A Demographic and Genetic Analysis of Minimum Viable Population Size to Inform the Population Reference Value for Wolves in Sweden

FINAL REPORT

Analyses conducted by:
Philip S. Miller, Ph.D.
Director of Science, Single-Species Planning
IUCN SSC Conservation Planning Specialist Group

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Summary

In May 2022, the Swedish Government commissioned the Swedish Environmental Protection Agency (SEPA) to investigate, based on the best available knowledge and scientific expertise if, and under what circumstances, the population reference value for the wolf (*Canis lupus*) as defined for favorable conservation status according to the European Union Habitats Directive, could be between 170 and 270 individuals in Sweden as stated in the parliament proposition from 2012 (prop. 2012/13:191). This report details an independent analysis requested by SEPA to inform future decision-making for wolf conservation in Sweden. Based on the distinction between minimum viable population (MVP) and favorable reference population (FRP) value as described in the Habitats Directive guidance documentation, the analyses described in this report specifically address the identification of a minimum viable population size for wolves in Sweden. Translation of this MVP value to a population abundance incorporating larger-scale ecosystem functionality, representation evolutionary genetic considerations – the FRP value – requires a process of "upscaling" to a larger population abundance. The translational process is outside the scope of this analysis and is instead to be conducted by SEPA after receipt of this PVA.

Another important issue governing the interpretation of this PVA concerns the ambiguity around the explicit definition of population viability in the Habitats Directive and supporting documents. To be fully operational, a definition of viability for a specific population should be quantitative and reflect an acceptable level of risk tolerance over a defined time frame. Because this quantitative definition was provided by neither the EU nor SEPA, it is not possible to provide a definitive interpretation of the PVA results in terms of what combinations of characteristics constitute a viable wolf population in Sweden. The process of setting quantitative thresholds for acceptable risk is a complex normative process that must be conducted by policy makers and not within the species research community. In the absence of such a defininition, simulation model results can be viewed on the basis of alternative definitions of viability in order to provide guidance to policy makers in their exploration of attitudes on acceptable risk.

This analysis was conducted using the simulation software Vortex, an individual-based demographic modeling package used around the world for exploring threats to endangered species and evaluating alternative management strategies. The wolf population in Scandinavia, distributed across south-central Sweden and southeast Norway, was considered to be a single population for purposes of simulating population dynamics. In addition, the population of wolves in Finland/Russia was included as a separate demographic unit to simulate occasional immigration of wolves into the Scandinavian population from this source. The core model structure featured two timesteps per year (each six months in duration) in order to more precisely account for reproduction in the spring and the population census to take place in the winter. The dataset of known living wolves in Scandinavia as of 1 October 2022 (N = 463) was used to initialize the predictive models, with the full pedigree of these individuals and their ancestry used to establish the starting population genetic structure. This valuable information influences the rate of retention of genetic variability (gene diversity) into the future as a function of relatedness among individuals and the inbreeding that can occur as adults form pairs in order to reproduce. Average rates of reproduction and survival, including both natural sources of mortality and anthropogenic mortality in the form of legal and illegal culling, were assembled from the literature and used to generate a population dynamics model with an expected realized annual population growth rate of approximately 2% which has been observed in the wild over the past decade of detailed census counts. The model explicitly counts population abundance at a point in the simulated annual cycle that generally corresponds to the actual wild population census taken as of 1 October.

Because the current population of wolves in Scandinavia is larger than the range of population reference values (170 to 340) tested in the analysis, the simulations feature gradual removal (culling) of wolves over the first five to seven years in order to reduce the population to an abundance consistent with

a given minimum population abundance threshold value. After that point in time, the population is maintained at or above the abundance threshold through the use of legal harvest when necessary (i.e., culling is not performed if the population is assessed to be less than the stated threshold). Wolves identified as valuable to the genetic viability of the population, especially immigrants from the Finland/Russia population, are exempt from removal. This selection process works to minimize the genetic costs of the removal program. Occasional immigration of wolves from the Finland/Russia population is simulated using random dispersal mechanics, with average immigration rates ranging from no immigration (an isolated Scandinavian population receiving no more wolves) to, on average, one wolf immigrating into the Scandinavian population every three years (a time interval that is roughly similar to the average generation length for this population). Immigration rates considered in this analysis are the actual rates, with each new migrant being at risk of dying before they successfully reproduce and, therefore, incorporate their genetic variation into the local population. The impact of their immigration on local population genetic viability, however, is observed through their reproductive success (determined by defined probabilities in the stochastic modeling environment) before mortality removes them from the population.

A total of 30 model scenarios, defined by unique combinations of population reference value and mean expected immigration rate, formed the core of the analysis. Demographically, the simulation models performed as expected, with long-term wolf abundance in the Scandinavian population governed by the expected mean rate of population growth and reaching a type of equilibrium after approximately ten years near the appropriate population reference value. This stable abundance was about 20% - 25% larger than the scenario-specific population reference value, owing to the production of new pups in early spring preceding the 1 October census. The simulated populations would decline to a number much closer to that value after the October – April timestep when winter mortality and, if necessary, removal of wolves occur. Because of the relatively larger starting abundance combined with the mean positive long-term population growth rate, extinction risk across the range of scenarios tested here was quite low, exceeding 0.01 over 100 years in just three of the 30 scenarios making up the analysis and never exceeding 0.02.

As expected from theoretical principles of conservation genetics, simulated populations maintained at smaller population abundance threshold values would show a more rapid rate of loss of genetic variation (gene diversity) over time, particularly if future immigration did not occur. Across the range of values tested here, immigration of wolves from the Finland/Russia population improved gene diversity retention over time. More frequent immigration (one wolf every three to six years) resulted in the Scandinavian population retaining at least 95% of the gene diversity present at the start of the simulation over the full duration of the simulation (100 years) across nearly all tested population reference values. When immigration averaged one wolf every three years, this retention increased to 99% to 100.5% of the original value, owing to the infusion of new genetic variation into the Scandinavian population from the Finland/Russia source. The process of retaining high levels of gene diversity in a population is influenced by stochastic (random) variability, however, resulting in a risk that these particular genetic goals may not be achieved even under favorable conditions. Therefore, choosing a genetic criterion for population viability should not only specify the desired level of gene diversity retention, but also the degree of confidence with which that desired level of retention is likely to be achieved.

Given the nature of the current models discussed in this report, and acknowledging the assumptions built into these simulations as described above, the analysis suggests that the wolf population in Scandinavia (south-central Sweden and southeast Norway) can potentially be considered viable within the interval of 170 to 270 individuals in accordance with the broad definitions presented in the European Union's Habitats Directive. However, this condition requires the following processes to be maintained through time:

- The Scandinavian wolf population must have the demographic characteristics to, at a minimum, sustain a positive population growth rate, ideally similar to or greater than what has been observed over the past decade of detailed observations of reproduction and survival (annual growth lambda $\lambda \geq 1.02$, with the possibility of considerably higher growth rates in the absence of legal harvesting of wolves); and
- Immigration of wolves from Finland/Russia into Scandinavia should be, on average, no less than one individual every three years.

The above discussion defines conditions for maintaining a viable population of wolves in Scandinavia. A similarly viable wolf population in Sweden would also require the same general demographic conditions: reproductive and survival parameters that result in a capacity for sustained population growth, and consistent immigration of wolves from the recognized source population in Finland/Russia. However, because the Swedish population represents only a portion of the total wolf population in Scandinavia, any specification of a minimum viable population for the purposes of setting a favorable reference population in Sweden would require proper scaling of the larger regional population. In addition, it is critically important to recognize that the precise demographic characteristics of a viable population in Sweden or elsewhere cannot be specified until a clear demographic and genetic definition of wolf population viability is presented by the appropriate national or regional authorities.

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Introduction

In May 2022, the Swedish Government commissioned the Swedish Environmental Protection Agency (SEPA) to investigate, based on the best available knowledge and scientific expertise if, and under what circumstances, the population reference value for the wolf (*Canis lupus*) as defined for favorable conservation status according to the European Union Habitats Directive, could be between 170 and 270 individuals in Sweden as stated in the parliament proposition from 2012 (prop. 2012/13:191). In response to this commission, SEPA sought out two conservation biologists to conduct independent analyses in order to inform future decision-making for wolf conservation in Sweden. This report details one of those independent analyses.

Key concepts and issues underlying the scope of the SEPA commission

To place the work described in this document in proper context, it is important to highlight key underlying concepts and their definitions as presented in the European Union's (EU) guidance document on implementing their Habitats Directive (DG Environment 2023). The guidance document defines "Favourable Reference Population" as "*Population in a given biogeographical region considered the minimum necessary to ensure the long-term viability of the species*..." (DG Environment 2023: 21). This definition invokes the concept of estimating a minimum viable population (MVP) size using methods of population viability analysis (PVA) that are customized for the species under consideration and the specific management situation for a given geographic region. The MVP typically represents the abundance required to eliminate or largely minimize the risk of extinction of the population or species over a defined time frame, usually 100 years from the date of analysis (e.g., Gilpin and Soulé 1986). In some instances, this metric also includes consideration of maintaining a minimum level of genetic variation (heterozygosity) over time that helps to avoid detrimental levels of inbreeding and associated fitness impacts (inbreeding depression).

However, the guidance document goes further and recognizes the value of adopting a more expansive definition of viability – one that explicitly incorporates ecological functionality of a species within its native landscape in order to promote more robust ecosystems through time (e.g., Sanderson 2006; Redford et al. 2011). The guidance document (DG Environment 2023: 25) addresses the clear relationship between these two concepts:

> *"It is therefore important for favourable reference populations to reflect the 'long-term viable component of the natural habitat' at the level of the species across its natural range and distribution, rather than solely a minimum viable population."*

In light of the EU's position, the analyses described in this report specifically address the identification of a minimum viable population size for wolves in Sweden. Translation of this MVP value to a population abundance incorporating larger-scale ecosystem functionality and representation – the favorable reference population (FRP) value – requires a process of "upscaling" as described in the guidance document (DG Environment 2023). It is understood that this "upscaling" to a larger population abundance value representing the FRP value is outside the scope of this PVA and is instead to be conducted by SEPA after the current work is completed.

Another important issue governing the interpretation of this PVA concerns the ambiguity around the explicit definition of population viability in the Habitats Directive and supporting documents (e.g., DG Environment 2023). To be fully operational, a definition of viability for a specific population should be quantitative and reflect an acceptable level of risk tolerance over a defined time frame. Because this quantitative definition was provided by neither the EU nor SEPA, it is not possible to provide a definitive interpretation of the PVA results in terms of what combinations of characteristics constitute a viable wolf population in Sweden. The process of setting quantitative thresholds for acceptable risk is a complex normative process that must be conducted by policy makers and not within the species research community (e.g., Vucetich and Nelson 2018). In the absence of such a defininition, simulation model results can be viewed on the basis of alternative definitions of viability in order to provide guidance to policy makers in their exploration of attitudes on acceptable risk.

Using population viability analysis for conservation decision-making

The work described here uses tools and processes based in population viability analysis (PVA) to critically evaluate the demographic and genetic properties of a simulated wolf population under a range of alternative scenarios. In this case, these scenarios are defined by paired combinations of (1) an assumed population reference value for wolves in Scandinavia, and (2) an assumed rate of immigration of wolves into the Scandinavia population from an external source – here, Finland/Russia. [Note: From this point onwards, the wolf population in Sweden and Norway will be referred to as the Scandinavian population, while the source population of immigrants to the north will be referred to as the Finland/Russia population.] The overall goal of the analysis is to generate information on the demographic and genetic characteristics of a Scandinavian wolf population that would conform with the EU Habitat Directive's general definition of favorable conservation status.

PVA is a valuable tool used by wildlife conservation researchers, non-government organizations, and national and regional government agencies to assess threats to endangered wildlife populations and to evaluate management options designed to improve population or species status in their wild habitats (Beissinger and McCullough 2002; Moris and Doak 2002). These analyses are typically done using computer simulation modeling tools to project wildlife population abundance into the future. In particular, the process of conducting a PVA helps to stimulate information sharing and discussion among species experts, and provides a framework in which assumptions about our collective understanding of the system of interest are expressed and clarified.

That said, it is important to recognize that PVA methodologies are not intended to give absolute and accurate "answers" for what the future will bring for a given wildlife species or population. Many practitioners caution against the exclusive use of absolute results from a PVA in order to promote specific management actions for threatened populations (e.g., Ludwig 1999; Reed et al. 2002; Ellner et al. 2002; Lotts et al. 2004; Lacy 2019). Instead, we can best use PVA results to make comparisons of the relative performance of a simulated population under alternative management activities or different assumptions of environmental conditions. Even in this comparative framework, however, results from PVA efforts can provide a critical base of evidence when deriving meaningful and justifiable quantitative targets for endangered species recovery (Himes Boor 2014; Doak et al. 2015).

General Approach to the Analysis

Initial discussions around project scope, wolf population data availability and PVA model structure began in early 2022 with an online meeting between the author of this report and a group of wolf biologists that are part of the Scandinavian Wolf Research Project (SKANDULV). Participants in this meeting are listed in Appendix I. A very preliminary report on model development was submitted by the author to SEPA in May 2023; following this early progress report, more intensive work on model structure, input data analysis and scenario construction began in June 2023. A draft report was submitted to SEPA in October 2023 and, following revision of the report based on peer review comments, a final report was submitted on 1 April 2024.

Choice of software for PVA

As noted previously, population viability analysis is typically conducted through the use of computer simulation modeling tools. The tool chosen for this analysis is Vortex version 10.6 (Lacy and Pollak 2022). Vortex models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. Vortex simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, dispersal among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. The software has a number of benefits inherent to its design, including:

- Individual-based model structure allows for explicit simulation of random (stochastic) variation in annual birth and death rates among age-sex classes, and the impact of this variation on the growth dynamics of small populations.
- Ability to define individual, population, or global state variables that can be used to derive complex expressions for age/sex-specific demographic rates, which can change over time in response to evolving environmental conditions, management regimes, etc.
- Capacity for incorporating metapopulation structure, with multiple populations that are linked by occasional dispersal and distributed across a landscape.
- Incorporation of detailed genetic processes, such as mating between known relatives (as tracked through kinship calculations between selected parents) leading to inbreeding depression, or erosion of genetic diversity over time through random genetic drift.

