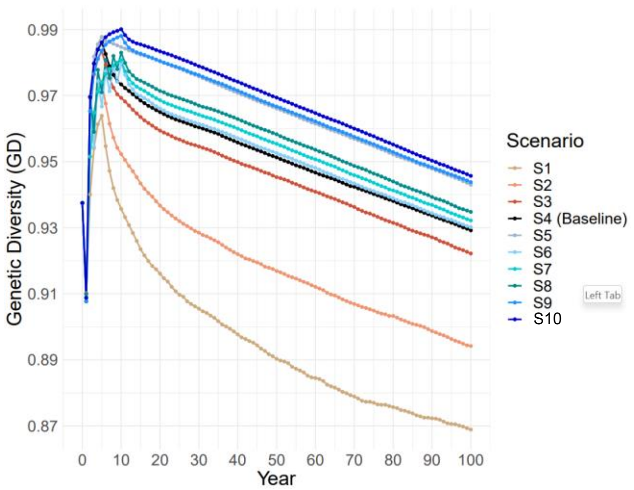
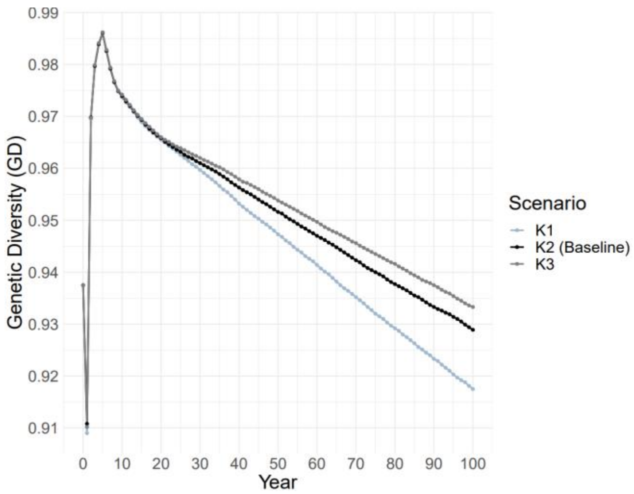
APPENDIX A

Genetic diversity over 100 years under scenarios of a) supplementation, b) carrying capacity, c) dispersal, d) collision mortality, e) persecution and f) disease

