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A stage-based life cycle implementation for individual-based population viability analyses of grey wolves (*Canis lupus*) in Europe

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ABSTRACT

Population viability analyses (PVA) are important tools for decision-making and planning of adaptive wildlife management actions. While earlier approaches on individual based PVAs have often been age-based, analyses of species with strong social structure might benefit from a stage-based model approach. In this study, we designed an individual-based and stage-based PVA within the software Vortex. As a case study, we applied our model to the German part of the European wolf population, making use of comprehensive data sets originating from the German monitoring regime including individual genotypes. Genetic diversity and inbreeding were important considerations in our analysis, as they could greatly impact population dynamics. We aimed to assess the population's trajectory, extinction risk, and genetic integrity under different scenarios while analyzing factors that could affect its survival. We found that mortality rates at different life cycle stages had varying effects on population growth. Higher mortality rates among pups and dispersers led to negative growth and increased the risk of extinction. In comparison, higher mortality rates among yearlings and subdominant wolves still resulted in positive growth but at a slower rate. Mortality among the breeding individuals within the pack (territorials) had the highest impact on population trajectory. Although the German wolves represent a rather recently founded population, our simulations predicted generally good genetic diversity as long as the population was not held at artificially low numbers.

Ultimately, we present a generic, easy-to-use-and-adapt model built within the Vortex environment, that after appropriate modification, calibration and testing could be used within conservation practice and management in collaboration with scientific research. Our study highlights the importance of stage-based modeling for understanding the demographic traits of social species like wolves.

1. Introduction

1.1. *Adaptive wildlife management*

Wildlife management typically involves decision-making under various levels of uncertainty. As a concept to embrace that uncertainty, adaptive wildlife management relies on comprehensive situation analysis and evidence-based decision-making (Organ et al., 2012). Hence, high-quality data about population dynamics and viability is needed (Legendre, 2020). While a lot can be learned by periodic monitoring and assessments, management actions should also be conceived and evaluated based on their future impact on the dynamics of the targeted population. As such, scenario planning is integral to adaptive wildlife management, where multiple possible futures can be considered (McLane et al., 2011).

Therefore, population models are needed that allow for forward-in-time simulations that can be used to develop and evaluate management actions (Marescot et al., 2013). Population viability analyses (PVAs) are standard tools in modern wildlife management to assess the persistence of a population and predict the population dynamics under various circumstances (Lacy, 2019). Individual-based models (IBMs) have proven to be especially suited for social species to account for their individual life histories (Pitt et al., 2003). Within IBMs, the individuals of a given species or population can be parameterized with virtually any

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characteristic relevant to the species (i.e., survival and reproduction rates, behavior, social status, etc.).

As bottom-up approaches, IBMs allow for population-level results by modeling individual-level mechanisms (Bauduin et al., 2020). As flexible as they are, IBMs for PVA can be built in many ways concerning their spatial and temporal scale. Earlier approaches were mostly age-based, quantifying vital rates per year using Leslie matrices (Caswell, 2001; Leslie, 1945). However, age-based models are not always appropriate, especially if age does not determine an individual's fate or its vital rates (most notably, survival and reproduction rates) (Caswell, 2001). This might be the case for highly social species, where vital rates depend on their social status (Legendre, 2020; Marescot et al., 2012).

In such species, stage-based models present suitable alternatives. Within these, stages are defined based on the target species' life cycle (representing the individuals' reproductive status, social status, etc.; Lefkovitch 1965; Chapron et al., 2003). Transition rates are then defined to determine the probability of transition of individuals from one stage to another per iteration of the simulation (Caswell, 2001).

1.2. Modeling approaches

As one of the most studied carnivore organisms in recent decades, the grey wolf (*Canis lupus*) was subject to many studies employing a wide range of different modeling approaches. Among others, models have been used to conclude from the number of packs to census size (Chapron et al., 2016), to evaluate recovery plans (Carroll et al., 2019), or to understand individual social dynamics (Bauduin et al., 2020). Accordingly, modeling approaches have been quite different, ranging from mathematical models built from scratch to pre-built software, including easy-to-use graphical user interfaces. While the body of scientific literature is promising and indicative of a highly active community, the knowledge transfer into practical decision-making and management is still restricted by the complexity of the models and their application. Yet, member states of the European Union, as well as parties of the Bern Convention, are currently faced with the necessity of designing and evaluating management concepts (cf. Bull 2006; Bruford 2015; Duchamp et al., 2017; Heikkinen et al., 2021; Hatlauf and Hackländer 2022; Institute of Wildlife Biology and Game Management 2022). As such, member states are urged by the European Commission to collect and submit scientific data on wolves to inform international decision making (European Commission, 2023). Within adaptive management by local authorities, easy-to-use applications that can be built-up and adapted rapidly are required (Hatlauf and Hackländer, 2022). The software Vortex offers such a framework. Vortex is an individual-based, stochastic simulation application for wildlife populations and allows for the parameterization of demographic, environmental, and genetic traits (Lacy and Pollak, 2021). It can be accessed via a graphical user interface, seeded with actual data originating from monitoring regimes and adapted to user-specific requirements by implementing personalized functions. In 2020, an update was issued with version 10.5.0, easing the option for Vortex population models to be transformed into a stage-based model (Lacy and Pollak, 2021).

1.3. Situation of grey wolves in Europe

Within Europe, the wolf has been under strict protection since 1979 by the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) and throughout the EU since 1992 by the Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC, FFH Directive) (Trouwborst et al., 2017). The Central European wolf population is considered a large meta-population with several distinct subpopulations; only the Iberian subpopulation is not interconnected with the others (Boitani et al., 2022; Kaczensky et al., 2021; Szewczyk et al., 2021). The expansion of the grey wolf in Europe has gained increasing momentum since the beginning of the 21st century, resulting from national and international conservation efforts (Boitani et al., 2022; Chapron et al., 2014). All countries in mainland Europe now have records of wolves, some of them in large numbers (e.g., Bulgaria, Greece, Italy, Poland, Romania, Spain and Ukraine with more than 1000 individuals), while others have few individuals due to their small size or because they have only recently been re-populated. Nineteen of 34 countries reported increasing numbers (Boitani et al., 2022). Common to them all is the dependence on reliable data. Despite the challenges of the data assessment and the combination of data from different countries, the overall population estimates based on the best currently available data reached approximately 19,000 individuals in the 27 EU Member States and exceeded 21,500 individuals in geographic Europe (excluding Belarus and the Russian Federation) (Boitani et al., 2022). However, a certain variation due to differing methods and accuracy leads to large fluctuations in estimates of wolf numbers and essentially affects thresholds for conservation assessment (Boitani et al., 2022; Hackländer et al., 2021; Kaczensky et al., 2021) or projections in population models (Hatlauf and Hackländer, 2022). Population estimates can vary over time due to research efforts, the dynamic dispersal process and the new settlement of packs.

Moreover, growth rates are tied to resource availability, habitat constraints (capacity limits) and mortality rates (Duchamp et al., 2017). Accordingly, a growth curve flattens once the maximum capacity is reached (Vogt et al., 2020). Wolf populations in Central European countries are subject to different growth rates and have, for example, increased in Italy while becoming smaller in France or Slovenia in recent years (Wolf Alpine Group, 2022). Exponential growth has been shown in some populations, especially in recent years and often at the beginning of the colonization phase, among others for the German part of the European population (Jarausch et al., 2021).