For more information on the features of Vortex and its application to wildlife population management, see Lacy (2000; 2019) and Lacy et al. (2021).

Vortex has been used by the author in recent detailed analyses of wolf population dynamics and management in North America to successfully inform decision-making by government agencies for management of the Mexican wolf (*Canis lupus baileyi*: Miller 2017; USFWS 2022) and the red wolf (*Canis rufus*: Miller 2023; USFWS 2023). More importantly, the current use of Vortex provides a form of continuity with the most recent analysis of Scandinavian wolf population viability (Bruford 2015) that used an earlier version of the software. Substantial and significant changes have been made to the software since Bruford's analysis; while some of the limitations noted in that earlier analysis may be largely addressed in the present analysis, there are likely other aspects of Scandinavian wolf biology and/or management that we cannot fully accurately capture in the present analysis. The potential impacts of these limitations will be noted throughout this report.

Key features of the Scandinavian wolf PVA model

Important characteristics of the population dynamics model are listed below. More detailed information on the specifics of these characteristics is given in the following section.

- The commission from the Swedish Government for this analysis clearly states that the most recent analysis by Bruford (2015) is not being questioned for its validity, but that new information on wolf demographics, etc. favor an update to that analysis. In the spirit of that assessment, some of the input data used in the 2015 analysis are used without modification as appropriate in the present analysis.
- The focus of this analysis is the full Scandinavian wolf population distributed across south-central Sweden and southeast Norway, which can be considered demographically a single population (Figure 1). Therefore, the actual numbers of wolves in each country are not considered here; users of this analysis will need to employ additional information to determine, at any specified time in the future, the estimated proportion of the total Scandinavian population that resides within Sweden.

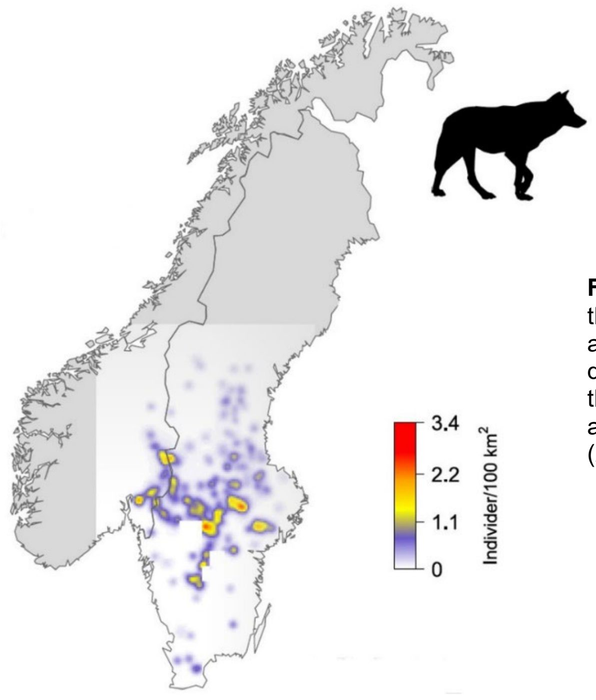


Figure 1. Spatial extent (light gray rectangle) of the Scandinavian wolf population used in this analysis. The figure includes data on wolf density and range for winter 2022-2023, but these data are not used specifically in this analysis. Figure adapted from Milleret et al. (2023).

- A separate population of wolves distributed across northern Finland and Russia is also included as a source of immigrants that occasionally disperse through northern Sweden and Norway to become incorporated into the resident Scandinavian population.
- The census of the wild Scandinavian population is reported as of 1 October, which is some months after the production of wolf pups from that year's breeding season. Therefore, in order to more realistically simulate the timing of annual population monitoring with the underlying population demographics, the model features two distinct timesteps per annual cycle, with each timestep assumed to be six months in duration (Figure 2). This is a structural modification of the default use of Vortex that is typically based on an annual pre-breeding census structure. With this modification, breeding takes place only in the "even-numbered" timesteps corresponding to the time period 1 April – 1 October. In contrast, mortality is imposed in both "even-numbered" and "odd-numbered" timesteps, with estimates of annual survival from the literature (e.g., Milleret et al. 2023) decomposed into numerically equivalent estimates of survival over the shorter six-month time periods.
- Each scenario (defined by a unique combination of input parameters, described in more detail in the following section) making up this analysis begins as of 1 October 2022, which is the date of the most recent available published Scandinavian population size estimate (N_{Total} = 463: Milleret et al. 2023). For the Scandinavian population, this initial population is fully described by a pedigree that lists all the ancestors of each member of the population alive as of the start date. By using this pedigree information, we can accurately describe the current genetic structure of this population (extent of relatedness among living individuals, kinship among paired individuals, mean level of inbreeding in the population, overall retention of gene diversity) and how that structure is expected to change in the future under different minimum population abundance thresholds and the extent of immigration from the Finland/Russia population.

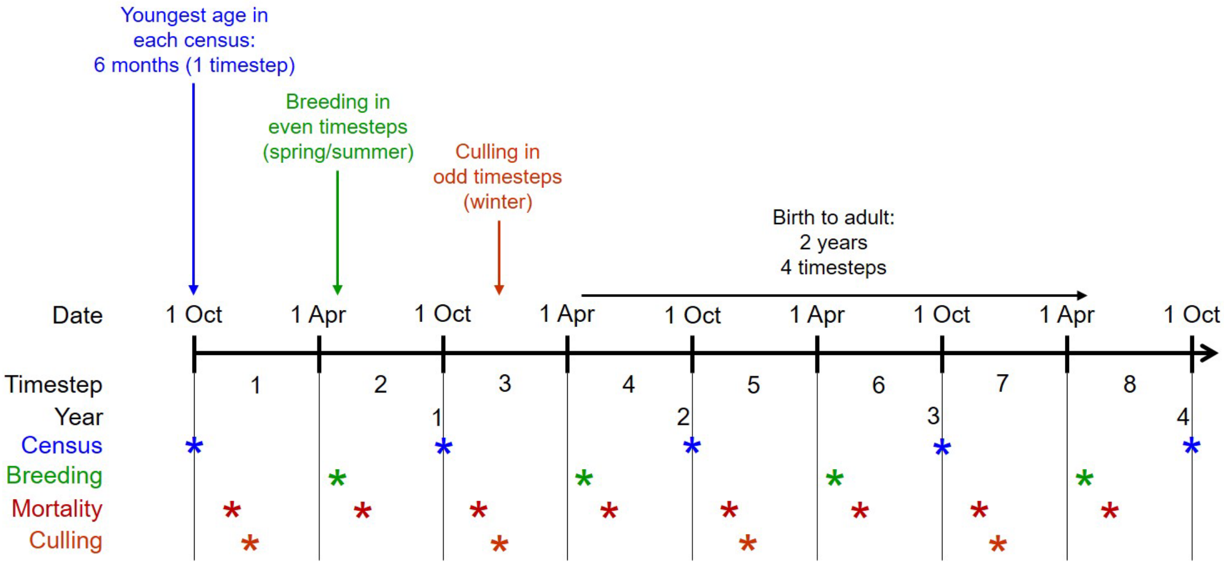


Figure 2. Diagram of Scandinavian wolf PVA simulation timeline, showing the decomposition of the typical annual demographic cycle into two timesteps of equal duration. The timing of each specific event across the annual cycle (designated by asterisks) is relative to other events in that cycle and is not meant to be exact.

- Because each scenario in the analysis is initialized with a wolf population size that exceeds the range of population abundance threshold values examined here, the decision was made to include in this PVA an expanded rate of wolf removal that in the shorter term is designed to reduce the existing wolf population size to the threshold value defining that scenario. A removal rate of reduced intensity can then be implemented in the longer term to maintain the population at the abundance threshold value to be evaluated. Threshold abundances tested in this analysis are:
    - 170 (lower end of the interval proposed by the Swedish government)
    - 210 (lower end of the interval with the addition of 40 individuals in Norway)
    - 270 (higher end of the interval proposed by the Swedish government)
    - 300 (current population reference value for wolves in Sweden)
    - 310 (higher end of the interval with the addition of 40 individuals in Norway)
    - 340 (current population reference value with the addition of 40 individuals in Norway)

  Note that this strategy is a significant departure from the previous analysis of Bruford (2015), which included scenarios that evaluated demographic and genetic characteristics of wolf populations across a wide range of potential population sizes as large as 2000 individuals. In keeping with the author's interpretation of the commission put forward by the Swedish Government, the structure of the present analysis is meant to realistically examine the validity of the proposed population threshold values in the context of the current abundance of wolves across southern Scandinavia.
- The minimum population abundance threshold values used in this analysis are defined on the basis of total population size, in other words, all individuals in the population aged six months and older (in keeping with the timing of reproduction and population monitoring discussed above). All plots of population size in this report will therefore conform to this definition. However, recognizing that the EU Habitats Directive reporting guidelines specify that population size estimates should also be restricted to adults, additional tabulation of adult population size (two years of age and older) is included along with tallies of subadults (between one and two years of age) and juveniles (from birth to one year of age).

- A given minimum population abundance threshold value is interpreted in this analysis to represent the minimum target population size, and not its long-term mean where actual population size could occasionally be less than the target. This interpretation underlies the population harvest mechanics as well as the interpretation of population size output from each scenario.
- In order to generate reasonable and internally consistent estimates of reproduction and age-specific mortality for the Scandinavian wolf population, this analysis uses published population size estimates dating back to the 1 October 2013 census (as reported in Milleret et al. 2023) to calculate a mean annual realized population growth rate (λ, lambda) across the time period 2013 – 2022. The calculated mean growth rate $\lambda = 1.018$ provides a reference point on which to calibrate population demographics with the goal of reproducing that mean growth rate into the future. By using this method, we assume that future population growth will be generally similar to that observed over the past decade. Note that this is a realized growth rate and not a true (much higher) potential growth rate that could be achieved in the absence of various sources of anthropogenic mortality that limit population growth.
- Key model output metrics that can inform the question of minimum population abundance threshold value include:
  - Probability of population extinction, expressed as the proportion of replicate simulations for any given model scenario that decline to zero individuals (or animals of only one sex) within the simulation timeframe.
  - Proportional retention of population genetic diversity (defined here as gene diversity or expected heterozygosity), expressed as both (1) the more theoretical proportion of diversity retained relative to the presumed source of the Scandinavian population, and (2) the proportion of diversity retained in the Scandinavian population relative to the value present in that population at the beginning of the simulation, in other words, 1 October 2022.

Detailed Summary of PVA Model Input

This section gives additional detail on the core numerical input used in the PVA models used for this analysis. A summary of the input parameters can be found in Table 1, with a more detailed presentation of input data for a specific scenario given in Appendix II. Unless specified otherwise, demographic data for the Finland/Russia population are equivalent to those for the Scandinavia population.

Initial population size, structure

Scandinavia: Milleret et al. (2023) used open population spatial capture-recapture (OPSCR) models on an extensive database of non-invasive genetic samples, carcass recoveries, etc. to estimate the number of wolves in Scandinavia as of 1 October 2022 to be 463 individuals (95% credible interval: 441 – 488). In addition, the kinship (relatedness) structure of this population is represented by a pedigree of all animals alive as of 1 October 2022, with their ancestry dating back to the founding immigration event in the 1980s (summarized most recently in Åkesson et al. 2023). A small number of young individuals known or presumed to be alive as of the model start date were not recorded in the pedigree; to account for these wolves, juveniles and subadults were added to the pedigree and assigned sex and parentage at random to bring the final population up to the desired abundance. Finally, adults that were known to be paired as of the model start date were assigned the ID of their mate so that the simulations could begin with an accurate expected breeding structure across the population. With these data included in the PVA model, the starting values of population mean inbreeding coefficient and gene diversity are known quantities. Initial population gene diversity is estimated by "dropping" alleles (two unique alleles per founder) through the known pedigree and calculating expected heterozygosity from the resultant distribution of final allele frequencies (Frankham et al. 2010). A portion of the full pedigree file, listing the original founders and all individuals presumed to be alive as of 1 October 2022, is given in Appendix III.

While a total of ten individuals are known to have immigrated from Finland/Russia into what is now the Scandinavian wolf population, only seven wolves are represented genetically in the current population and are therefore considered as founders. These animals are identified as follows:

- G1-83 (male) and D-85-01 (female) of the Nyskoga pair, immigrated in 1983
- G1-91 (male) of the Gillhov pair, immigrated in 1991
- M-09-03 (male) of the Galven pair, immigrated in 2008
- M-10-10 (male) of the Kynna pair, immigrated in 2008
- G31-13 (female) of the Tivenden pair, immigrated in 2013
- G187-19 (male) of the Setten pair, immigrated in 2021 (alive as of 1 October 2022).

Three additional individuals immigrated into the existing population, but are no longer genetically represented in the current population:

- G23-13 (male) of the Tivenden pair, immigrated in 2013
- G15-16 (male) of the Tunturi pair, immigrated in 2016
- G325-17 (female) of the Svartedalen pair, immigrated in 2017

As is common practice in pedigree analysis methodologies, we assume that all founders are unrelated to one another in the absence of detailed genetic data that might establish more definitive estimates of founder relatedness. This assumption is likely to be inaccurate for certain founder animals, as specific animals may share common recent ancestry.