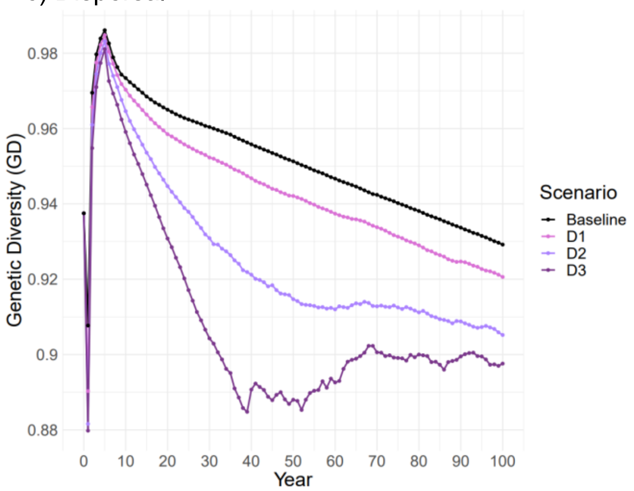
a) Supplementation



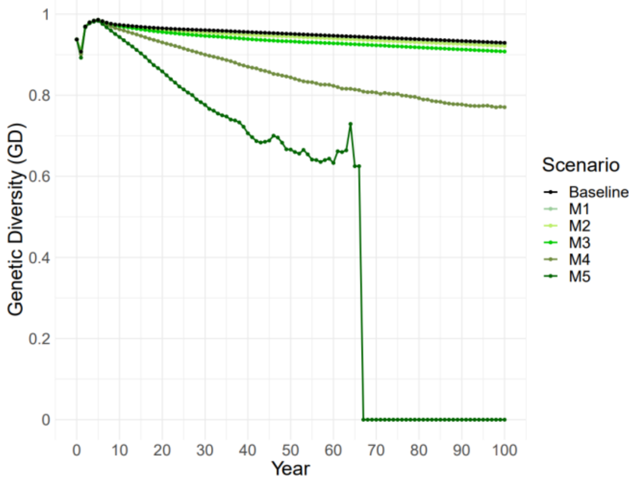
b) Carrying capacity



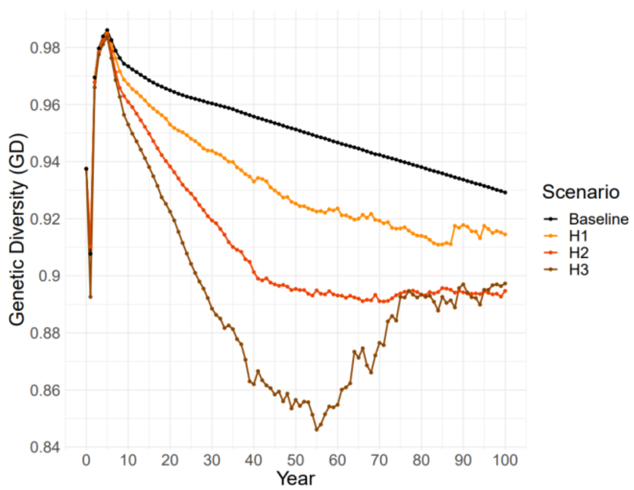
c) Dispersal



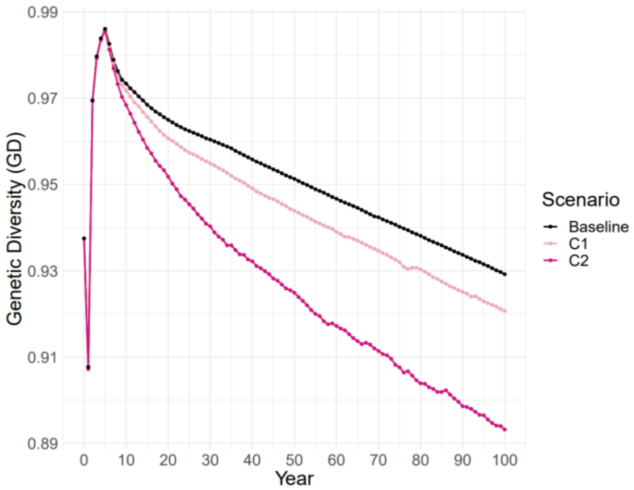
d) Collision mortality



e) Persecution



f) Disease

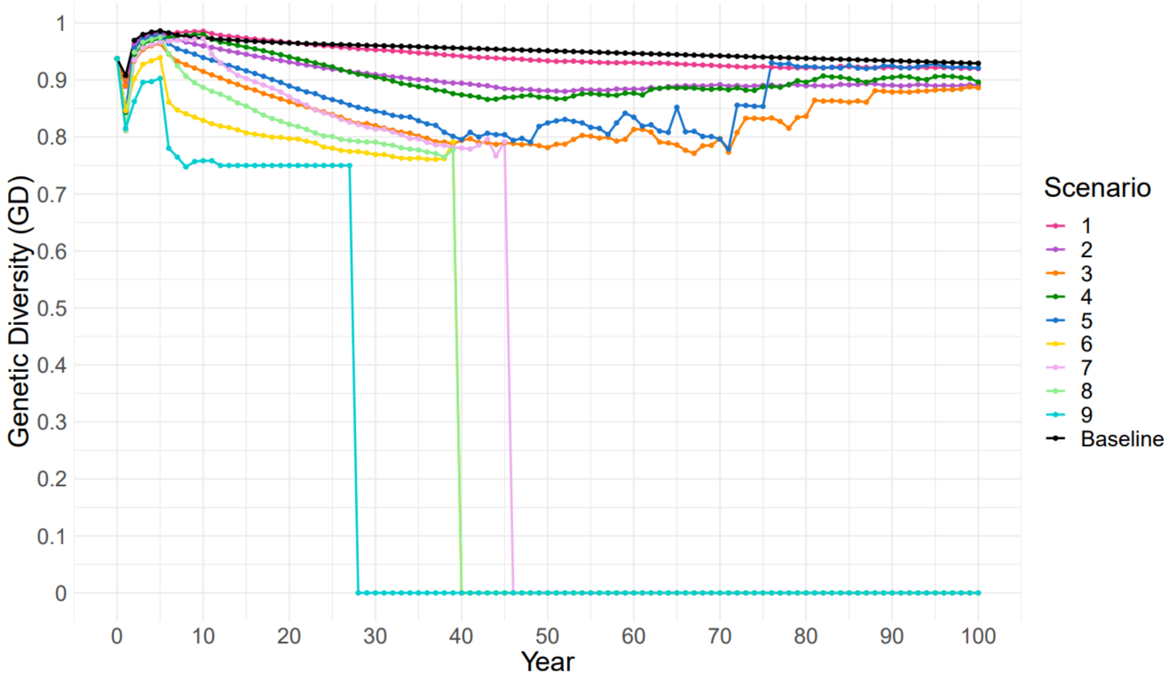


Appendix A. Genetic diversity (GD) over 100 years under each scenario of a) supplementation, b) carrying capacity, c) dispersal, d) collision mortality, e) persecution and f) disease-based catastrophes. Within each graph, each coloured line represents a different severity of each scenario.