Germany's first reproducing wolf pack was detected in Saxony in 2000 (Reinhardt and Kluth, 2007). Since then, the population has been steadily increasing, and the species is spreading with an annual growth rate of approximately 36 % (Reinhardt et al., 2019). This rate is higher than what is reported for the Scandinavian wolf population (29 % during population expansion, Wabakken et al., 2001, and 18 % during a period of steady growth in 1999–2011, Chapron et al., 2012) but similar to the reported rates for the western Polish population (38 %; Nowak and Mysłajek 2019). In more recent years, the German wolves started showing signs of a sigmoid population trajectory, although monitoring records might still be complemented (database of the DBBW, the Federal Documentation and Consultation center on Wolves, https://www.dbb-wolf.de/home). Within Germany, the wolf is a strictly protected species according to the Federal Nature Conservation Act (§ 7 paragraph 2 No. 14). In the current Red List of Mammals of Germany (prompted 2020), the wolf is classified in the category "endangered". The leading causes of this endangerment are high mortality in road traffic and illegal killings (Boitani et al., 2022; Musto et al., 2021). However, while between 2000 and 2004, only two successful breeding pairs were known within Germany (Jarausch et al., 2021), in the monitoring year 2020/21, at the federal level, a total of 203 wolf territories (including 157 wolf packs, 27 pairs, and 19 territorial individuals) were recorded (DBBW database, https://www.dbb-wolf.de/home).

To mitigate wolf-based conflicts and implement EU-law conform wildlife management, management plans build the framework for monitoring and compensation or other conflict-reducing and coexistence-promoting measures (cf examples Sächsisches Staatsministerium für Umwelt und Landwirtschaft (SMUL) 2014). Decisions need to be based on reasonable biological and data-driven facts (Duchamp et al., 2017), and political stakeholders, as well as management authorities, need support on the grounds of scientific facts and research (Hatlauf and Hackländer, 2022). As such, authorities and other acting bodies need flexible, easily adaptable modeling solutions to build projections regularly incorporating the most recent data. As wolves are social animals with population dynamics centered around the pack as a functional unit (Chapron et al., 2016; Mech and Boitani, 2003), vital rates depend on the individual's social status. Hence, stage-based IBMs are ideally suited to represent wolf populations and study potential population development.

In this study, we aimed 1) to develop a species-specific stage-based transition model for Central European wolves and 2) to implement it into Vortex using functions for individual state variables. As a case study, we applied our model to the German part of the European wolf population to project population trajectory and genetic parameters under various realistic yet hypothetical scenarios. Ultimately, we provide an easy-to-use-and-adapt set of Vortex functions for future wolf PVA to be used by scientists, authorities and practitioners to inform adaptive management and decision-making.

2. Materials and methods

2.1. Developing a stage-based transition model for wolves

We built a life cycle model for European wolf populations, with stage classes representing the life stages of a wolf individual (Fig. 1). Being born as a pup, an individual will stay within its pack as a yearling and later as a subdominant (including subadults and non-breeding adults). However, individuals of all three stages might become dispersers, looking to establish their pack or overtake an existing one. If successful, dispersers will become territorial and advance to the dominant, breeding individuals within their pack. In rare cases, the subdominant individuals within a pack might also become the dominant ones (Chapron et al., 2003; Okarma and Herzog, 2019). Based on an extensive literature review we parameterized the life cycle model with transition rates describing the probability of an individual changing from one stage to another (Haight and Mech 1997; Marescot et al., 2012; Chapron et al., 2016; Bauduin et al., 2020 and references therein). Transition and survival are separate processes (Caswell, 2001), and transition rates must add up to 100 %. Hence, we modeled transition and survival to be separately applied per individual (Table 1). The in-stage self-loops represent the probability of individuals remaining in the respective stage.

2.2. Implementing the stage-based transition model into Vortex

We used Vortex 10.5.6 (Lacy and Pollak, 2021) to build an individual-based PVA that allows for the projection of population trajectory and genetic parameters. To improve the flexibility and power of a Vortex model, state variables can be used to describe additional characteristics of the modeled species and population. All state variables are referenced by either a variable ID or label. Users can also overwrite pre-built functions within Vortex. This allows Vortex to serve as a highly flexible modeling environment. By creating a set of Individual State variables (ISvars), we adapted the default age-based structure of Vortex into a stage-based structure and implemented wolf-specific life history parameters (Table 1). As we built an individual-based model, we did not use Global State variables (GSvar) or Population State variables (PSvar). Sensitivity tests in Vortex were conducted to examine the impact of uncertainties and variations in input parameters on model outcomes. By varying specific parameters, we were able to analyze how robust population estimates and predictions were to changes in these parameters.

Within our model, IS1 is used to specify the number of offspring that depend on their mother for a defined period, 1 year in our model. If the mother dies, all presently dependent offspring will be killed by the simulation. IS2 was used to adapt the default age-based model structure into a stage-based one by altering the built-in AGE function. By default, AGE tracks the individual’s age during the modeling process. Using our altered function, AGE now tracks the life cycle stage according to our life cycle model (Fig. 1). Within each time step, a random draw decided about an individual’s transition. Thereby, we prevented individuals from being duplicated into two stages simultaneously. Due to this approach, our stage-based transition model included further inherent stochasticity. The initialization function (starting value for each individual at the beginning of the simulation was coded with an "A," representing the starting stage (instead of the former AGE) of each individual in the dataset used to seed the model. The birth function (value for each newborn individual) was coded with a "0″, representing stage 0 (pups). To complete the modification of the model structure from age to stage, the "AGE" step within the “Order of events in a Vortex year" had to be removed so that AGE (tracking stage) did not automatically increment yearly. As we overwrote the default age-based model, we had to redefine maximum lifespan, mortality and reproduction, as these functions depend on the AGE variable. Hence, we used IS3 to create a new variable tracking age, IS4 to implement a maximum life span of 15 years (according to Bauduin et al., 2020) based on IS3, and IS5 - IS9 to implement mortality rates per stage (i.e., survival rates, cf. Table 1). Regarding IS4 - IS9, the initialization and birth function were always set to 1. Reproduction was modeled in the Vortex interface tab "Reproductive system" using stages 0 - 4 instead of specific ages. The overall time step in our model comprised one year, as we assumed that within wolves, reproduction happens once a year (Okarma and Herzog, 2019). For each time step, every individual was subject to the following processes and the same order of events (assessable in "Scenario Settings"): EV, ISUpdate (including transition), Breed, Disperse, Supplement, rCalc, Ktruncation, Census.

2.3. Case study: a stage-based PVA in Vortex for wolves in Germany

We used the German part of the European wolf population as a case study to apply our stage-based transition model within Vortex and support the development of an adaptive management process. Germany established a state-wide wolf monitoring program with the main objectives to record the area of occurrence and population size (specified as minimum numbers of packs with reproduction), territorial pairs, and individual wolves annually (Jarausch et al., 2021; Reinhardt et al.,

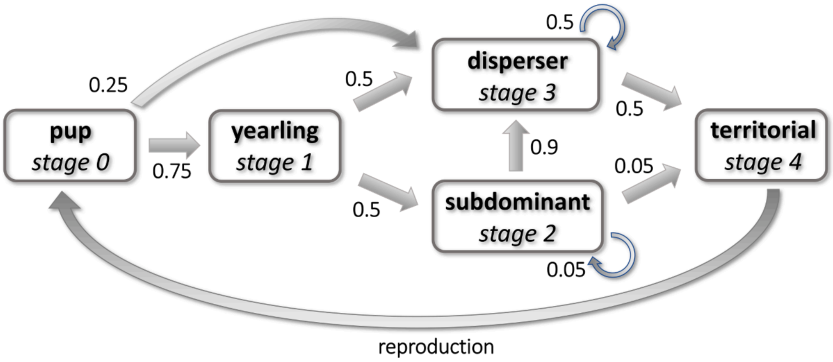

Fig. 1. Stage-based life cycle model for Central European grey wolves, with stages as boxes and transition rates in between. The arrows and values indicate the average transition rate of individuals growing from one life stage to another. Reproduction occurs only in stage 4, based on parameters described in Table 2.

Table 1
Formulas and description of coded Individual State variables (ISvars) used to implement a stage-based transition model in Vortex.