Finland/Russia: The model includes a generalized estimate of 500 wolves in the Finland/Russia source population. The geographic boundaries of this population, considered in the context of this analysis, are undefined. As a result, the goal here is to create a wolf population of a sufficient size that can serve as a source of immigrants to the Scandinavian population. Because of uncertainty in this parameter, a set of additional scenarios were constructed that assessed the impact of starting the models with a smaller abundance of wolves in this population (see the section titled "Testing model sensitivity to select demographic input parameters" below). Additionally, this population is not initialized with a detailed pedigree; consequently, the model lacks a detailed description of genetic structure in this population. However, in recognition of the fact that some moderate level of inbreeding is likely to be taking place among localized subsets of the population, the mean inbreeding coefficient across all individuals in the population at the start of the simulation is assumed to be 0.1.

To summarize, we have two important assumptions about population genetic structure built into this model: (1) the genetic relatedness among immigrants incorporated into the Scandinavia population in the past – those that are currently identified in the pedigree as founders of that population – is unknown; and (2) the genetic relatedness among future immigrants added to the Scandinavian population from the Finland/Russia source population, and their relatedness to past founders of the Scandinavian population, is also unknown. When considering future loss of gene diversity in the Scandinavian population, the above assumptions imply that the degree of relatedness among new wolves immigrating into Scandinavia from Finland/Russia is no different than the relatedness of founders of the Scandinavian population to each other. This is likely to be a plausible assumption, and should facilitate informative interpretation of the genetic results of the PVA scenarios described here.

Population carrying capacity

In the typical Vortex modeling framework, a population is allowed to increase in abundance under favorable demographic conditions (and without explicit specification of density dependence) until the carrying capacity *K* is reached. When this occurs, individuals are randomly removed (simulating additional mortality under these limiting conditions) according to the age and sex structure of the population in order to bring the population back down to the value of *K*. In this manner, we therefore simulate a ceiling-type density dependence.

Both the Scandinavia and Finland/Russia populations have an assumed carrying capacity of *K* = 800 individuals. These values are somewhat arbitrary, but the overall structure of this PVA means that carrying capacity is not expected to be a factor informing the viability of the Scandinavian wolf population. There is no evidence that the current Scandinavian population is being regulated by natural ecological processes, and the range of identified population abundance threshold values tested in this analysis are lower than the initial abundance used here (N_{2022} = 463). Note that the value of *K* used for the Scandinavian population in the recent analysis by Bruford (2015) was as high as 2000 individuals – likely to be quite unrealistic and uninformative in the analysis described here. Nevertheless, because of some uncertainty in this parameter concerning the Finland/Russia population, a set of additional scenarios were constructed that assessed the impact of starting the models with a smaller value of *K* in this population (see the section titled "Testing model sensitivity to select demographic input parameters" below).

Reproduction

For the purposes of this PVA, wolves are considered to have a long-term monogamous breeding system, where adult pairs will remain together until one of its members dies. Additionally, female breeding is defined as the birth of a litter of pups. The data presented by Bruford (2015) are used for this analysis, where it is assumed that a mean of 60% ± 10% of all adult females will pair with an adult male and produce a litter. The standard deviation given above reflects annual variation around the mean arising from stochastic variability in the environment (for example, annual weather effects, prey availability, individual animal health, etc.). Females that already paired at the beginning of the breeding timestep will retain their mate, while unpaired females have the specified chance of pairing with a similarly unpaired adult male. If one of the pair members dies, the living individual is returned to the pool of available breeders to pair with a suitable mate. Effectively all paired females in a season are assumed to produce a litter. Unpublished data from SKANDULV (time period 2011 – 2022) suggest that the proportion of adult females breeding is slightly higher than 60%. A set of additional scenarios was constructed that assessed the impact of an alternative value for this parameter (see the section titled "Testing model sensitivity to select demographic input parameters" below).

Given our definition of reproduction above, mean litter size reported in the literature – which records the number of pups surviving to 1 October – must be adjusted to reflect the number of pups alive at the beginning of the April – October timestep. In this case, data on the mean number of pups counted in October (taken from Liberg et al. (2005)) and on the mean inbreeding coefficient measured in the population in recent years (taken from Åkesson and Svensson (2022); see below) suggest a mean of 4.5 ± 1.5 pups born in the beginning of the April – October timestep. This mean value was adjusted slightly to 5.3 ± 1.5 pups per successful female in order to generate a simulated population growth near the rate observed over the past decade as reported in Milleret et al. (2023).

Inbreeding depression affecting pup survival

Liberg et al. (2005) examines the effects of inbreeding on the number of pups per litter that survive and are counted in winter (1 October census). The authors of that study transformed their data to generate a standardized estimate of the intensity of inbreeding depression, expressed as the number of lethal equivalents per diploid genome (Morton et al. 1956). The Scandinavian wolf population was assessed to have 6.04 lethal equivalents affecting survival of pups to winter, with 50% of that load comprised of fully lethal alleles (and, therefore, more easily purged from a population through the process of purging). This framework for describing the demographic effects of inbreeding depression is explicitly included in the Vortex model structure. Note that a more recent examination of inbreeding in Scandinavian wolves (Smeds and Ellegren 2022) emphasizes the significance of genetic load in this population, although techniques for estimating fitness effects like those reported by Liberg et al. (2005) are not currently available.

Mortality

The non-invasive genetic sample data used to estimate Scandinavian wolf population size was also used by Milleret et al. (2023) to summarize key population demographic processes (see Table A.7 in their report). Specifically, they estimated annual age-specific survival rates for "scent-marking" individuals and for other individuals across the time period 2013 – 2022. Additionally, they separated legal culling as a separate source of mortality from the more general category of "other" mortality (both natural and anthropogenic causes other than culling). This "other" mortality was used to specify base age-specific mortality in the model, with culling mortality treated separately (see "mechanics of wolf removal" below). Data for scent-marking individuals were used to classify mortality for paired adults, and data for other individuals used to classify mortality for unpaired adults and younger individuals. As observed in the Milleret et al. (2023) dataset, and in keeping with the previous analysis of Bruford (2015), there is no difference in mortality rates between males and females. Note that the present estimate of annual pup mortality (0.323) is significant greater from the equivalent estimate in Bruford (2015) of 0.05. Details of how that original rate was estimated are unavailable but is likely to follow from a slightly different functional definition of reproduction that already accounts for early mortality in the annual cycle.

Timestep-specific survival rates were obtained by calculating the square root of the annual rates, therefore assuming a constant mortality risk across the full annual cycle. Finally, survival estimates were transformed to their corresponding mortality rates for use in the model. This assumption applies only to the specification of "other" mortality per Milleret et al. (2023), and not to the bulk of culling mortality which is treated separately in the model as discussed above. Small adjustments were made to age-specific mortality rates where appropriate in an attempt to generate the desired population trajectory (realized annual growth rate $\lambda = 1.018$) as described earlier.

Catastrophic variation in demographic rates

An outbreak of a generic infectious disease was included here as a "catastrophe", defined in the context of PVA models as a rare event but with the potential for significant negative impacts to rates of reproduction and/or survival. Every year of the Vortex simulation, a random number draw is used to determine if a catastrophe occurs in that year and, if so, a specified multiplicative modifier is applied in that year to normal rates of reproduction and/or survival.

Without detailed data to the contrary, the catastrophe used in the Bruford (2015) PVA was carried forward to this analysis. When an outbreak occurs, the impacts include a complete elimination of successful reproduction in that year (reproduction multiplicative modifier = 0) as well as a 50% reduction in survival across all age and sex classes (survival multiplicative modifier = 0.5). Despite the significant fitness impacts in the year of the catastrophe, the event's very low frequency of occurrence results in a minimal impact of this catastrophe on the long-term trajectory of population abundance.

Metapopulation connectivity through inter-population dispersal

The Scandinavian and Finland/Russia wolf populations are assumed to make up a metapopulation, with occasional exchange of individuals through dispersal. For the purposes of this model, it is assumed that dispersal occurs only from the Finland/Russia population to the Scandinavian population. This may be an unrealistic assumption, as there are reports of wolf immigration from Scandinavia to Finland (Mäntyniemi et al. 2022). However, these data were not available for review for this analysis, and it is unclear if the recorded immigration events involved wolves that were residing in the Scandinavian population analyzed here, or if they were transients that were returning to the Finland/Russia population before integrating into the Scandinavian population.

The model simulates only natural dispersal and not human-managed translocation. This natural dispersal is implemented as a stochastic process in the Vortex PVA environment by specifying a probability that a given individual in the Finland/Russia population of either sex will disperse to the Scandinavian population within the six months defining the model timestep. The dispersal event is assumed to take place only in the October-April (odd-numbered) timestep, with all male and female subadults and adults capable of dispersing. Individuals that have dispersed to the Scandinavia population are assumed to be immediately subject to the same rates of reproduction and survival as native wolves born into that population.

This PVA includes a range of expected mean immigration (dispersal) rates that are in keeping with previous analysis such as Bruford (2015) and are broadly consistent with observed rates of individual wolves dispersing into the Scandinavian population from Finland and neighboring areas. Specifically, immigration rates tested here include:

- No dispersal (isolated populations)
- One wolf every 12 years (annual probability of dispersal = 0.083)
- One wolf every 9 years (annual probability of dispersal = 0.111)
- One wolf every 6 years (annual probability of dispersal = 0.167)
- One wolf every 3 years (annual probability of dispersal = 0.333)

Note that this mechanism of metapopulation connectivity explicitly simulates demographic immigration; it is possible that some wolves will immigrate to the Scandinavian population and die before reproducing. While some may see this as a simplification of the model, the consequences of this true dispersal with subsequent reproduction when possible are readily apparent in the genetic components of the model results (see next section). Also note that this dispersal mechanic does not account for individuals that leave the Russia/Finland population but die before reaching the Scandinavian population. In other words, all individuals in the simulation that leave the Russia/Finland source are successful in immigrating into the Scandinavian population. Therefore, there may be a slight underestimate of the genetic cost to losing individuals from the northern source that are not integrated into the Scandinavian wolf population.

Mechanics of wolf removal

For the purposes of this PVA, “removal” refers to legal harvest (culling) of wolves in Scandinavia. This process occurs only in odd-numbered timesteps (October-April) as this is the time of the year when the bulk of the legal culling process takes place (R. Ekblom, pers. comm.). The initial base scenario used to calibrate demographic rates and, by extension, recent population growth rate, includes a separate culling (harvest) process in which a proportion of each age-sex class is removed from the population. This proportion is based on the estimated culling mortality rates presented in Table A.7 of Milleret et al. (2023). Therefore, this mortality is treated distinctly from the “other” mortality from Milleret et al. (2023) that is used to specify base annual mortality rates.

The removal process used here features a number of specific constraints within any given model scenario in an attempt to improve the realism of the simulation (note that these constraints apply only to the Scandinavian population):

- Culling occurs only when the number of wolves across all age classes exceeds a numerical threshold value that is equivalent to that scenario’s designated minimum abundance threshold value. If the total population abundance is less than this threshold, legal culling of any kind does not occur.

- Individuals that immigrate from the Finland/Russia population – new founder animals – are not removed in order to retain their genetic value while they are alive. This is a simplified rule relative to what is practiced in reality, where offspring of founders are also exempt from culling. The precise parameters defining this rule, e.g., if this applied only to first-generation offspring or more distant descendants, is not known and were therefore not employed here.
- There is an additional genetic constraint on removals, in which wolves are targeted for removal only if their mean kinship value (the average degree of relatedness of that individual to all other living individuals in the population) is greater than 50% of the average mean kinship within that population. This constraint – intended to simulate actual decisions on culling individuals from the Scandinavian population – is designed to remove individuals that are relatively less genetically valuable to the population as they have a relatively high degree of relatedness to many individuals in the population. Because of this constraint, the retention of population-wide gene diversity is improved over a removal strategy that does not take individual mean kinship into account. As this may not be consistently applied in practice, a set of additional scenarios was constructed that assessed the impact of relaxing this rule and allowing culling of any individual except for living immigrants from the Finland/Russia population (see the section titled "Testing model sensitivity to select demographic input parameters" below).
- In order to reduce the initial population size to a given minimum abundance threshold value, an attempt is made to somewhat gradually remove individuals over the first few years of the simulation. Specifically, removal is relatively more gradual during the first six years, after which time the removal rate is increased to accomplish the necessary reduction and then maintain the population at or near the desired target reference value for the remainder of the simulation.
- If removal is triggered during a specific timestep (total population size is greater than the minimum population abundance threshold value), both female and male wolves are removed in approximate proportion to the expected age-class distribution of a population growing at the current rate calculated from Milleret et al. (2023): pups, 36%; subadults, 31%; adults, 33%. Since removal is implemented probabilistically, the actual number of wolves removed may be greater or less than the target number.

Additional model characteristics

The specific software package used in this analysis is Vortex version 10.6.0.0 (10 May 2023). Each model scenario was run with 1000 replicate iterations to account for stochastic variability in demographic rates, population genetic processes, etc. Output discussed in the next section shows the mean outcome of those iterations with, where appropriate, estimates of variation around the mean (standard deviation). All scenarios were run for 100 years (200 timesteps), with results presented graphically from even-numbered timesteps that corresponds to the October population census (in model terms, at the end of those timesteps).

A Note on PVA Scenario Structure

As noted previously, the present PVA is based on the previous analysis of Bruford (2015) in terms of software choice as well as general structure and function of the simulations. Insights from the earlier analyses exploring the sensitivity of model output to uncertainty in such input parameters as the number of lethal equivalents making up the population genetic load, the proportion of that load composed of lethal alleles, characteristics of catastrophes, etc. are expected to remain valid in the present analysis. Consequently, this analysis does not repeat those explorations of model sensitivity.

Instead, this PVA attempts to focus on the central question commissioned by the Swedish Government: the necessary conditions for a wolf population in Sweden to be maintained at an abundance of between 170 and 270 and to be considered to satisfy the broad definition of viability per the EU Habitat Directive guidelines. To accomplish this task, this PVA includes a set of 30 distinct scenarios that feature different combinations of six different minimum population abundance threshold values (see page 5) paired with five different assumed immigration rates (see page 10). Where appropriate, additional scenarios have been developed to explore identified areas of uncertainty and their impact on insights into the central question posed above.