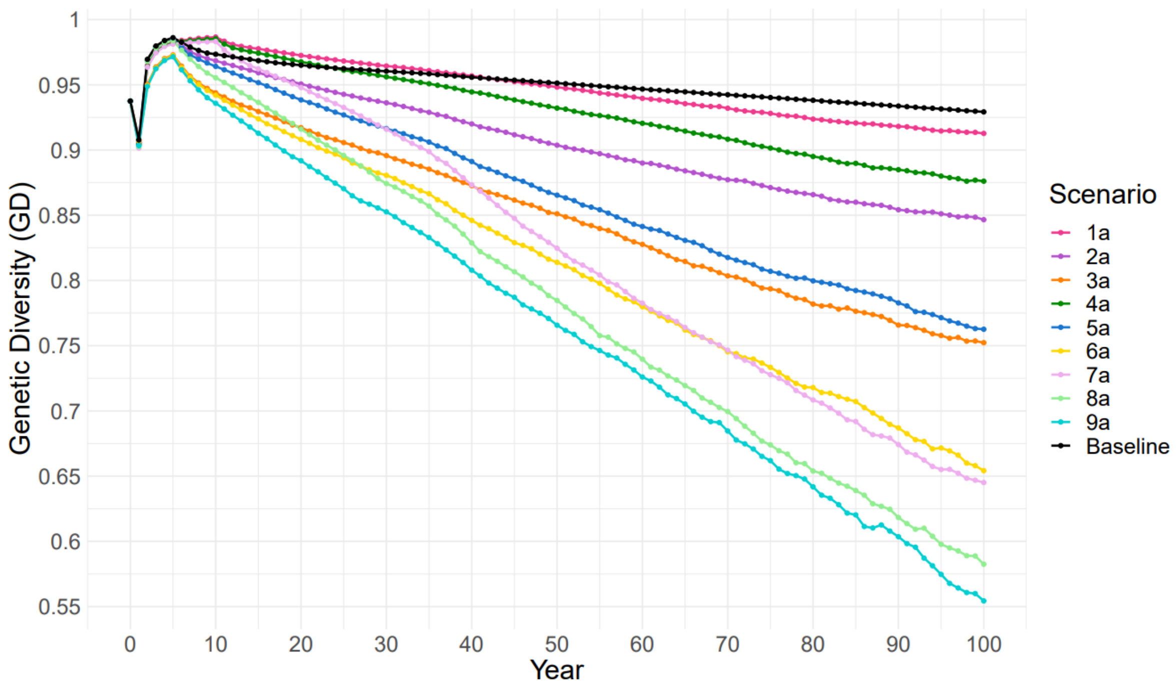
APPENDIX B

Genetic diversity over 100 years for combined loss models a) 1-9 and b) 1a-9a

a) Models 1-9



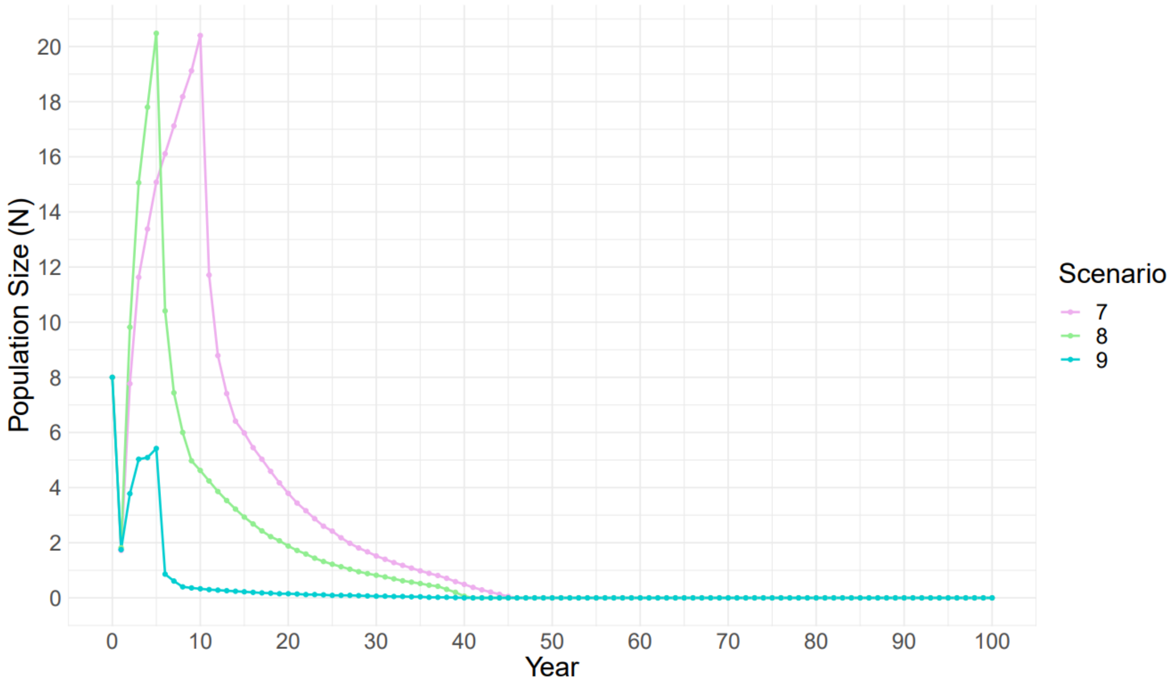
b) Models 1a-9a



Appendix B. Genetic diversity (GD) over 100 years under combined population loss models with different levels of supplementation, a) 1-9 and b) 1a-9a, simulated in a VORTEX PVA (100 years, 1000 iterations).

APPENDIX C

Population size (N) trajectories over 100 years for combined high loss models 7-9



Appendix C. Population size (N) over 100 years under the combined high loss models 7-9, simulated in a VORTEX PVA (100 years, 1000 iterations).