Variable ID	Label	Initialization function	Birth function	Transition function	Explanation
IS1	Dependent Offspring	0	0	=IS1	ISvar (IS1) is automatically created by Vortex to specify the number of newborns that depend on their mother until they become X years old. X is specified within the Vortex interface, see Table 2.
IS2	AGE	A	0	=IF(*A* = 0;IF(RAND>0,25;1;3);IF(*A* = 1;IF(RAND>0,5;2;3); IF(*A* = 2;IF(RAND>0,1;3;(3)OR(4));IF (*A* = 3;IF(RAND>0,5;4;3);IF(*A* = 4;4;4)))))	The main transition function adapts the model structure from default age-based to stage-based. Based on the transition rates, individuals start in stage 0 and will transition into further stages (Fig. 1).
IS3	IS3	0	0	=IS3+1	Tracking the age of individuals by advancing a counter per year.
IS4	ALIVE	1	1	=IF(IS3=15;0;1)	Implementing maximum lifespan (15 years) by removing individuals from the simulation when 15 is reached.
IS5	ALIVE	1	1	=IF((*A* = 0)AND(RAND>0,5);0;1)	Stage 0 (pups) survival rate, modeled by setting ALIVE to 0 if a random number exceeds the survival rate (50 %).
IS6	ALIVE	1	1	=IF((*A* = 1)AND(RAND>0,82);0;1)	Stage 1 (yearlings) survival rate, modeled by setting ALIVE to 0 if a random number exceeds the survival rate (82 %).
IS7	ALIVE	1	1	=IF((*A* = 2)AND(RAND>0,82);0;1)	Stage 2 (subdominants) survival rate, modeled by setting ALIVE to 0 if a random number exceeds the survival rate (82 %).
IS8	ALIVE	1	1	=IF((*A* = 3)AND(RAND>0,69);0;1)	Stage 3 (disperser) survival rate, modeled by setting ALIVE to 0 if a random number exceeds the survival rate (69 %).
IS9	ALIVE	1	1	=IF((*A* = 4)AND(RAND>0,82);0;1)	Stage 4 (territorials) survival rate, modeled by setting ALIVE to 0 if a random number exceeds the survival rate (82 %).

2013). Data collection is carried out by each federal state. Since 2009, efforts are made to establish state-wise uniform standards for wolf data collection and publication, with most of the data being made publicly available in the DBBW database. This collection includes wolf occurrence in the form of territorial packs, pairs, and individuals, along with their geographic location. Furthermore, models of habitat suitability and selection provide important knowledge about inhabitable area and consequently carrying capacity (Kramer-Schadt et al., 2020; Planillo et al., 2023). Additionally, genetic monitoring is conducted (further described in Jarausch et al., 2021).

2.4. Data gathering and analyses

We built the PVA within Vortex seeded with data from the DBBW and the genetic monitoring (Jarausch et al., 2021). We used the R programming language version 4.2.2 (R Core Team, 2022) to handle and process the data. The DBBW data was acquired on the 07.10.2021 using the package *rvest* (Wickham, 2022). The packages *dplyr* (Wickham et al., 2021a), *tidyr* (Wickham et al., 2021b), *stringr* (Wickham, 2019), and *purrr* (Wickham and Henry, 2020) were used for data processing. Graphs were generated using the package *ggplot2* (Wickham, 2016). The forward simulations were initiated using the known German wolves in the year 2015. Between 2005 and 2015, approximately 96 % of the breeding pairs in Germany were genotyped (Jarausch et al., 2021), resulting in 524 individuals identified by microsatellites. Thanks to the state-wide unique ID of each wolf individual, we could link the genetic data with further information from the DBBW. The ratio of genetically identified individuals was not constant among monitoring years and decreased from 2013. We chose 2015 as the starting year for further simulation as the number of identified breeding pairs and the ratio of genetically identified individuals was still high (85.3 % and 79.4 % for females and males, respectively). We seeded the Vortex forward simulations using a studbook including the following variables per individual: ID, sire, dam, sex, alive, stage, population and the genotypes of 13 microsatellite loci. Sire (father), dam (mother) and sex were extracted from the DBBW (the Federal Documentation and Consultation center on Wolves) data. For 33 individuals, a cause of death was known. Individuals with unknown status (death or alive) were assumed to be alive if detected within 2013, 2014, or 2015 or known to be territorial individuals. Out of all non-territorial individuals that have not been detected in these past three years, 10 % were randomly set to dead, as we assumed that not all undetected individuals from these years had survived. The initial life cycle stage of recent individuals was modeled depending on their age. As data about the birth year was available for some individuals (from the DBBW), we calculated the mean age at first detection of those individuals using an intercept-only model with Poisson error. We then used the model coefficient to randomly draw years of age for all individuals with unknown age from a Poisson distribution at first detection. Microsatellite genotypes per individual were supplied to Vortex in genepop format using GenAlEx 6.503 (Peakall and Smouse, 2012, 2006).

Simulations are generally highly dependent on the correct choice of input parameters (Patterson and Murray, 2008); hence, great care needs to be taken during model parametrization. As such, we based our model parameterization on a vast body of literature on recently reported life history parameters of comparable wolf populations and, if not reported, calculated parameters from data. Simulation input parameters are given in Table 2 and explained in detail in Appendix A.

Vortex was then run, including fifteen realistic yet hypothetical scenarios (Table 3), with simulations running for 30 years each. As Vortex is a stochastic engine, we replicated each scenario 1000 times. The population is considered closed throughout the scenarios, except for scenarios where "Supplementation" is simulated (S4).

After the simulations, we visualized the demographic curves of the scenarios with their standard deviation and extracted the probability of extinction. We further extracted the genepop output per run for thirteen scenarios (excluding S4, as the genotypes of Vortex-simulated individuals were not based on known frequency distributions and hence were not feasible in analyses). We calculated and visualized standard measurements of genetic diversity over all replicates, including the number of alleles per locus N_A, observed heterozygosity H_O, expected heterozygosity H_E and inbreeding coefficient F_{IS} with confidence intervals using the R packages *adegenet 2.1.1* (Jombart, 2008; Jombart and Ahmed, 2011) and *hierfstat 0.5–7* (Goudet, 2005).

3. Results

From the fourteen scenarios beside the default scenario, nine resulted in an increasing population size trend, while two resulted in a stable or decreasing population size trend and three scenarios displayed a reasonable probability of extinction within the next 30 years (Table 4, Fig. 2).

Following the assumptions of the default scenario, the carrying capacity based on Kramer-Schadt et al. (2020) for the German part of the

Table 2
Summary of input parameters and associated data sources for the default scenario of the population viability analysis of the grey wolf in Germany.

Parameter	Value and source
Number of iterations	1000
Number of years	30/100
Duration of each year in days	365
Extinction definition	Only individuals of one sex remain
Census each year for the first	Yes, for all 1000 iterations
Lethal equivalents	6.29 (O'Grady et al., 2006)
Reproductive System	Long-term monogamy
Maximum number of broods per year	1
Make offspring dependent	Yes, for 1 year
Proportion of reproducing females	Calculated via linear model (cf. Supplemental material)
Number of pups per litter	Randomly drawn from a Poisson distribution with an alpha value of 6.1, based on Bauduin et al. (2020) and Šuba et al. (2021), with a maximum limited to 13 (=POISSON(6.1))
Maximum number of pups per litter	13 (this is the indicated maximum number of pups within the German wolf monitoring; DBBW)
Sex-ratio	1:1 (Chapron et al., 2003; Lovari et al., 2007)
Stage of reproduction	Only individuals in stage 4 (territorial) can reproduce
Maximum age	15 years (Bauduin et al., 2020)
Mortality stage 0	50 % (Bruford, 2015; Nowak and Mysłajek, 2016)
Mortality stages 1 and 2	18 % (Bauduin et al., 2020; Marucco et al., 2009; Nilsson, 2004)
Mortality stage 3	31 % (Bauduin et al., 2020; Blanco and Cortés, 2007)
Mortality stage 4	18 % (Bauduin et al., 2020; Marucco et al., 2009)
Average pack size	6.4 (Romański et al., 2018)
Carrying capacity (K)	Estimation of potential ecological carrying capacity for wolf territories (1400, from Kramer-Schadt et al., 2020) times average number of individuals per pack (6.4, from Romański et al., 2018) results in 8960 individuals
Supplement	=POISSON(10) (scenario S4b implemented a stochastic function, drawing the number of immigrants from a poisson distribution with mean 10)
Number of loci that are modeled and can mutate	14 (13 microsatellite loci from Jarausch et al. (2021) and one default locus by Vortex; with a mutation rate of 4.5^{-4}, Whittaker et al., 2003)

Table 4
Summary statistics of the vortex simulation output per scenario. Stoch-r mean stochastic growth rate (as experienced in the simulations, averaged over all years the population was extant), SD(r) standard deviation of the stochastic growth rate, PE probability of extinction after the simulated period, meanTE mean time to extinction in years.