Table 1. Summary of core input parameter values used in simulation models of wolf population dynamics.

	Parameter Value		
Model Parameter	Scandinavia	Finland/Russia	Source (Scandinavia)
Initial population size	463	500	Milleret et al. (2023)
Carrying capacity	800	800	This study
Reproduction[1]			
Age of first reproduction	2 years	2 years	Wikenros et al. 2021
Maximum age of reproduction	13 years	13 years	2022 pedigree
Mean adult females breeding (%)	60 ± 10	60 ± 10	Bruford (2015)
Mean litter size[2]	5.3 ± 1.5	5.3 ± 1.5	Liberg et al. 2005
Age-specific mortality (annual)[3]			
Pups (Age-0 to Age-1)	0.323 ± 0.05	0.323 ± 0.05	Milleret et al. (2023)
Subadults (Age-1 to Age-2)	0.300 ± 0.05	0.300 ± 0.05	Milleret et al. (2023)
Adults (Age-2+)	Paired: 0.25 ± 0.06 Unpaired: 0.36 ± 0.06	Paired: 0.25 ± 0.06 Unpaired: 0.36 ± 0.06	Milleret et al. (2023)
Inbreeding depression	6.04 LEs; 50% lethal	6.04 LEs; 50% lethal	Liberg et al. (2005)
Catastrophe			
Annual frequency	0.01	0.01	Bruford (2015)
Severity	Breeding: 0.0 Survival: 0.5	Breeding: 0.0 Survival: 0.5	Bruford (2015)

1. Reproduction defined as birth of pups, not the time of onset of sexual maturity or the time of mating.
2. Pups assumed to be present at birth, not at subsequent 1 October count.
3. Related to “other” mortality reported in Milleret et al. (2023). Legal culling mortality treated separately.

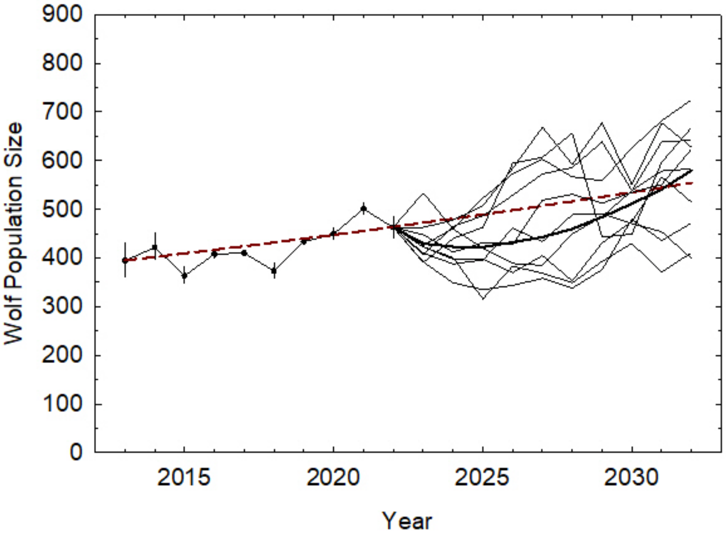
Results of PVA Simulations

Demographic performance of the base scenario

The base scenario in this analysis features the demographic input described in the previous section and projects the pedigreed Scandinavian population forward in time. All rates of reproduction and survival – reflecting both culling mortality and other sources of mortality – are assumed to continue into the future. In addition, the model includes occasional immigration of Finland/Russia wolves (approximately one wolf every six years). The simulation runs for ten years (20 timesteps) to match the number of years comprising the Milleret et al. (2023) dataset used to generate recent population size estimates.

The results of this scenario are shown in Figure 3. Note the slight reduction in mean population size in the first two years of the prospective trajectory; this is likely caused by the initial age structure of the population, particularly regarding the addition to the starting pedigree of a group of younger individuals that have yet to reach the adult stage. Once the age structure begins to readjust after a few years, the population grows in a generally consistent manner compared to the actual ten years of data compiled in Milleret et al. (2023) – mean growth rate λ = 1.022. In addition, specific iterations of the prospective trajectory occasionally show significant changes in population size, which is likely to result from a combination of environmental variability in mean demographic rates, a rare infectious disease outbreak, and proportional culling rates that may differ markedly from annual expectations. Overall, however, the results of this scenario provide a satisfactory level of confidence that the demographic rates used as model input result in a simulated Scandinavian wolf population that grows at a similar rate to that observed in the recent past. Consequently, this model can be used as the foundation for additional scenarios that explore the impacts of a range of population reference values and immigration rates on demographic and genetic measures of population viability.

Figure 3. Trajectory of the Scandinavian wolf population size (census as of 1 October) as estimated using analysis of non-invasive genetic sampling over the time period 2013 – 2022 (line and scatter plot: data from Milleret et al. 2023) and as simulated using the demographic and genetic input data comprising this PVA over the time period 2022 – 2032 (heavy solid line). Vertical bars in the historic dataset are 95% credible intervals around the population size estimate. Red dashed line shows the expected mean population trajectory assuming a constant realized growth rate (lambda, λ) of 1.018 as calculated from the historic data. Light gray lines are ten representative iterations of the PVA model base scenario. See text for more information on model structure and input data.



The demographic data used for this base model were also used in a companion scenario with a simplified structure that allowed the calculation of mean generation length. This companion scenario gave a mean generation length of T = 3.8 years (detailed results not shown here), which is consistent with recent observations of decreasing generation length in Scandinavian wolves (Wikenros et al. 2022).

Demographic performance of the Scandinavian population without immigration

An initial set of scenarios was created that features management of Scandinavian wolves across the range of minimum population abundance threshold values, but without immigration of individuals from the Finland/Russia source. This serves as a type of "control" to better compare the relative response of the simulated population to increasing levels of occasional immigration from the source population.

Following a period of population reduction through wolf removal over approximately seven years (in keeping with the removal mechanic described previously), each of the simulated populations reaches a stable mean abundance that, on average, is maintained across the duration of the simulation timeframe (Figure 4). This stability results from the inherent capacity for population growth given the underlying demographic rates used in the base scenario (see Figure 3). Measures of statistical variability around the mean abundance values have been omitted from Figure 4 for clarity; detailed inspection of the results show that the standard deviation of mean population size after 100 years is typically around 20% to 25% of the mean value (see Table 2). The number of adults (i.e., individuals at least two years of age) in the population consistently make up approximately 38% - 40% of the total abundance as calculated at the end of the simulation (Table 2).

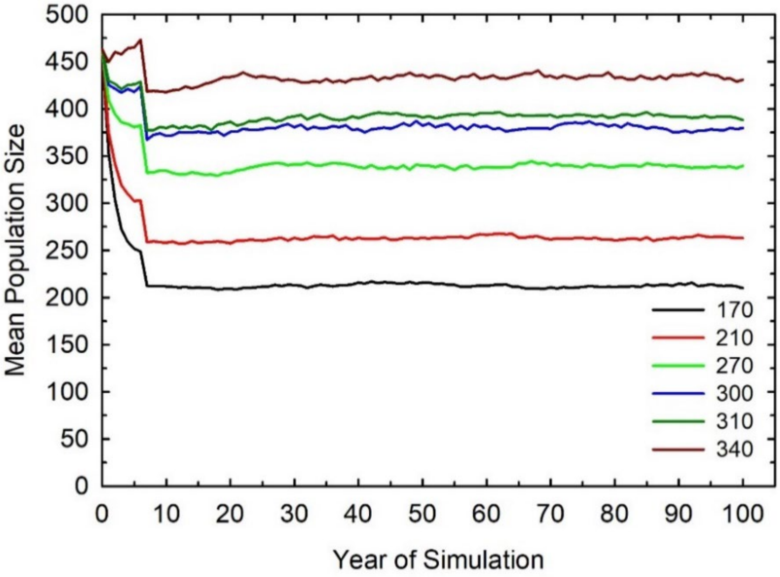


Figure 4. Projections of mean extant population size (census as of 1 October) for the Scandinavian wolf population across the range of minimum population abundance threshold values and assuming no immigration from Finland/Russia. Extant population size for a given scenario is calculated using only those iterations that did not become extinct. See accompanying text for more information on model structure and function.

While the long-term wolf population size shows significant stability over time in these simulations, the mean abundance is consistently larger than the minimum population abundance threshold value used to guide maintenance of the population at that desired abundance. For example, when the threshold is set at 170 individuals, the long-term average population size seen in Figure 4 is approximately 210 animals – about 23% greater than the population reference value. At larger reference values, the long-term mean abundance is approximately 25% greater than the corresponding reference value. This occurs because that the model's annual census event takes place in October which is after the production of pups in the spring, which is itself after the legal culling of wolves the preceding winter (see Figure 2 for the graphical depiction of the model's annual cycle). A pre-breeding census taken just before reproduction in the spring would show population abundance closer to the desired threshold value.

This dynamic can be examined in more detail by showing the total population abundance at each model timestep in order to see the impacts of different events that occur across the annual cycle (Figure 5). The figure shows a segment of just five years (ten timesteps), beginning just after the population census in October at the onset of model year 40. The first timestep features a general mortality event (including both natural mortality and some illegal hunting mortality), which is then followed by a culling event that is conditional on the population abundance relative to the specified minimum threshold. If the abundance exceeds the threshold, culling occurs as is evident in the first timestep shown in Figure 5. The population is now at or very near the threshold as of 1 April. The second timestep (April – October) now features a breeding event followed by mortality. These events will increase population size which will be recorded in the subsequent October census at the beginning of model year 41. In this next year, pup production declines stochastically, meaning that the mortality event takes the population below the minimum threshold by the 1 April model census. Therefore, culling was not necessary in this second year. Another round of reproduction increases the population to an abundance of about 200 individuals at the 1 October census that initiates model year 42. Because of the timing of the 1 October census in the model, as in reality, and if only the 1 October census data are displayed graphically as model output, the active maintenance of the population at or near the minimum threshold as reflected in the model's 1 April census is not readily apparent. It is recognized that the exact mechanism of setting annual culling targets in the model does not precisely replicate those mechanisms in reality, but the overall intention and outcome of the simulated culling process is generally realistic.

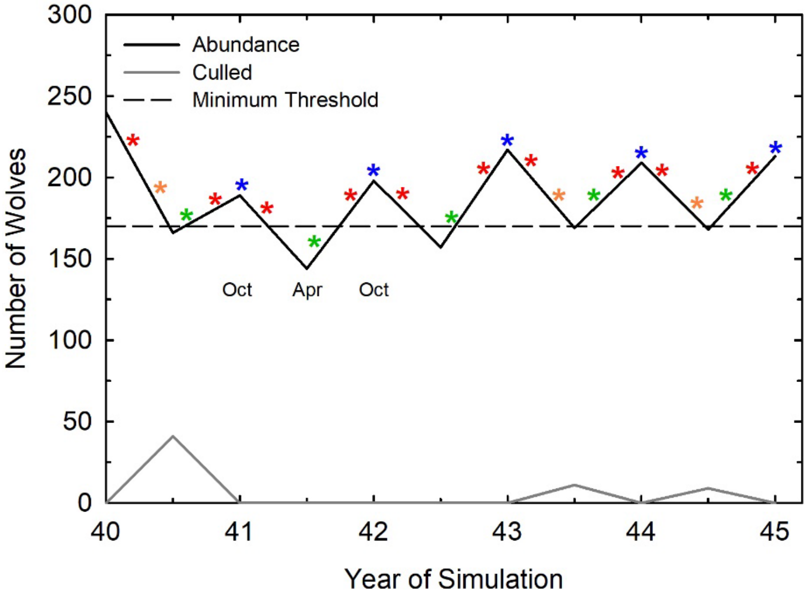


Figure 5. Five-year segment of a single iteration from the scenario featuring a minimum abundance threshold of 170 wolves (horizontal dashed line). Plots show the total wolf population abundance (black) and the number of wolves culled (dark gray) in the two timesteps making a single calendar year. The symbols represent specific events within each timestep, with mortality (red) and culling (orange) occurring in the October-April step and breeding (green) and mortality occurring in the April-October timestep. The population census event (blue) takes place in October. See accompanying text for more information on model structure and function.

Genetic output from the simulated populations in the absence of immigration from Finland/Russia shows short-term improvement in both the population mean inbreeding coefficient (Figure 6) and the retention of gene diversity (Figure 7). The initial gene diversity is estimated to be 0.802, with some very slight variation across scenarios resulting from the stochastic process of randomly "dropping" unique founder alleles through the known pedigree to initialize population genetic structure. After this improvement over six to seven years, models show consistent increases in mean inbreeding levels and a gradual erosion of gene diversity over the timeframe of the simulations. The short-term improvement is likely a result of the genetic contributions of the newly-arrived founders to the Scandinavian population and, to a lesser extent, the removal of genetically less valuable wolves through selective culling. The populations that are maintained at the smaller abundances accumulate inbreeding and lose gene diversity through random genetic drift more rapidly than those populations maintained at larger target abundances. It is important to observe here that even those simulated populations maintained at the largest abundance values (310 to 340 individuals) show higher levels of inbreeding and a gradual loss of gene diversity. While these populations are relatively large on the scale examined here, the consequences of isolation will inevitably result in reduced genetic viability over time.