Scenario	Years of simulation	Stoch-r	SD(r)	PE	meanTE
DS	30	0.1251	0.0747	0.0000	0.0
S1	30	0.1259	0.0748	0.0000	0.0
S2a	30	0.0051	0.1156	0.0000	0.0
S2b	30	0.0897	0.0827	0.0000	0.0
S2c	30	0.1082	0.0719	0.0000	0.0
S2d	30	-0.1332	0.2433	0.4310	27.2
S3a	30	-0.0926	0.2101	0.1080	27.6
S3b	30	-0.0253	0.1270	0.0010	30.0
S3c	30	0.0244	0.0973	0.0000	0.0
S3d	30	0.0674	0.0838	0.0000	0.0
S4a	30	0.1320	0.0745	0.0000	0.0
S4b	30	0.1499	0.0745	0.0000	0.0
S5a	30	0.0430	0.3011	0.2140	21.9
S5b	30	0.0952	0.1977	0.0030	27.3
S5c	30	0.1396	0.0953	0.0000	0.0
S2a	100	-0.0380	0.1834	0.4970	88.0
S3c	100	0.0046	0.0879	0.0260	87.3
S3d	100	0.0633	0.0532	0.0000	0.0

Central European wolf population could be reached in 25 years, translating approximately to the year 2040. As the DS is based on the most likely life history parameters and seeded without further assumptions, it provides a basis for comparisons with other scenarios. Only one scenario showed an enhanced increased population trend compared to DS, scenario S4b (with higher immigration rates). Reducing the maximum number of pups per litter from 13 (DS) to 7 (S1) had no immediate effect on population growth. Increasing mortality, however, affected population growth differently, depending on the life cycle stage. An increase in pup mortality (stage 0) from 50 % (DS) to 76 % (S2a) resulted in a negative population growth (however no extinction within 30 years). The increase of disperser mortality (stage 3) from 31 % (DS) to 78 % (S2d) lead to an extinction probability of 43 %. An increase in yearling mortality (stage 1) from 18 % (DS) to 40 % (S2b) and in subdominant mortality (stage 2) from 18 % (DS) to 40 % (S2c) however showed positive population growth, yet lower than in the DS. Within territorial individuals (stage 4), increased mortality led to decreasing population growth for S3d (increase from 18 % to 25 %) and S3c (increase from 18 % to 30 %). While the population showed slight growth in these scenarios, only marginal to no growth could be detected when territorial mortality increased to 30 % (S3b) and 40 % (S3a), leading to average extinction probabilities of 12 % and 43 %, respectively. The immigration of wolves from outside Germany (S4a, S4b) positively affected the population's growth curves. Naturally, the effect was stronger when more wolves immigrated, leading to the only scenario that reached the carrying capacity earlier than the DS. Artificially reducing carrying

Table 3
Description of all scenarios used in the PVA for German wolf.

Scenario name	Scenario label	Verbal description of the scenario
Default	DS	The default scenario represents the most likely scenario (based on the parameters in Table 2)
Reproduction	S1	The maximum number of offspring in this scenario was reduced to 7
Mortality	S2a	The mortality in stage 0 (pups) was increased to 76 %, based on a study in the Western Alps (Marucco et al., 2009)
	S2b	The mortality in stage 1 (yearling) was increased to 40 %, based on a study on Scandinavian wolves (Bruford, 2015)
	S2c	The mortality in stage 2 (subdominant) was increased to 40 %, based on a study on Scandinavian wolves (Bruford, 2015)
	S2d	The mortality in stage 3 (dispersers) was increased to 78 %, based on a study on dispersers in Schleswig-Holstein and Denmark (Sunde et al., 2021)
Mortality (stage 4)	S3a S3b S3c S3d	Given that only territorial individuals can reproduce, mortality in that stage was assumed to impact population trajectory directly. Hence, different gradations between 25 % and 40 % of mortality were implemented in the scenarios based on 3a = 40 %, 3b = 35 %, 3c = 30 %, 3d = 25 %
Immigration	S4a	Immigration into the population was defined as one individual per year (per sex), i.e., two per year. Immigrating individuals are simulated by Vortex
	S4b	Immigration into the population was defined as ten individuals per year per sex (drawn from a poisson distribution). Immigrating individuals are simulated by Vortex
Carrying capacity	S5a	Carrying capacity was reduced to 50 individuals.
	S5b	Carrying capacity was reduced to 100 individuals.
	S5c	Carrying capacity was reduced to 500 individuals.

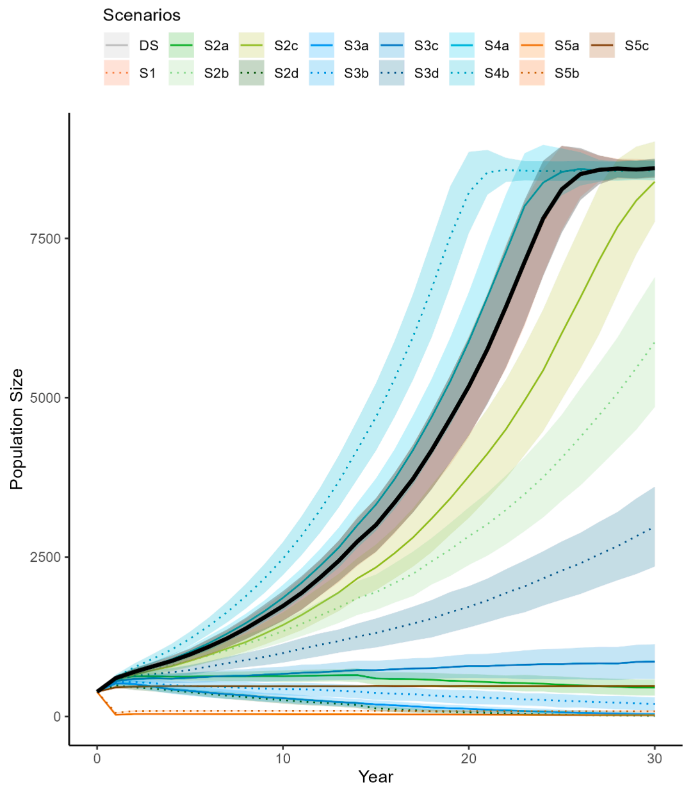

Fig. 2. Overview of all simulated scenarios by year with standard deviation. The black line shows the DS (which overlays with S1, as their population trajectory is quite similar).

capacity (S5a, S5b) to low population sizes (50 and 100) resulted in an increased probability of extinction.

Although the German part of the Central European wolf population cannot be considered a closed population (Szewczyk et al., 2021), the scenarios DS to S3d and S5 did not include immigration to enable analyses of genetic summary statistics. Alleles of simulated immigrating individuals are unknown and unfeasible to model without detailed knowledge about the originating population allele frequencies. Hence, we excluded scenarios with immigrating individuals from our genetic analyses. Within measurements of genetic diversity (Table 5), the mean number of alleles per locus differed strongly between scenarios, as N_A generally depends on N (Table 5, Fig. A3). All scenarios showed comparable measurements in observed and expected heterozygosity expect for scenarios with low carrying capacity (S5a, S5b), and inbreeding coefficients were low and insignificant for all scenarios (Fig. A4).

Table 5
Mean genetic summary statistics of the simulated population after 30 years and the seed population (2015) used to seed the Vortex runs taken from Jarausch et al. (2021), rounded. For the summary statistics of the seed population, only individuals that were deemed alive have been included in the analyses. N number of individuals in the resulting population, N_A mean number of alleles per locus, H_O observed heterozygosity, H_E expected heterozygosity, F_{IS} inbreeding coefficient. Based on 95 % confidence intervals, no inbreeding coefficient was significant. Note that we did not calculate genetic summary statistics for S4a and S4b, as the genotypes of simulated immigrating individuals were unknown.

Scenario	N	N_A	H_O	H_E	F_{IS}
2015/seed population	387	6.2	0.566	0.568	0.0027
DS	8580	19.1	0.584	0.584	-0.001
S1	8583	19.	0.584	0.583	-0.0009
S2a	472	6.6	0.580	0.575	-0.0078
S2b	5813	14.5	0.583	0.582	-0.0019
S2c	8436	17.6	0.583	0.582	-0.0011
S2d	15	2.7	0.554	0.555	-0.0474
S3a	41	3.5	0.558	0.566	-0.0118
S3b	211	5.1	0.573	0.567	-0.0139
S3c	847	7.1	0.578	0.575	-0.0061
S3d	3029	10.8	0.582	0.581	-0.0026
S5a	25	2.6	0.482	0.483	-0.0380
S5b	82	3.5	0.534	0.542	0.0006
S5c	478	5.6	0.576	0.572	-0.0074

4. Discussion

4.1. *Stage based vs age based*

PVAs and the software to build them have been improved steadily since their development about 35 years ago (Lacy, 2019). What started as an implementation of matrix population models (Caswell, 2001) has soon moved to modular simulation engines accounting for a comprehensive set of confounding factors affecting a population's development. As such, age-based modeling approaches have been widely applied to model wolf populations in the past two decades to answer various questions (Bruford, 2015; Carroll et al., 2019, 2014; Chapron et al., 2012; Jensen and Miller, 2001; Marescot et al., 2012; Miller, 2017; Nilsson, 2004). However, as a social species, several life stages define typical behavioral characteristics independent of the individual's age which are fundamental for mortality or reproduction probabilities. Dispersing individuals (stage 3 in our model) face different mortality than territorial individuals within a pack (Sunde et al., 2021) and population dynamics are centered around the pack as a breeding unit (stage 4 in our model). As such, its life cycle and vital rates are best represented within a stage-based modeling approach. Neglecting social structure might lead to skewed projections and might ultimately misinform decision-making (Marescot et al., 2012). Stage-based modeling approaches allow to model the full complexity of demographic traits of social species (Chapron et al., 2016). Additionally, they enable analyses of responses to management actions, as those are typically set per life stages (especially for species where age cannot be assessed easily).

Chapron et al. (2003) developed a life-cycle model for wolf populations based on social stages. Within their IBM, stages were age classes based on months alive, as data to parameterize vital rates and transition rates per social status were few at the time. In 2016, the model was advanced and applied to the Scandinavian wolf population (Chapron et al., 2016). Although based on a life cycle model comparable to ours, the model's implementation and intention differed from the concept of a PVA. The model comprised individual, pack, and population levels and proceeded in monthly time steps, including the transition between stages, to estimate population size from counts of one segment of the population (Chapron et al., 2016). Marescot et al. (2012) also developed a comparable yet female-only life-cycle model. Besides differences in the life cycle models and temporal scales used, our approach adds to these models by allowing individuals to remain within one stage, implemented via self-loops.

Using Vortex and implementing our life cycle model, we created a PVA for wolves based on the social structure rather than the age. Vortex has already been used successfully in studies on the management of the Mexican Wolf (*C. lupus baileyi*) (Carroll et al., 2019, 2014) or the red wolf (*C. rufus*) (Miller et al., 2023). While self-coded functions expanded these models on factors like the proportion of females breeding and inbreeding-dependent litter size, among others, behavioral factors influencing the population dynamics could only be accounted for in a simplified way (Carroll et al., 2019). However, projections initiated with PVAs of these kinds can vary greatly in their outcome depending on the distribution of individuals per stage (Mills, 2012), showing the importance of using actual data originating from thorough monitoring regimes. Hence, we built our model based on the known wolf population within Germany and carefully chose parameters best representing the life history of German wolves. As such, the default scenario (DS) mainly focused on generating reasonable predictions and comparing the effect of changing life history parameters on the population trajectory and genetic integrity. Therefore, the default scenario did not include extreme assumptions and ignored additional population-threatening aspects, i.e., due to catastrophes. While this allows the default scenario to serve as a valid baseline for scenarios, it should be noted that stochastic catastrophes should be accounted for when building models primarily for predictions (e.g. sarcoptic mange in wolves, Fuchs et al., 2016). This can easily be incorporated via the Vortex tab for catastrophes.

Our model is intended as a generally applicable and adaptable framework for grey wolf populations in Europe, hence we did not include any form of spatial substructure. As such, mate choice is assumed to be unaffected by geographic proximity or other spatial factors. As dispersing wolf individuals searching for mates are known to overcome large distances and unsuitable areas (Ražen et al., 2016; Wabakken et al., 2007), we did not expect to overestimate genetic diversity by sparing to account for substructure, especially during phases of population expansion. Yet, we advise users of our model to critically evaluate their target population and whether spatial substructure should be accounted for. Within the Vortex environment, any spatial substructure can readily be implemented by dividing the individuals into subpopulations using the studbook input, allowing for different life history parameters per subpopulation and any form of migration between subpopulations. Within our case study, we refrained from including any spatial substructure, as wolves within Germany are considered part of the larger Central European population (Szewczyk et al., 2021). On a small spatial scale, we might have overestimated genetic diversity to a minor degree given that habitat availability with Germany (Planillo et al., 2023) might restrain wolf mate choice to some extent.

Our model does not account for age-dependent senescence besides a maximum life span of 15 years. With an increasing body of proof and population dynamic data, our model could, however, be extended to include such, for example, by implementing an age-dependent decrease in fecundity (reproduction rate) or increase in mortality. Such an extension would be possible via the “RATE” and “AGE” functions. We also suggest future implementations to include forced transitions driven by years spent in the same life stage, as our functions theoretically allow for individuals to stay within their life stage until the age of 15 (although highly unlikely). We implemented density-dependence via estimated carrying capacity for wolves in Germany (based on Kramer-Schadt et al., 2020, Table 2), with Vortex removing excess individuals. However, we did not account for density-dependent effects on life history parameters in our model, as German wolves are currently not impeded by lack of space (Planillo et al., 2023) or prey (Greiser et al., 2023). We advise users of our model to review their target populations in detail and evaluate whether or not density-dependent effects on life history parameters should be included and reliable data is available. In such case, the effects of density-dependence could be implemented by expanding our set of individual state variables (Table 1) including functions for a decrease in reproduction and an increase in mortality as a response to the total number of individuals approaching carrying capacity. Additionally, our model did not account for specific increase in pup mortality or decrease in reproduction rate in the case of the loss of one of the breeding mates. While this was observed for wolf populations in Alaska (Borg et al., 2015) and within a data re-analysis of field studies (Brainerd et al., 2008), it seemed to have no effect on overall population dynamics (Borg et al., 2015).

By incorporating the stage-based functions into Vortex, built-in functions for catastrophes and harvest cannot be included per default because these parameters refer directly to mortality rates, which we had to overwrite using our functions to build the stage-based model. Furthermore, some of the deterministic output results, like effective population size or growth rate (r), are not meaningful because of these adaptations in programming. These challenges could be met in future implementations of Vortex, enhancing its usability even further.

4.2. Case study on German wolves

Our stage-based model was applied to assess the German part of the European wolf population. Thereby, we could seed our PVA using data from the actual population, including the distribution of sexes, stage classes and genotypes, and to parameterize the life history parameters through reported or data-derived values. By implementing scenarios varying the life history parameters, we were able to pinpoint their effect on the population trajectory, extinction probability and genetic integrity of the population.

S1 explored the effect of the maximum number of pups per litter. As such, it has wide implications for monitoring regimes, indicating whether or not high efforts should be made to monitor the complete litter size or stop above a certain threshold of monitored pups per litter. Our simulations showed that the first counted pups in the context of reproductive monitoring are much more important than the recording of the 12th or 13th pup. Focusing on the survey of reproducing packs, with good knowledge of the average number of pups, seems more meaningful than spending many resources to monitor all pups per litter (cf. Chapron et al., 2016). In summary, exceptionally large litter sizes did not play an important role in population trajectory, whereas average litter size showed significant effects, as expected.