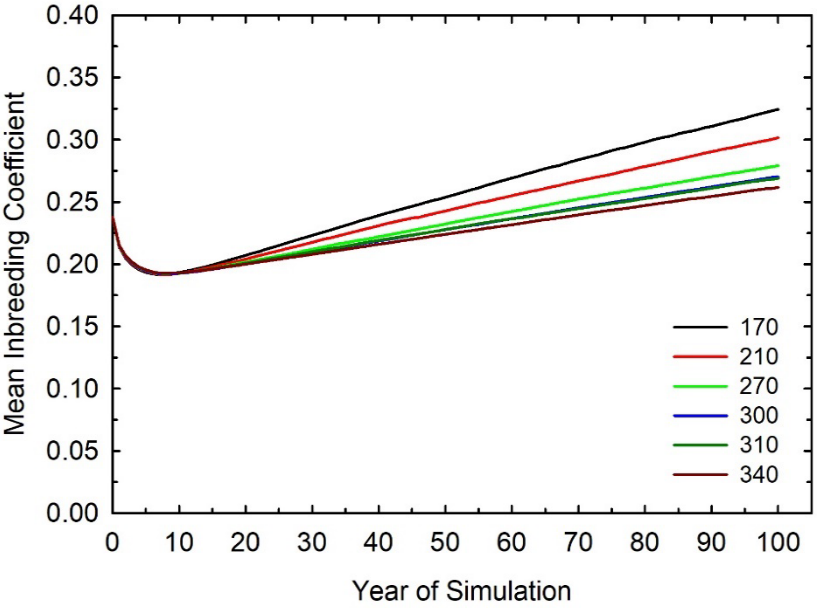


Figure 6. Projections of mean inbreeding coefficient in the Scandinavian wolf population across the range of minimum population abundance threshold values and assuming no immigration from Finland/Russia. Initial values of mean inbreeding in the population are based on pedigree information used as input for all simulations. See accompanying text for more information on model structure and function.

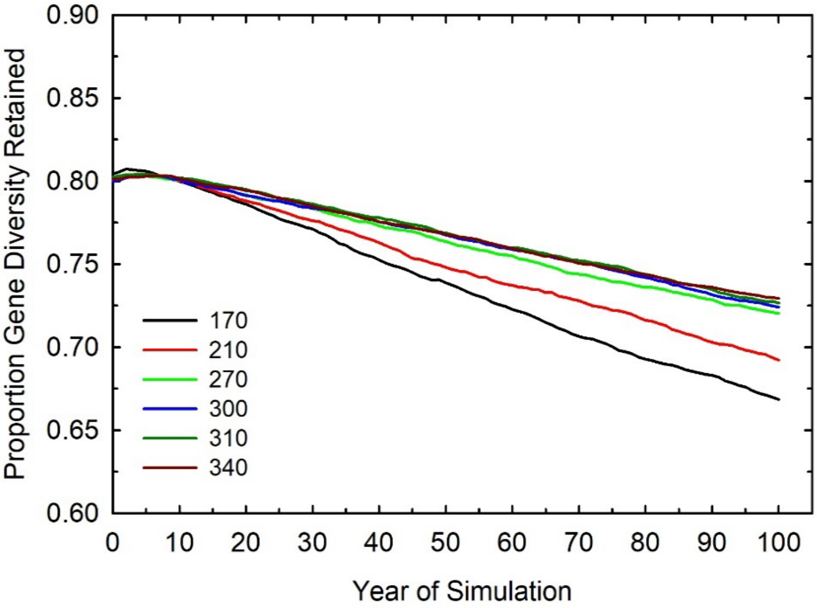


Figure 7. Projections of proportional gene diversity (GD) retained in the Scandinavian wolf population across the range of minimum population abundance threshold values and assuming no immigration from Finland/Russia. Initial GD values in the population are based on pedigree information used as input for all simulations. Retention values reported in this figure give the estimated theoretical proportion of diversity that remains in the population relative to the ancestral population source (Finland/Russia). See accompanying text for more information on model structure and function.

Analysis of genetic benefits of immigration into the Scandinavian wolf population

The simulations discussed in this report do not feature changes to the underlying rates of reproduction or age-specific mortality among Scandinavian wolves. As described in the section "Demographic performance of the base scenario" (page 12), the simulated Scandinavian wolf population grows at a mean realized annual rate of approximately 2% (in the presence of natural and anthropogenic sources of mortality including licensed hunting), which is consistent with the past ten years of data analyzed by Milleret et al. (2023). Consequently, it is assumed that the observed rate of population growth in simulations either excluding or including occasional immigration of wolves from the Finland/Russia population into the Scandinavian population will be effectively identical. This assumption has been verified in observations of mean population growth rate and mean long-term population size in simulations featuring the range of immigration rates tested as part of this analysis (detailed results can be found in Table 2). Therefore, analysis of scenarios featuring immigration into the Scandinavian population will focus on the potential genetic benefits of that immigration process.

Across the full range of minimum population abundance threshold values and immigration rates tested in this analysis, occasional addition of wolves from the source Finland/Russia population leads to a reduced rate of gene diversity loss over time in the Scandinavian population, compared to a "control" scenario excluding immigration (Figure 8, Table 2). This benefit is more pronounced at the lower end of the range of population abundance threshold values (170 to 270 individuals), where smaller isolated populations lose gene diversity more rapidly through increased rates of inbreeding and accelerated genetic drift. As expected, increased frequency of immigration into the Scandinavian population leads to an enhanced genetic effect – lower rates of inbreeding and increased retention of population gene diversity.

The absolute values of proportional gene diversity retained that are shown in Figure 8 are calibrated to the starting value of gene diversity expected to be captured from the historical set of founders that immigrated into the Scandinavian population from Finland and Russia ($GD_0 = 0.802$). More precisely, this starting value is the expected heterozygosity in the population at the start of the simulation, determined by the historical data on founder immigration events and the mating structure among individuals as given by the full population pedigree dating back to the first immigration event in the early 1980s. As explained previously, a statistical technique is used to "drop" unique founder alleles through the pedigree to estimate current allele frequencies, and, by extension, expected heterozygosity. In addition to this presentation of absolute gene diversity retention, another expression of gene diversity retention can be calculated as the relative proportion of the starting value that is retained in the Scandinavian population at the end of the 100-year simulation. This relative retention metric can readily identify situations where introgression of new genes from recent immigrants can effectively offset the loss of existing diversity from past founders.

Figure 9 summarizes gene diversity outcomes for the full range of scenarios making up this analysis. Proportional gene diversity retained over 100 years relative to the simulation starting conditions ranges from a minimum of 0.834 (minimum population abundance threshold value of 170 in the absence of immigration) to 1.003 – 1.005 (minimum population abundance threshold values of at least 270 and with an average of one immigrant entering the Scandinavian population every three years).

Proportional gene diversity retention values of 0.95 or 0.90 over 100 years can be used as candidate measures of genetic viability for the purposes of interpreting these results. Using the 0.95 retention metric, the results in Figure 9 indicate that if the mean immigration rate equates to one wolf added to the Scandinavian population every three years, then all minimum population abundance threshold values within the tested range exceed the genetic viability criterion. For a mean immigration rate of one wolf every six years, minimum population abundance threshold values of 270 and above satisfy the 0.95 genetic viability criterion. A population reference value of 340 wolves can satisfy the 0.95

criterion when the immigration rate is reduced to an average of one wolf added to the Scandinavian population every nine years on average. If the 0.9 retention metric is used, only isolated populations below the threshold of 300 and a population threshold of 170 with the lowest immigration rate fail to meet the genetic viability criterion (see Table 2 for the full results).

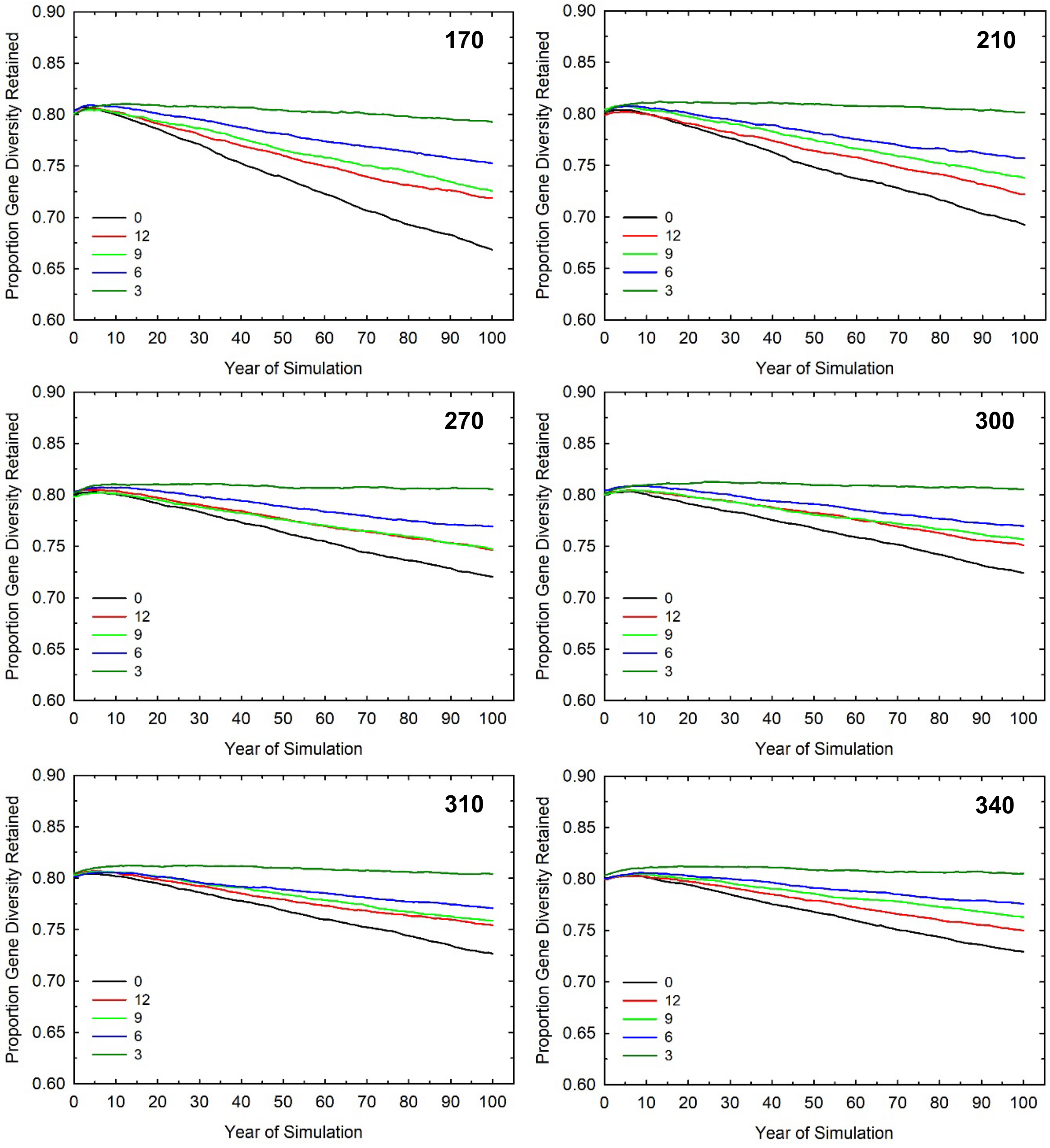


Figure 8. Projections of proportional gene diversity (GD) retained in the Scandinavian wolf population across the range of minimum population abundance threshold values and expected rates of immigration of wolves from Finland/Russia. The value in the top-right corner of each panel is the minimum abundance threshold value for that set of scenarios. Each plot legend defines the expected immigration rate, with numerical values equal to the average number of years between immigration of one individual (male or female) into the Scandinavia population. Initial population GD values are based on pedigree information used as input for all simulations. Retention values reported in this figure give the estimated theoretical proportion of diversity that remains in the population relative to the ancestral population source (Finland/Russia). See accompanying text for more information on model structure and function.

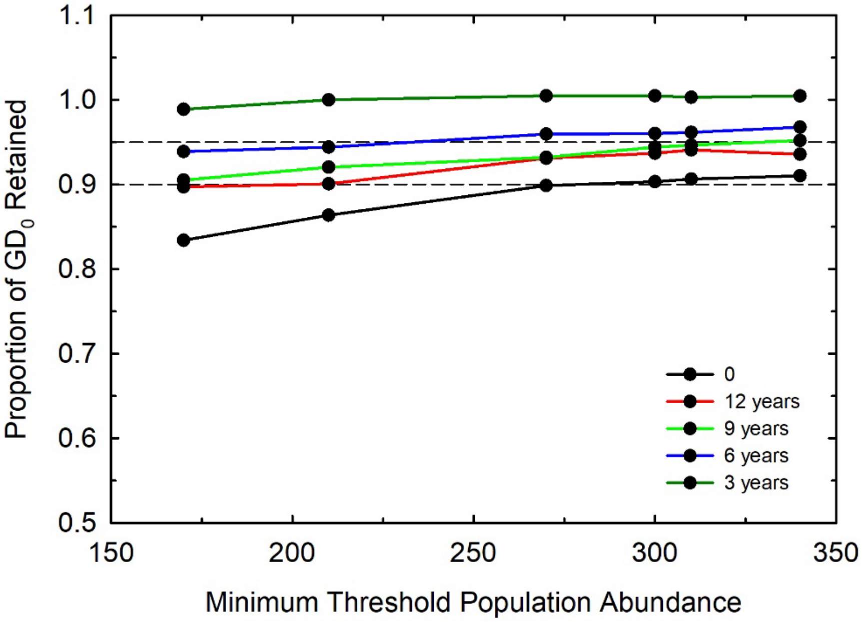


Figure 9. Scandinavian wolf population gene diversity (GD) retained after 100 years, expressed as the proportion of the estimated initial value in the population at the beginning of the simulations. Horizontal dashed lines identify 90% and 95% GD retention levels often used for identifying genetic viability metrics. See accompanying text for more information on model structure and function.