A major cause of mortality in wolves is interactions with humans. Wolves tend to show higher survival rates where settlement and road densities are lower (less than 0.6 km / km2; Lovari et al., 2007). Traffic accidents are also among the most common mortality in Germany (Reinhardt et al., 2020). S3a (increased mortality of territorial individuals to 40 %) resulted in an increased probability of extinction within the next 30 years. According to a simulation on Scandinavian wolves (Chapron et al., 2012), none of the simulated populations were viable within 100 years when their overall mortality was set to around 39 %; in our presented case, even after 30 years this effect was documented. Additionally, we ran three scenarios for a 100-year time-span to explore probability of extinction. These additional simulations resulted in a probability of extinction of 2.6 % for scenario S3c (mortality of stage 4 with 30 %) after 87 years on average. Further, S2a showed an extinction probability of 54 %. However, simulations over a longer time period become increasingly unspecific and results are less precise. Especially from a management perspective, 30 years is already a long enough period to conceive and evaluate management actions. If a study does not aim at understanding long-term effects such as the impact of climate change for example, it is much more informative to reduce the time horizon of the prediction, enhancing realism and precision.

Overall, the mortality of territorial (stage 4) wolves greatly influenced population trajectory. Mortality rates hereby differ between studies (24 % for Scandinavian wolves in Chapron et al., 2012, 18 % for Italian wolves in Marucco et al., 2009, or 25–34 % in Caniglia et al., 2014), which is why we designed several scenarios. Mortality may also be density-dependent and might increase with increasing pack size (due to intraspecific aggression, prey availability, etc.; Cubaynes et al., 2014). However, as we lacked reliable data on such density-dependence effects, we refrained from including it in our simulations.

Within PVAs, genetic effects are known to interact with demographic effects affecting the population trajectory and hence need to be included (Mills and Smouse, 1994). Scenarios S5a and S5b resulted in higher extinction risks due to negative growth rates. This population decrease was explained by the effect of inbreeding within our model, as additional runs for S5a and S5b without the inclusion of inbreeding (same settings expect for inbreeding depression unchecked within Vortex) resulted in the respective population to become stable at the level of carrying capacity (Fig. A2). As such, inbreeding depression played a major role especially in populations with low carrying capacity and severely affected their probability of extinction. Strong effects of inbreeding are known for several wolf populations, including the Isle Royale wolves (Hedrick et al., 2014), the Scandinavian population (Åkesson et al., 2016) or the Finnish population (Jansson et al., 2012).

By seeding our PVA with real genotypes, we could simulate the genetic integrity of the projected future populations. After a bottleneck, small populations originating from few founder individuals could still show high levels of genetic diversity and small levels of inbreeding within the first few generations. But within the following generations, although census sizes might grow exponentially, such populations could, seemingly unintuitive, display trends of decreasing diversity and increasing inbreeding due to genetic drift and forced inbreeding. This was observed for the Scandinavian and the Finnish wolf populations following a severe bottleneck (Jansson et al., 2012). Within wolves, parent-offspring mating events are known to occur (Sidorovich and Rotenko, 2019) and were documented for the German wolves as well (Jarausch et al., 2021). Hence, while quite good levels of genetic diversity within the German wolves of 2015 (12 years after their first reappearance) were found (Jarausch et al., 2021), high uncertainty about their future genetic diversity remained. Within our simulations, we found genetic diversity (H_O, H_E) and inbreeding (F_{IS}) of all scenarios expect S5a and S5b to be comparable with the original wolf population in 2015 (Table 4). Hence, no decreasing trend could have been detected as long as the population is not artificially reduced to low numbers (as in S5a and S5b). High mortality naturally led to smaller population sizes, increasing variance in genetic diversity (scenarios S2a to S3d in Fig. A4 and Table 5), but did not induce significant deviation between expected and observed heterozygosity (as no F_{ST} value was significant). The genetic diversity of our simulated populations in 2050 was generally good compared to other Palearctic wolf populations (Aspi et al., 2009; Jansson et al., 2012; Jarausch et al., 2021; Lucchini et al., 2004; Žunna et al., 2023 and references therein). Potential negative effects due to a founder effect within the German wolves could have been avoided probably due to the high proportion of immigrating individuals in the first years of establishment (Jarausch et al., 2021), which was shown to affect genetic diversity significantly (Carroll et al., 2019). As our simulations did not show a decrease in genetic diversity over time as long as the population was not held at low numbers, we conclude that the initial population in 2015 was sufficient in genetic diversity and population size to maintain genetic diversity, at least for the time period simulated.

4.3. Conclusion

PVAs are promising tools for adaptive wildlife management because they can provide important information for scenario planning. Hereby, especially easy-to-use approaches will help bridge the gap between scientific analysis and decision-making and hence increase transparency. Yet, the main reason for PVAs lies within scientific uncertainty about population sizes, vital rates and confounding effects, and stochastic events affecting the population dynamics (Lacy, 2019). In this light, PVAs must be applied and interpreted cautiously (Carroll et al., 2019), and great care must be laid on several aspects, especially if results are meant to inform decision-making.

At their core, matrix population models are a set of deterministic functions (Caswell, 2001), yet implementing transition and vital rates leads to several levels of stochasticity. Hence, PVAs should not be used for precise predictions but to rank and evaluate management actions while accounting for their uncertainty (Lacy, 2019; Mills, 2012). Central to every population dynamics modeling approach is a life cycle model. However, besides the decision about the stages, the distribution of the initial individuals within these stages affects population growth (Mills, 2012). Hence, simulations should be seeded with monitoring data to represent the targeted population. Additionally, modeling genetic effects within a PVA is crucial as demographics and genetics are known to interact, especially in small populations (Mills and Smouse, 1994).

If applied thoughtfully, easy-to-use applications of PVAs will allow for important fundamentals, ultimately supporting evidence-based decision-making (Carroll et al., 2019). While PVAs are not exclusive to people in the scientific sector and should find entrance into local authorities and practitioners, they must not be done alone. Complex simulation models, even if easy to use, might still need much different expertise. Hence, PVA technicians might need to be assisted by various experts in species biology, genetics, behavior, and stakeholders representing economic or sociocultural aspects (Lacy, 2019).

After wolf population models have been implemented in Netlogo (Bauduin et al., 2020; Recio et al., 2020), as IBM within a Bayesian framework (Chapron et al., 2016), as an open-population spatial capture-recapture (OPSCR) model (Bischof et al., 2020) or as an age-based model within Vortex (Carroll et al., 2019 and references therein), we now supplement these by providing an individual-based, stage-based implementation for European grey wolf to be used in Vortex. Ultimately, we provide an easily accessible and ready-to-use model framework which can readily be expanded with appropriate adaptions for density-dependence, spatial substructure, age-dependent senescence, environmental stochasticity and more. Such a model, if thoughtfully tested for reliability, can serve as a valuable tool to inform management decisions, especially in situations where more complicated models are not feasible.

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Relationships

There are no relationships to disclose.

Ethics approval

Not applicable.

CRediT authorship contribution statement

J. Hatlauf: Writing – review & editing, Writing – original draft, Software, Project administration, Methodology, Formal analysis, Conceptualization. **F. Kunz:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Conceptualization. **P. Griesberger:** Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Conceptualization. **F. Sachser:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **K. Hackländer:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The funding organization had no direct or indirect influence on the study design, methods, results, or interpretation and was not involved in generating this manuscript in any way. The authors declare no conflict of interest.

Data availability

The data used is publicly available.

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Appendix A

Input parameters for the Vortex simulation of German wolves

Various modeling approaches of wolf populations (e.g., on the Mexican wolf *Canis lupus baileyi* (Carroll et al., 2019) or wolves in France (Duchamp et al., 2017), as well as spatially explicit studies for Austria (Crook and Paulus, 2016) have included either assumptions or actual data. The life history parameters, in general, are always debated because inaccurate values can lead to inadequate predictions (Patterson and Murray, 2008). In the presented case study on the German part of the Central European wolf population, we mainly referred to repeatedly cited models from Central Europe and, regarding life history parameters, primarily focused on studies of surrounding wolf occurrences like in France (Bauduin et al., 2020; Chapron et al., 2016, 2003; Duchamp et al., 2017) or in Poland (Nowak et al., 2017; Reinhardt et al., 2013). Missing parameters were subsequently supplemented using studies from Scandinavia (Bruford, 2015; Bull, 2006; Chapron et al., 2012; Nilsson, 2004) or Belarus (Sidorovich et al., 2007). The following parameters were considered within our model: **reproduction, survival** (mortality) and **dispersal**.

Reproduction

Reproduction within Vortex is defined as the number of offspring produced per female wolf in a given period in a given population. The proportion of reproducing females was calculated via a logistic regression model based on the known ratio between reproducing females over all females detected in a given year (Fig. A1). Empirical studies showed that average litter size typically varies between four and nine pups (Fuller, 1989; Mech and Boitani, 2003; Miller et al., 2002; Webb et al., 2011). Studies from Europe place the average litter size between 4.4 and 7.7 (Sidorovich et al., 2007), 6.6 (Bruford, 2015) and 6.1 (Bauduin et al., 2020; Šuba et al., 2021). For reproducing females, the number of pups was randomly drawn from a Poisson distribution with an alpha value of 6.1, based on Bauduin et al. (2020) and Šuba et al. (2021). We limited the maximum number of pups per female and year to 13 to ensure an ecologically realistic maximum value.

The percentage of territorial females that reproduce in a year could be derived from the available DBBW data in this study. The average expected percentage of territorial females and the year-to-year variability were estimated using a linear model. The proportion of successfully reproducing females (± SE) based on DBBW data (as of August 2021) was 77.9 % ± 3.5 %. Normal distribution was used as the link function to implement the results adequately in Vortex subsequently (see Table 2). For this study, the first monitoring years (up to and including) 2010 were discarded because they were subject to high random fluctuations due to a small population size of less than ten territories.

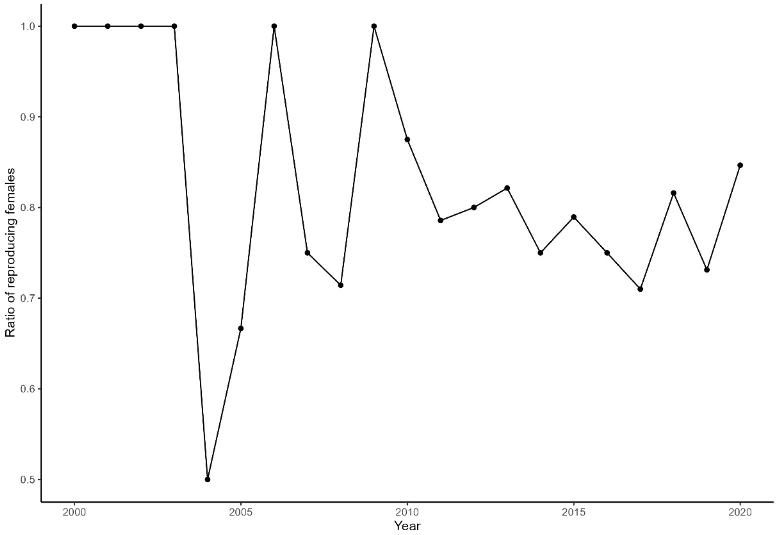

Fig. A1. Ratio of reproducing female wolves (proportion of territorial females detected) in Germany based on DBBW data (as of 12/13/2021).

Mortality

The parameters for mortality in Vortex encompass natural mortality due to diseases, starvation, predation, age-related factors, and anthropogenic mortality stemming from human activities, such as hunting or road accidents. Studies on the German part of the European wolf population have indicated that territorial wolves exhibit significantly higher survival probabilities within military training areas (Reinhardt et al., 2019; Sunde et al., 2021). Traffic mortalities accounted for approximately 37 % to 78 % of the dead wolves in Germany (Sunde et al., 2021). Wolf pups are much more sensitive to environmental influences than adult wolves. Consequently, mortality rates are significantly higher in the juvenile age class in contrast to subadults and adults. In general, mortality is expected to increase with the exploration of juveniles outside the den (Mech, 1970). Disease and weather conditions have a strong effect on survival. Often, mortality within the den cannot be recorded at all, and most studies work with data about pups from the time they leave the den (see f.e. Cubaynes et al., 2014). Pup mortality rates in Miller (2017; for the Mexican wolf) were 28.2 % ± 10 %, with two phases integrated here: the first phase was calculated from the first observation immediately after emergence from the den to the time of dispersal in September; the second phase was calculated from the time of dispersal to the next reproductive season (Carroll et al., 2019). In other wolf populations, pup mortality rates have been estimated to range between 11 % and 52 % (Fuller, 1989) or between 57 % and 94 % (Mech, 1970). Bauduin et al. (2020) assumed mortality rates of 60 % for modeling the French wolf population based on (Smith et al., 2010). In a recent study on the Scandinavian population, a pup mortality of 50 % was assumed (Bruford, 2015). Nowak and Mysłajek (2016) similarly recorded annual pup mortality of 50 % in the Polish study areas.

Given the assumption that pup mortality in Germany is largely comparable to that in Polish study areas, a mortality rate of 50 % was used as a baseline assumption for our simulation (Bruford, 2015; Nowak and Mysłajek, 2016).

For mortality rates in stages 1 and 2, we opted for 18 %, based on a study of mortality in the western Alps (Bauduin et al., 2020; Marucco et al., 2009). In a study of wolves in Europe, Chapron et al. (2012) selected mortality for dispersers with a probability between 35 % and 55 % under different scenarios. (Bauduin et al. (2020) assumed 31 % mortality for dispersers based on a study from Spain by Blanco and Cortés (2007), which we adopted for our study. We selected 18 % as the mortality probability for stage 4 in the default scenario (based on an Italian study by Marucco et al., 2009 and Bauduin et al., 2020). This rate is at the lower end of rates observed in other growing wolf populations. For example, an average mortality rate of 22.9 % was assumed for adults in the Greater Yellowstone Area (Smith et al., 2010) and 25 % for Scandinavian areas (Bruford, 2015). Chapron et al. (2012) selected a rate between 15 % and 35 % (for stages 1,2 and 4). Due to the strong influence of mortality on population growth and a recent study by (Sunde et al. (2021) with high mortality rates, several scenarios with alternative estimates of mortality values were developed. It should be noted that different mortality rates can also be observed across the year, as mortality is generally assumed to be higher in wintertime (Marucco et al., 2009). Specifically, adult mortality is elaborated through diverse scenarios, as this parameter is an essential factor in population dynamics for wolves and species with similar life histories (Carroll et al., 2019, 2014).

Dispersal

The dispersal rate is the proportion of individuals, typically young wolves, that leave their natal territory and establish new territories elsewhere (Morales-González et al., 2022). Dispersal is essential for maintaining genetic diversity, preventing inbreeding, and colonizing new areas. Dispersal is considered crucial for wolves to adjust their numbers to prey availability or to compensate for deaths (Cubaynes et al., 2014). Dispersal rates generally vary with sex and age in this regard (Boyd and Pletscher, 1999; Gese and Mech, 1991), as well as of subdominant animals between different packs. The death of leading animals can also affect dispersal behavior (Chapron et al., 2003). Because of their high dispersal ability, wolves can recolonize distant areas (Ciucci et al., 2009; Kojola et al., 2006; Ražen et al., 2016), traveling distances of up to 800 km (Andersen et al., 2015). Despite this potential, many dispersing individuals settle within 100 km of their natal range (Caniglia et al., 2014; Jarausch et al., 2021; Recio et al., 2020). In Germany, linear dispersal distances between natal territory centers and the territory of first reproduction ranged from 0 to 359.5 km (Jarausch et al., 2021), with no significant difference between sexes. Thus, the median dispersal distance was 26.4 km for females and 35 km for males. Migration from and to Germany has been confirmed in the past decades (Hindrikson et al., 2017; Jarausch et al., 2021).