The gene diversity retention results displayed in Figure 9 are mean values calculated over 1000 model iterations for each scenario. The specific probability that the final gene diversity would actually meet or exceed a candidate genetic viability criterion for any given scenario is given in Figure 10. This probability is calculated by storing the final GD value at model year 100 for each of the 1000 iterations run for a given scenario, and calculating the proportion of those values that meet or exceed a candidate criterion. When considering the smallest population abundance threshold of 170 individuals, the probability of meeting or exceeding the 0.95 retention criterion is 0.711 under the highest rate of immigration (one individual every three years on average) and declines to just 0.172 when immigration is absent (Figure 10A). The probability of achieving or exceeding the 0.90 retention criterion increases to 0.837 under the highest immigration rate and to 0.368 assuming no immigration from Finland/Russia (Figure 10B). If the population abundance threshold is increased to 340, the probability of achieving or exceeding the 0.95 retention criterion ranges from 0.781 (one immigrant every three years) to 0.450 (no immigration). The 0.9 retention criterion can be achieved or exceeded with a probability ranging from 0.891 (one immigrant every three years) to 0.645 (no immigration).

If immigration is absent from the analysis, the proportional retention of gene diversity is a comparatively strong function of the minimum population abundance threshold value. As the immigration rate increases, this relationship is less pronounced; interestingly, under the highest rate of immigration tested here (mean one individual every three years) there is rather little influence of population abundance threshold on the final extent of gene diversity retained. In other words, the models appear to be more sensitive to the rate of introgression of wolves from the Finland/Russia source population than they are to the minimum population abundance threshold imposed across the timeframe of the simulation. It is also important to recognize that the achievement of genetic viability as defined here is observed to be a probabilistic phenomenon and, therefore, is not guaranteed given a specified set of biological and management conditions. A precise definition of population viability can incorporate metrics on both overall gene diversity retention over a specified period of time and the expressed confidence in achieving that outcome.

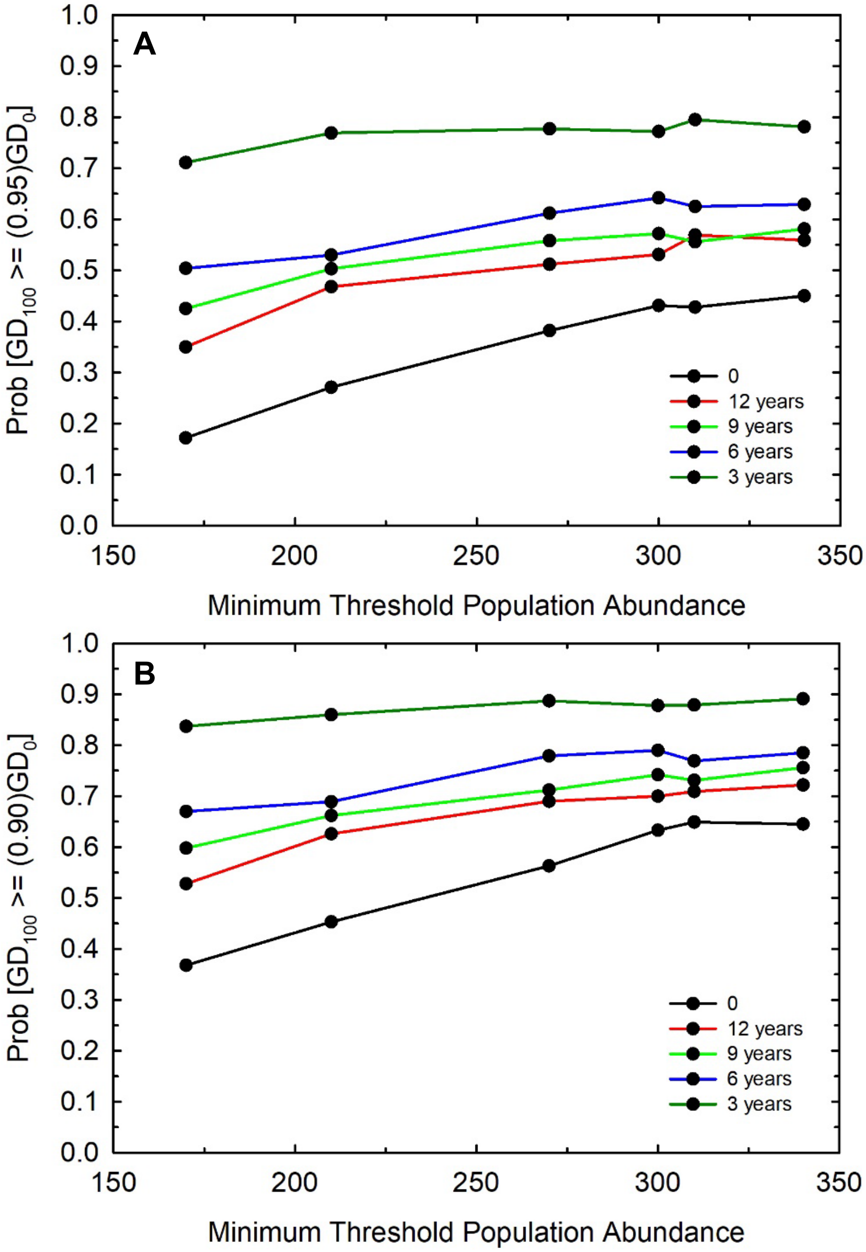


Figure 10. Probability that the gene diversity retained in the Scandinavian wolf population is at least 95% (A, top panel) or 90% (B, bottom panel) of the initial value at the beginning of the simulations. Curves represent different rates of immigration of wolves from the Finland/Russia population, expressed here as the mean time interval between immigration events (single wolf entering the Scandinavian population). See accompanying text for more information on model structure and function.

Table 2. Key output metrics for Scandinavian wolf population dynamics simulations. Shaded cells indicate those scenarios in which the Scandinavian population retains at least 90% (light green) or 95% (darker green) of initial population gene diversity after 100 years.

Column headings: Min N, minimum population abundance threshold; D, mean number of successive years between individual wolves immigrating from the Finland/Russia population into the Scandinavian population; P(E), probability of population extinction within 100 years; $N(Ext)_{100}$ (SD), mean total population size (as of 1 October) across extant populations at 100 years (standard deviation); $N(Ad/Sub/Pup)_{100}$ (SD), mean number of adults/subadults/pups (as of 1 October) across extant populations at 100 years (standard deviation); GD_{100} (SD), mean population gene diversity after 100 years (standard deviation); % GD_0, proportion of population gene diversity retained after 100 years relative to the initial value estimated at the beginning of the simulation; Prob ≥ ($0.95/0.90GD_0$), probability that the final population gene diversity value is at least 95% / 90% of the initial value at year 0; F, mean population inbreeding coefficient.

Min N	D	P(E)	$N(Ext)_{100}$ (SD)	$N(Ad)_{100}$ (SD)	$N(Sub)_{100}$ (SD)	$N(Pup)_{100}$ (SD)	GD_{100} (SD)	% GD_0	Prob ≥ ($0.95GD_0$)	Prob ≥ ($0.90GD_0$)	F
170	0	0.020	209.9 (109.1)	87.1 (45.7)	48.8 (29.9)	76.3 (50.3)	0.669 (0.121)	83.4	0.172	0.368	0.324
	12	0.010	204.6 (84.3)	83.0 (34.7)	47.9 (25.5)	75.6 (42.0)	0.719 (0.107)	89.7	0.350	0.528	0.296
	9	0.007	211.5 (91.0)	85.6 (39.1)	48.9 (24.5)	79.5 (47.5)	0.726 (0.105)	90.5	0.425	0.598	0.288
	6	0.003	208.8 (72.7)	82.9 (29.8)	49.0 (21.1)	77.9 35.0)	0.753 (0.095)	93.9	0.504	0.670	0.276
	3	0.006	211.3 (63.6)	81.8 (25.2)	49.7 (19.3)	80.4 (31.6)	0.793 (0.076)	98.9	0.711	0.837	0.246
210	0	0.017	262.9 (93.5)	106.0 (39.2)	60.8 (26.9)	98.0 (44.8)	0.692 (0.107)	86.4	0.271	0.453	0.302
	12	0.006	261.5 (92.6)	104.1 (38.6)	61.0 (26.7)	98.1 (43.5)	0.722 (0.101)	90.1	0.468	0.626	0.282
	9	0.009	258.3 (85.9)	102.1 (35.1)	60.3 (24.9)	97.1 (40.9)	0.738 (0.100)	92.0	0.503	0.662	0.274
	6	0.006	262.7 (81.1)	103.1 (32.7)	61.7 (24.1)	99.2 (40.0)	0.757 (0.088)	94.4	0.530	0.689	0.263
	3	0.002	262.6 (63.3)	101.2 (24.4)	61.4 (19.4)	100.7 (34.7)	0.802 (0.073)	100.0	0.769	0.860	0.237
270	0	0.012	339.7 (84.8)	133.6 (34.8)	78.8 (24.5)	129.2 (46.9)	0.720 (0.095)	89.9	0.382	0.563	0.279
	12	0.004	338.1 (85.4)	131.8 (34.0)	80.1 (25.5)	127.9 (46.3)	0.746 (0.090)	93.1	0.512	0.690	0.263
	9	0.001	343.7 (88.4)	132.9 (35.5)	80.6 (25.6)	131.7 (46.6)	0.747 (0.092)	93.2	0.558	0.712	0.258
	6	0.006	337.3 (88.3)	129.7 (34.5)	79.5 (25.9)	129.7 (46.8)	0.769 (0.081)	96.0	0.612	0.779	0.250
	3	0.000	347.2 (65.9)	131.4 (25.9)	82.5 (20.8)	134.0 (38.0)	0.805 (0.068)	100.5	0.777	0.887	0.229
300	0	0.002	379.7 (92.7)	148.3 (38.3)	88.9 (27.6)	144.6 (48.9)	0.724 (0.094)	90.3	0.431	0.633	0.270
	12	0.003	381.2 (91.8)	147.4 ()36.4	89.6 (27.3)	146.1 (50.3)	0.751 (0.087)	93.7	0.531	0.700	0.256
	9	0.001	380.4 (83.9)	146.5 (33.5)	88.6 (26.4)	146.6 (45.3)	0.757 (0.085)	94.4	0.572	0.742	0.253
	6	0.002	380.5 (78.2)	144.8 (30.1)	90.8 (24.5)	145.8 (43.5)	0.770 (0.079)	96.0	0.642	0.790	0.244
	3	0.001	385.9 (76.4)	144.9 (27.3)	91.0 (23.9)	150.5 (43.2)	0.805 (0.067)	100.5	0.772	0.878	0.226

Table 2. (Continued)

Min N	D	P(E)	$N(Ext)_{100}$ (SD)	$N(Ad)_{100}$ (SD)	$N(Sub)_{100}$ (SD)	$N(Pup)_{100}$ (SD)	GD_{100} (SD)	% GD_0	Prob ≥ ($0.95GD_0$)	Prob ≥ ($0.90GD_0$)	F
310	0	0.007	388.1 (98.9)	151.6 (39.6)	91.1 (28.7)	147.5 (52.3)	0.727 (0.091)	90.6	0.428	0.649	0.269
	12	0.001	393.1 (88.9)	150.7 (36.2)	93.4 (25.6)	150.2 (46.7)	0.754 (0.084)	94.1	0.569	0.709	0.255
	9	0.002	387.8 (97.8)	149.0 (37.6)	92.0 (27.8)	148.2 (51.7)	0.759 (0.083)	94.6	0.556	0.731	0.251
	6	0.001	399.0 (85.1)	151.9 (32.5)	93.4 (24.9)	154.9 (48.1)	0.771 (0.078)	96.2	0.625	0.769	0.244
	3	0.000	401.3 (81.2)	150.3 (30.3)	95.9 (24.3)	155.9 (46.7)	0.804 (0.073)	100.3	0.795	0.879	0.225
340	0	0.003	430.8 (106.1)	166.8 (41.4)	100.7 (31.9)	165.3 (53.9)	0.729 (0.097)	91.0	0.450	0.645	0.262
	12	0.001	431.7 (103.1)	165.4 (41.2)	101.8 (31.2)	167.7 (57.4)	0.750 (0.087)	93.6	0.559	0.722	0.250
	9	0.000	427.9 (95.8)	163.3 (36.7)	101.8 (29.6)	164.0 (50.3)	0.763 (0.079)	95.2	0.581	0.756	0.246
	6	0.001	436.2 (90.8)	165.8 (33.9)	101.2 (27.0)	170.4 (51.4)	0.776 (0.078)	96.8	0.629	0.785	0.239
	3	0.002	439.0 (87.9)	164.7 (33.1)	102.4 (26.3)	173.0 (50.2)	0.805 (0.069)	100.5	0.781	0.891	0.223

Testing model sensitivity to select demographic input parameters

Reviewers of the initial draft version of this report identified a subset of input parameters with relatively higher levels of uncertainty that, as a result, could be the subject of additional sensitivity testing in order to determine the impact of this uncertainty on model outcome. Three parameters were chosen for this additional analysis:

- <u>Proportion of adult females breeding</u>: All models in this PVA assume that, on average, 60% of adult females produce a litter of pups each year. This estimate was carried over from the most recent PVA model developed by Bruford (2015). Unpublished population data compiled by SKANDULV over the time period 2011 to 2022 indicates that this estimate of reproductive success is in fact 64%. A subset of new models was run created this as the new mean value for the percentage of adult females breeding (producing pups) each year.
- <u>Genetic rule for population culling</u>: Based on conversations with members of the PVA model development team (Appendix I), the assumption was made that culling of individuals each year was conditional on their genetic makeup – measured by their mean kinship to other members of the population. In particular, individuals that are deemed to be relatively more genetically valuable, as measured by a low mean kinship value, would not be subject to legal removal. Subsequent discussions during the review process suggests that this practice is not presently practiced, although regulations do in fact specify that immigrants and their offspring are exempted from legal harvest. A subset of new models was created that removed the genetic condition on harvesting individuals, while retaining the restriction on harvesting immigrants. [Note that model restrictions do not allow for identification of the full range of immigrant offspring for similar harvest restrictions.]
- <u>Size of the source population in Finland/Russia</u>: The core set of models set the initial abundance of the Finland/Russia population at 500 individuals, and with a habitat carrying capacity (*K*) of 800. These figures were chosen somewhat arbitrarily, primarily with the goal of maximizing the ability of that population to successfully serve as a source of immigrants to the Scandinavia population. Subsequent discussion argued for a smaller population in Finland/Russia, as well as a reduced value for the habitat carrying capacity. In light of these discussions, and informed by a recent report on analysis of wolf population viability in Finland (Mäntymiemi et al. 2022), a subset of new models was created in which the initial abundance in the Finland/Russia population is assumed to be 300, and with a habitat carrying capacity of 600.

The set of five scenarios featuring a minimum population abundance threshold value of 270 individuals was used as the basis for this analysis, as this represents a value approximately mid-way across the range of tested abundances. Each of the three parameters identified above were revised to their alternate values independently in order to evaluate their specific impact on population performance. Proportional retention of gene diversity relative to the starting value was chosen as the output metric for analysis.

Overall, the identified modifications to each of the three input parameters resulted in only very small changes in the chosen output metric, with the changes generally observed to shift gene diversity in the predicted direction (Figure 11). Relaxing the genetic rules governing removal of individuals each year – effectively defined as random removal of living non-immigrants – would be expected to result in removing some individuals of relatively higher genetic value and, consequently, a higher rate of gene diversity loss in the population. The model results confirm this expectation, although the absolute magnitude of reduced gene diversity retention is quite small: final proportional gene diversity retained differed from the baseline scenario results by 0.2% to 1.7%. Similarly, a smaller source population in Finland/Russia would, over time, be expected to result in immigrants entering the Scandinavian population with a higher mean relatedness and, by extension, a comparatively smaller positive contribution to gene diversity in the Scandinavian population. Again, the models generally confirm this expectation, although not with the same level of consistency and magnitude as was seen in the scenarios featuring a modification to the population culling rules (gene diversity retention change of 0.4% to 0.9% depending on immigration rate). Increasing the proportion of females producing pups each year was expected to produce minimal changes to the population genetic output metric. This change would result in a small increase in population growth rate; however, because of the mechanic built into these models that regulates population abundance at or just above the minimum population abundance threshold value, this apparent benefit would be largely offset by the correspondingly larger number of individuals subject to culling to keep the population at the desired abundance (gene diversity retention change of 0.1% to 0.8% depending on immigration rate).

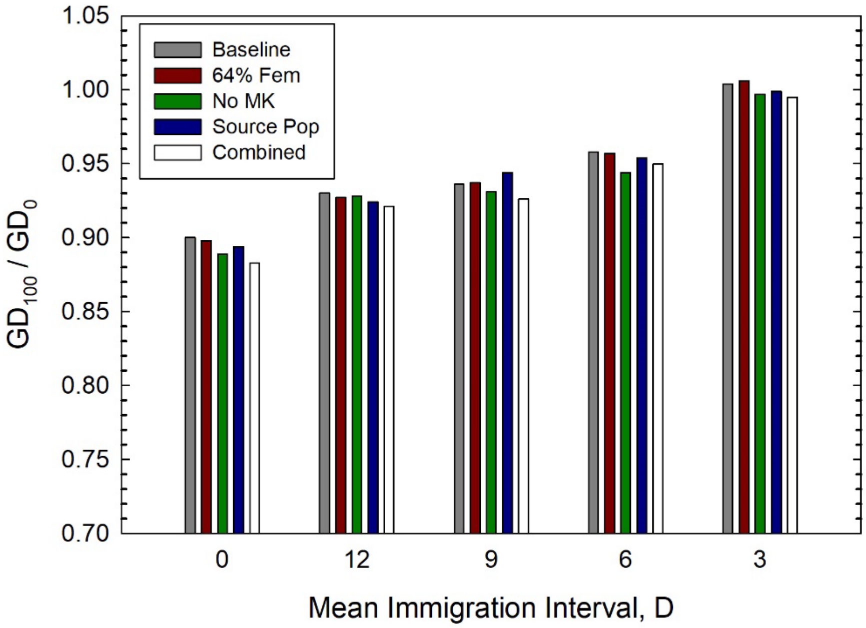


Figure 11. Results of sensitivity analysis scenarios, expressed as the proportional retention of population gene diversity at 100 years (GD_{100}) relative to the gene diversity present in the Scandinavian population at the beginning of the simulation (GD_0). See accompanying text for more information on sensitivity scenario parameter values and overall model structure.

Combining each factor into a single set of scenarios – featuring higher female breeding success, relaxing the genetic-based culling rule, and reducing the size of the Finland/Russia source population – yields results that generally conform to expectations. Gene diversity retention is reduced for each level of immigration relative to the baseline scenarios, but as before the absolute difference remains small at 0.8% to 1.9% compared to the baseline retention value, depending on the immigration rate.

Discussion and Conclusions

Interpreting the language of the EU Habitats Directive for this analysis

The key question posed by the Swedish Government in the context of guiding the construction and implementation of this population viability analysis (PVA) focuses on the conditions that are required for the reference value for the Scandinavian wolf population size, as defined for favorable conservation status according to the European Union Habitats Directive, to lie within the interval of 170 – 270 individuals. In order to properly address this question, it is important to understand the intended meaning of certain words and phrases in the above sentence.

First, the Habitats Directive guidance document (DG Environment 2023) considers the conservation status of a species to be "favorable" when "...the species is maintaining itself on a long-term basis as a viable component of its natural habitats". The author of this report assumes that the concept of favorable conservation status as applied to species in the above statement can also be applied to individual populations as is being done here for the Scandinavian wolf population. Furthermore, the phrase "...the species is maintaining itself on a long-term basis..." implies that the species or population is not declining in abundance and, at minimum, is demonstrating a mean trend in abundance over some specified time period that is at least stable (in other words, neither growing nor declining) and preferably increasing. Secondly, the Directive defines the concept of a favorable reference population (FRP) as the "...population in a given biogeographical region considered the minimum necessary to ensure the long-term viability of the species...".

Note that both of these definitions invoke the concept of viability. The Directive does not provide definitive guidance on how to precisely define the concept of viability and its dependence on a timeframe within which it is measured. In the absence of this definitive guidance, it may be necessary to refer to existing frameworks within which demographic and genetic definitions of viability have been proposed. For example, the Red List Categories and Criteria as defined by the International Union for Conservation of Nature (IUCN) define the risk-based boundary between threatened and non-threatened taxa at a 10% risk of species or population extinction within 100 years (IUCN 2012). The relatively newer addition of explicit genetic concerns in relation to wildlife population viability takes into account the retention of a quantitative threshold of genetic diversity in a population over a specified period of time. These thresholds – typically in the range of retaining 90% to 95% of the original founder gene diversity over a period of 100 years – originate from concepts guiding management of captive populations of endangered species where intensive management of breeding dynamics can be used to promote viability (for example, Lees and Wilcken 2009, 2011). As a working framework for interpreting the results of the present analysis, it may be instructive to adopt similar definitions of both demographic and genetic viability as diagnostic of favorable conservation status as presented in the European Union's Habitats Directive. The official definition of viability generated by government authorities may differ from this example.

Key attributes of PVA model structure and interpretation of results

It is important to clarify the mechanisms by which the range of minimum population abundance threshold values used in the simulations described here – serving as precursors to the associated range of favorable population reference values – are implemented. Before that can be done, however, it must be remembered that all scenarios in this PVA begin in October 2022 with a population of wolves in Scandinavia (Sweden and Norway: N = 463) that is larger than the upper bound of population reference values tested here. Because of this reality, and in light of the question posed by the Swedish Government that frames this analysis, the simulations include a mechanism by which wolves are removed on an annual basis in order to bring the population down to an abundance that is more compatible with the identified reference value. This removal of wolves is therefore considered a necessary activity within the modeling framework to examine a range of future population abundance thresholds while simultaneously acknowledging the need to initialize the simulations under existing conditions. Establishing hunting regulations in Sweden is certainly not without controversy (e.g., Laikre et al. 2022), and the best scientific information must be used to inform responsible decision-making for management of this endangered population. In implementing this component of the model, the author neither supports nor condones any level of wolf harvest or similar form of management.

The removal process implemented in these simulations is similar in theory to the "selective harvest" of Liberg and Sand (2012), in which genetically valuable animals are exempt from harvest in order to retain their genetic representation in the living population. In the Vortex simulations used here, all new immigrants from the Finland/Russia population (genetic founders to the Scandinavian population) are exempt from this harvest, as are individuals that have low levels of relatedness to other wolves as measured by individual mean kinship (calculated from the initial and derived pedigree over time). The current analysis does not explicitly restrict F1 offspring of new founders from harvest, but these individuals are almost certainly implicitly exempt due to their low levels of kinship to the rest of the population. All in all, the harvest mechanic used here made every attempt to be as realistic as possible and to reduce its impact on the genetic characteristics of the Scandinavian population.

Given this harvest element of the model, it should be recognized that the minimum population abundance threshold value used in any given scenario should not be interpreted as a form of population carrying capacity. The carrying capacity of a population (or, more precisely, the habitat within which the population resides) acts ecologically as a ceiling, restricting the population from further growth under favorable conditions. Instead, in this PVA the population abundance threshold value is meant to act as a floor – the lower bound of abundance, below which the population of interest should not decline. Harvest (set to occur in the winter timestep) only occurs if the population is larger than the reference value, thereby encouraging the population to grow to that value. In the case of this wolf population, the underlying realized annual growth rate of 1.5% to 2.0% should help the population recover from declines due to random drops in survival and/or reproduction or the occasional severe event like a disease outbreak. This growth rate can be significantly larger when the population is below the desired abundance threshold, as legal culling is no longer employed (both in the model and in reality) in favor of facilitating growth to the desired minimum abundance. When population abundance exceeds the threshold to a significant extent, culling is designed to reduce the population closer to that minimum abundance value.

Because this harvest is probabilistic, the simulation of this process will sometimes result in a smaller number of wolves removed than expected. This will result in a population count in the following October that is not reduced to the exact population reference value. Additionally, the observed abundance as of 1 October is the outcome not only of wolf removal the preceding winter, but also of the addition of new surviving pups in the spring, just before the October census is taken. As a result of the combined effects, the long-term abundance therefore equilibrates at a value that is greater than the desired abundance threshold. But this is consistent with the spirit of the Habitats Directive's broad definition of "viable population" as the minimum abundance needed to reduce of an adverse demographic or genetic outcome for the population in the timeframe of the analysis (100 years). To satisfy this viability criterion, the population abundance should ideally remain greater than the stipulated minimum, thereby reducing the likelihood of sustained reductions below that value and risking the destabilizing effects of the "extinction vortex" (Gilpin and Soulé 1986). In this way, the abundance threshold value is truly acting not as a cap on population abundance, but as a floor – below which the population should not decline.

The detailed description of model structure in the report by Bruford (2015) is often unclear, so it is difficult to reconstruct the process by which any type of similar harvest mechanic was implemented to examine different population reference value targets. Some of those models also did not use a pedigree file specifying the ancestral relationships among animals that were alive as of the start date of that analysis. Moreover, that earlier report included many simulations that featured carrying capacity values as high as 2000 – values significantly greater than the upper bound of the range of population reference values tested in this analysis. It is therefore not practical to make direct comparisons between the results of the present analysis and the earlier Bruford analysis.

While acknowledging the difficulties in comparing the present model structure to the most recent analysis of Bruford (2015), it is instructive to consider some potential weak points of this Vortex model and how those weaknesses could impact the results. At a fundamental level, there may be concerns that the relatively more "generic" structure of the software may not capture the potentially complex nuances of species like wolves that feature socially-stratified breeding dynamics. The basic Vortex framework does not include facilities for including this social stratification, but it can be done if the specific analytical questions call for it and if the relevant data are available. The ability in the current wolf model to specify long-term monogamous breeding, to accurately portray the starting population genetic structure by incorporating the historic pedigree data, and the ability to develop complex rules around population regulation are likely sufficient to create projections of wolf population dynamics that are useful for the larger decision-making process.

When investigating model structure and function at a finer scale, a few input parameters can be highlighted in a discussion of model accuracy and realism:

- Extent of genetic load: The specification of genetic load – the demographic cost of inbreeding, quantified by the number of lethal equivalents – is based on relatively old data from Liberg et al. (2005) that could potentially be updated if new information exists. The study by Bensch et al. was considered for this analysis, but the uncertainty around the precise demographic mechanism of an apparent inbreeding effect was a key factor in ultimately deciding to not include this potential effect in the present PVA. The authors of that study acknowledged that they were unable to determine of the higher success of heterozygous wolves to recruit to the breeding population was caused by selection on survival to breeding age or instead on factors determining pair formation and successful mating. Because of this ambiguity, there appeared to be a significant risk of overestimating the inbreeding effect, primarily by adding the signal detected by Bensch to the existing pup survival effect reported by Liberg et al. (2005). This risk of "double dipping" is real and, given some ambiguity about the mechanism of incorporating this study into our demographic description of wolf population dynamics, the choice was made to exclude it from the analysis.
- Catastrophes: The frequency of a generic catastrophic event as simulated in this analysis – occurring just once on average in a 100-year period – that reduces both survival and reproduction in Scandinavian wolves may be underestimated. Reed et al. (2003) suggested a much higher frequency of a significant event impacting vertebrate populations, and Miller (2017) specified a similarly higher frequency of an infectious disease outbreak in a PVA for Mexican wolves. If a catastrophic event with a higher frequency were included in this analysis, the impact would likely be more deleterious that considered here. The downstream consequences for identification of the minimum viable population abundance are less clear.
- Mean litter size: The mean litter size used for this analysis – an average of 5.3 pups born in April to successful females – may be an overestimate of the true estimate of fecundity in this population. Sand et al. (2014) estimates a mean of 3.5 pups per litter. An assumption for the present PVA is that this value represents an estimate of pups alive as of the 1 October census, which is a different parameter than what is used in this analysis (number of pups alive at birth in April). Assuming a survival rate of approximately 0.82 in the April – October time period (in line with the analysis of Milleret et al. (2023)), the estimated number of live pups at birth would be 4.3. This is in fact quite similar to the original estimated number of live pups at birth for this analysis (4.5) based on the analyses of Liberg et al. (2005). This number was adjust upwards to 5.3 to facilitate a simulated population growth rate matching that reported by Milleret et al. (2023). The fact that we see a wolf population in Scandinavia that is consistently growing in abundance, and given the rather robust

survival estimates presented in Milleret et al. (2023), the uncertainty in mean litter size in this population is likely to be of little consequence in the larger analysis.