Average pack size and carrying capacity

While most countries estimate the number of individuals, various methods are used, from very sophisticated models to simply estimating reproductive units (e.g., packs and pairs) or conversion factors to estimate the number of individuals from them. The conversion factors from packs to individuals can range from six to eight, from four (Belgium) to ten (Sweden). Since pack sizes of wolves in Germany vary considerably between 3 and 11 (Reinhardt and Kluth, 2007), an exact indication of the capacity limit of individuals is associated with uncertainty. The territory size of individuals in a pack can vary greatly depending on age, sex, reproductive status - and the analysis method (Reinhardt and Kluth, 2015). The average value of 6.4 individuals per pack (data from Poland, cf. Romański et al., 2018) for the maximum capacity in Germany. Similar to this value, the average pack size of Iberian wolves of 6.2 (SE ± 0.3) was also found during long-term monitoring (Nakamura et al., 2021). Causes for variation in size and the composition of individual packs include birth and mortality rates of pups, out-migration rates of older offspring, and general mortality of adult individuals.

For carnivores, carrying capacity is very hard to define a priori, and it is likely to shift over time, especially in human-dominated landscapes. It is likely to be influenced by the densities of wild and domestic prey. Therefore, excluding prey from the calculation effectively leads to underestimating carrying capacity (Trouwborst et al., 2017). We have integrated the results for the carrying capacity of wolves in Germany from a previous habitat model (Kramer-Schadt et al., 2020; Table 2) and tested artificially reduced numbers within scenarios S5.

Scenarios S5a, S5b and S5c without inbreeding

Scenarios S5 (a, b, and c) simulated the population with decreased carrying capacity. As simulations for S5a and S5b resulted in negative population growth after 30 years, we re-run the simulations for 100 years and additionally included the scenarios with same settings expect for disabling inbreeding depression, assuming the effect of inbreeding might be especially pronounced in limited populations. These runs without inbreeding depression resulted in positive population growth and hence stable population numbers at carrying capacity (Fig. A2). Hence, the inclusion of inbreeding depression in Vortex had a high impact on simulation outcome.

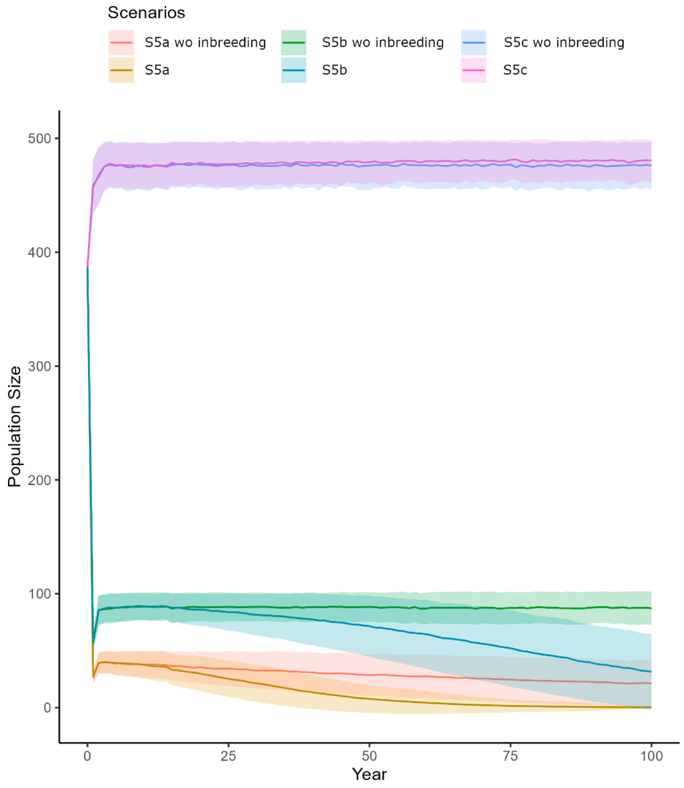

Fig. A2. S5a, S5b and S5c as well as repeated runs for S5a and S5b without inbreeding depression (denoted as "wo inbreeding").

Genetic summary graphs

Figs. A3, A4

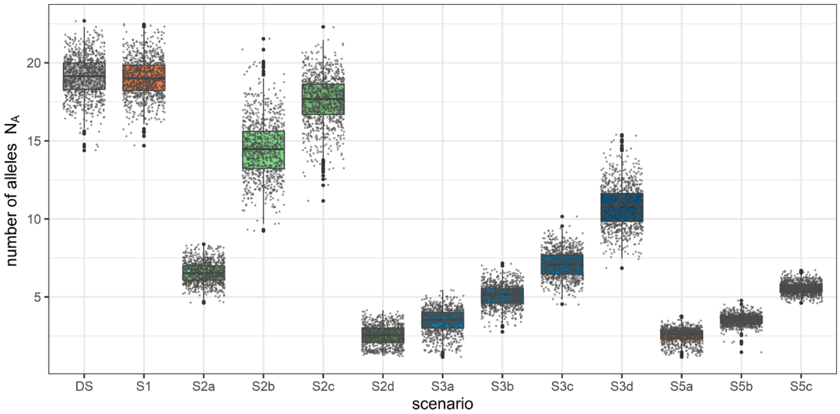

Fig. A3. Number of alleles (N_A) per scenario for the simulated German part of the European wolf population in the year 2045.

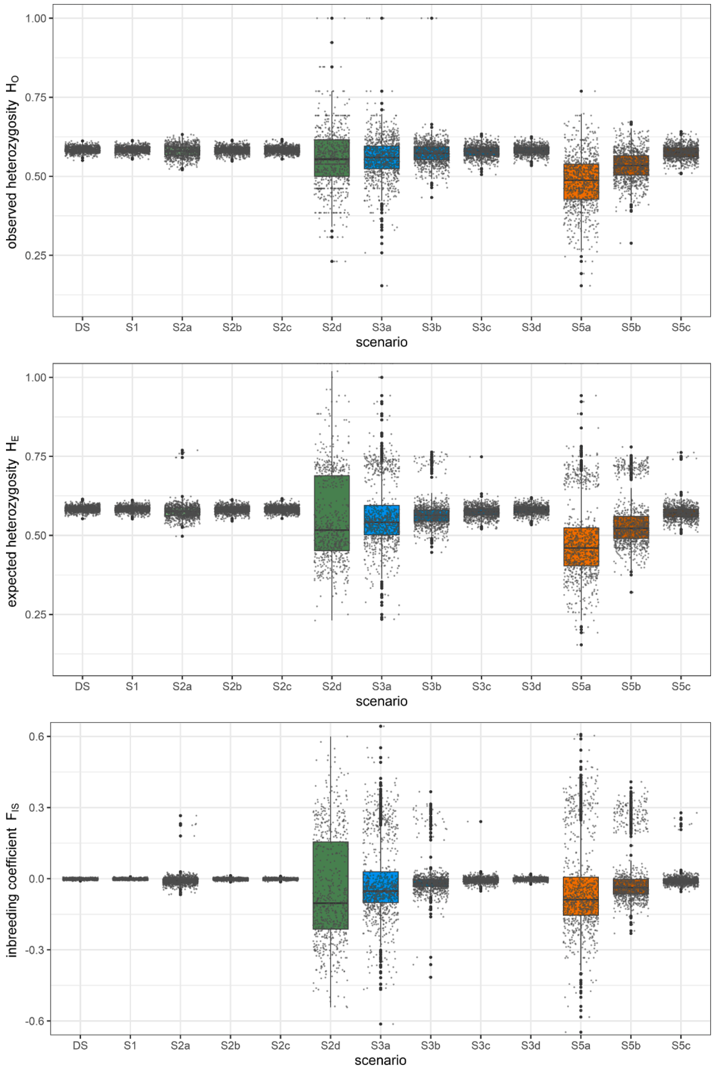

Fig. A4. Observed heterozygosity (H_O), expected heterozygosity (H_E) and inbreeding coefficient (F_{ST}) per scenario for the simulated German part of the European wolf population in the year 2045.

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