Another key element of the present analysis is the metapopulation structure defined by the presence of a second population representing wolves in Finland/Russia. In the Vortex model used here, the demographic and genetic characteristics of this population are not specified with the same level of detail as the Scandinavian population; this second population is designed primarily to serve as a source of animals that would occasionally disperse to the west and become immigrants into the Scandinavian population. This mechanism of probabilistic dispersal is believed to be more realistic than the analysis of Bruford (2015) in which immigration was typically simulated as a deterministic "supplementation" of a specified number of individuals over a specific time interval. Although it is unlikely within the model that more than one individual would immigrate into the Scandinavian population in any given year, the timing of those immigration events is random across years and across iterations so that greater or fewer numbers of wolves could immigrate into the population over the duration of the simulation.

Perhaps the most significant assumption influencing the results of this PVA concerns the relatedness among the founders of the Finland/Russia population and the kinship of that population to the Scandinavian wolves. Since we do not have a detailed pedigree for the Finland/Russia population, we are unable to specify the genetic relationships among those individuals. [This is also, of course, the assumption concerning the seven founders of the current Scandinavian population.] The model does specify that all individuals in the Finland/Russia population start with inbreeding coefficients and kinships amongst each other equal to 0.1, but this only acts to recalibrate the mean level of inbreeding in the starting population away from 0.0 in the default scenario where all starting individuals are unrelated. In turn, this will lead to immediate impacts of inbreeding in that population. This detail, however, does not set levels of relatedness among Scandinavian and Finland/Russia wolves.

There is strong reasoning to assume that wolves immigrating from Finland/Russia share some level of explicit genetic ancestry with the Scandinavian wolves, as the current population is derived from that geographic source (see Smeds and Ellegren 2022 for a review and new data concerning this topic). It is important to remember, though, that the necessary assumption regarding pedigree data is that the founders that started the Scandinavian population, as well as those continuing to immigrate to the west, are also unrelated to each other and to existing Scandinavian wolves. If new data become available that demonstrate a specific common ancestry among the identified Scandinavian population founders, then it would be possible to revise the existing 1 October 2022 pedigree with this new information and update the analyses. Without those data, we are forced to make the assumption that the degree of relatedness among new wolves immigrating into Scandinavia from Finland/Russia is no greater than or less than the relatedness of founders of the Scandinavian population to each other. In this comparative context, it is difficult to estimate the degree of error in the results of the current analysis, especially when assessing the suitability of candidate reference population values.

Even with this recognized uncertainty, there is an argument to be made that the key metric of interest in evaluating a genetic component of population viability is the <u>relative rate of loss</u> of population-level gene diversity, and not the <u>absolute value</u> of that diversity that is retained. Numerous examples exist in the wildlife conservation literature where current levels of gene diversity are already below thresholds commonly used to define viability (e.g., retention of 90% wild population gene diversity). For example, captive populations of both the Mexican wolf (*Canis lupus baileyi*) and the red wolf (*Canis rufus*) have gene diversity values that are below the standard gene diversity retention targets, owing to small founder numbers, earlier extinction of the taxa in the wild, and challenges in proper population management through the early phases of the breeding programs (USFWS 2022; 2023. Despite this undesirable starting point, the goal of population management is to minimize the loss of existing gene diversity in order to maximize opportunities for continued population growth and to improve parameters for long-term viability.

Finally, it may be instructive to note that the mean inbreeding coefficient in the Scandinavian population, as reported in Åkesson and Svensson (2022), has decreased from a maximum value of approximately 0.31 in 2006 to 0.24 in 2021 and has remained rather constant at the latter value since 2014. [Importantly, this analysis also appears to assume no genetic relatedness among founders since 1983.] This observation could imply that the assumptions built into the current Vortex model regarding relatedness among wolves within and between these populations may be reasonable.

Implications of PVA results for identification of MVP value for wolves in Sweden

The analysis described here is a dedicated attempt to create a sufficiently robust and realistic simulation of population dynamics and management that can ultimately inform the question of a favorable reference population (FRP) value for Scandinavian wolves. However, as described elsewhere in this report, the estimation of the FRP value must first be preceded by an analysis of the ecological and management conditions that can support maintenance of a minimum population abundance that can be considered viable according to specific criteria. A detailed demographic dataset was used to construct realistic rates of annual reproduction and survival for the population, and the genetic structure of the population was characterized by a complete pedigree of all living individuals and their ancestors dating back to the population's beginning about 40 years ago. Despite the depth of the dataset, the analysis required specification of some key assumptions about kinship among animals in the Scandinavian and Finland/Russia populations, and how this genetic ancestry may impact the benefits of immigration into Scandinavia from the source population to the north.

Given the nature of the current models discussed in this report, and acknowledging the assumptions built into these simulations as described above, the analysis suggests that the wolf population in Scandinavia (south-central Sweden and southeast Norway) can potentially be considered viable within the interval of 170 to 270 individuals in accordance with the broad definitions presented in the European Union's Habitats Directive. However, this condition requires the following processes to be maintained through time:

- The Scandinavian wolf population must have the demographic characteristics to, at a minimum, sustain a positive population growth rate, ideally similar to or greater than what has been observed over the past decade of detailed observations of reproduction and survival (annual growth lambda $\lambda \geq 1.02$, with the possibility of considerably higher growth rates in the absence of legal harvesting of wolves); and
- Immigration of wolves from Finland/Russia into Scandinavia should be, on average, no less than one individual every three years.

The above discussion defines conditions for maintaining a viable population of wolves in Scandinavia. A similarly viable wolf population in Sweden would also require the same general demographic conditions: reproductive and survival parameters that result in a capacity for sustained population growth, and consistent immigration of wolves from the recognized source population in Finland/Russia. However, because the Swedish population represents only a portion of the total wolf population in Scandinavia, any specification of a minimum viable population for the purposes of setting a favorable reference population in Sweden would require proper scaling of the larger regional population. For example, if a minimum viable population for Scandinavia were to be set at 250 wolves, and if we take the latest published data from Milleret et al. (2023) to assign approximately 85% of those wolves to Sweden, we would then identify a minimum viable population of wolves in Sweden equal to 210 to 215 individuals.

It is critically important to recognize, however, that the precise demographic characteristics of a viable population in Sweden or elsewhere cannot be specified until a clear demographic and genetic definition of wolf population viability is presented by the appropriate national or regional authorities. This is clearly demonstrated through detailed inspection of the results for gene diversity retention across the range of scenarios analyzed here. A demographic component of viability – often defined as risk of population extinction below a particular threshold value – appears to be met across the full range of scenarios evaluated here. Extinction risks do not exceed 0.02 over a timeframe of 100 years, which is far below the large majority of typical definitions of demographic viability found in the literature (e.g., Doak et al. 2015). In contrast, choice of a genetic viability criterion markedly changes the parameters for viability. If the criterion is 95% retention of today's gene diversity over 100 years, a rather restricted set of satisfactory candidate population abundance thresholds and immigration rates can be identified (see Figure 9). If 90% gene diversity retention is adopted as a viability criterion, a much more expansive set of satisfactory candidate population abundance thresholds and immigration rates can be identified. Moreover, the choice of which populations can be considered viable may also be constrained by the confidence one sees in the ability to achieve the specified genetic criterion. For example, authorities may wish to be at least 80% confident that their gene diversity retention can be achieved. As laid out in Figure 10, this decision on certainty significantly restricts the conditions within which population viability can be achieved.

The introgression of new genetic variation by immigration from the Finland/Russia population can be effective in offsetting the inevitable loss of variation in the Scandinavian population through inbreeding and random genetic drift. If immigrating wolves have a high degree of relatedness to the specific founders of the Scandinavian population, the benefits of this introgression will be reduced. It may be worth noting here that the immigration process being discussed is restricted to natural dispersal of individuals between populations. This process, therefore, does not technically fall under the definition of genetic rescue (Hedrick and Fredrickson 2010), in which unrelated individuals from another population are selected for managed introduction into the target population to reduce genetic load. The process of deciding if and when to adopt this more intensive approach to metapopulation management is beyond the scope of this analysis.

The simulations described here project future population characteristics over a time span of 100 years. The likelihood that current conditions for wolves in Scandinavia will persist in their current form for 100 years is, of course, extremely low. Researchers working in the field of PVA model development and improvement recognize the values – and the difficulties – of forecasting the ecological landscape for endangered wildlife as a function of the even more complex description of future economic, sociocultural, and political variables that determine the human-mediated natural environment (Miller and Lacy 2003; Lacy et al. 2013). Nevertheless, typical forecasts of population viability of both wild and captive populations are conducted for 100 years under the recognition that observing the predicted outcomes of alternative scenarios over many decades can help to strengthen the scope and intensity of recommended management activities designed to improve population viability in the shorter term (Frankham et al. 2010, 2014).

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Appendices

Appendix I
January 2023 Online Meeting Participants

Name	Organization
Robert Ekblom	Swedish Environmental Protection Agency
Øystein Flagstad	Norwegian Institute for Nature Research
Inari Helle	Natural Resources Institute Finland
Helena Johansson	Natural Resources Institute Finland
Baharan Kazemi	Swedish Environmental Protection Agency
Samu Mäntyniemi	Natural Resources Institute Finland
Phil Miller	IUCN SSC Conservation Planning Specialist Group
Håkan Sand	Swedish University of Agricultural Sciences
Linnéa Smeds	Uppsala University, Sweden
Hanna Dittrich Söderman	Swedish Environmental Protection Agency
Mia Valtonen	Natural Resources Institute Finland
Petter Wabakken	Inland Norway University of Applied Sciences
Camilla Wikenros	Swedish University of Agricultural Sciences

Appendix II
Example Vortex PVA Scenario Input Summary

The information presented below is taken from a selected scenario-specific input file created by Vortex – in this case, the scenario features a Scandinavian wolf population reference value (PRV) of 170 with a mean immigration rate of one wolf entering the population every six years. Additional interpretation of model input requires some knowledge of Vortex and the syntax for coding specific customized input variables and/or output metrics. More detailed explanations of this example input is available from the author upon request.

```
VORTEX 10.6.0.0 -- simulation of population dynamics

Project: ScandinavianWolves

Scenario: PopRV170_6yrs

25/10/2023

  2 populations simulated for 200 years for 1000 iterations

  Undocumented options: Q I1

Sequence of events in each time cycle:
  EV
  Breed
  Mortality
  ISUpdate
  PSUpdate
  GSUpdate
  Harvest
  Disperse
  PSUpdate
  Age
  Supplement
  rCalc
  Ktruncation
  Census

Extinction defined as no males or no females.

EV correlation between reproduction and annual survival - left at default 0.5

Inbreeding depression with a genetic load consisting of
  6.04 total lethal equivalents per individual, of which
  50% are due to recessive lethals, and the remainder are lethal equivalents not subjected to removal by selection.
```

```
Global state variables
  GS1: ReferenceValue    Initialization: 170    Transition: 170

Populations:

  SwedenNorway
  Population state variables
  PS1: PopInbrCoeff        Initialization: 0.238  Transition: =IMEAN2
  PS2: NumPups             Initialization: 176    Transition: =ITOT3
  PS3: NumSubadults        Initialization: 140    Transition: =ITOT4
  PS4: NumAdults           Initialization: 147    Transition: =ITOT5
  PS5: Culled              Initialization: 0      Transition: =HARVESTS
  PS6: Incoming            Initialization: 0      Transition: =IMMIGRANTS
  PS7: Outgoing            Initialization: 0      Transition: 0

  FinlandRussia
  Population state variables
  PS1: PopInbrCoeff        Initialization: 0.1    Transition: =IMEAN2
  PS2: NumPups             Initialization: 180    Transition: =ITOT3
  PS3: NumSubadults        Initialization: 120    Transition: =ITOT4
  PS4: NumAdults           Initialization: 200    Transition: =ITOT5
  PS5: Culled              Initialization: 0      Transition: =HARVESTS
  PS6: Incoming            Initialization: 0      Transition: 0
  PS7: Outgoing            Initialization: 0      Transition: =EMIGRANTS

  Individual state variables
  IS1: MATE                Initialization: -1             Birth function: -1   Transition: =IS1
  IS2: InbrCoeff           Initialization: =I             Birth function: =I   Transition: =IS2
  IS3: Pup                 Initialization: =A<2           Birth function: 1    Transition: =A<2
  IS4: SubAdult            Initialization: =(A=2)OR(A=3)  Birth function: 0    Transition: =(A=2)OR(A=3)
  IS5: Adult               Initialization: =A>3           Birth function: 0    Transition: =A>3
  IS6: Origin              Initialization: =P             Birth function: =P   Transition: =IS6


Correlation of EV among populations = 0.5

Both sexes disperse, from age 3 to age 25
Survival during dispersal: 100

Dispersal rates (as counts), from source (row) to destination (column):
                    SwedenNorway               FinlandRussia
  SwedenNorway                                       0
  FinlandRussia   =((Y%2)=1)*0.167
```

```
Reproductive System:

  Monogamy, with pairs maintained across years
  Females breed from age 4 to age 26
  Males breed from age 4 to age 26
  Maximum age of survival: 26
  Sex ratio (percent males) at birth: 50

Correlation of EV between reproduction and survival = 0.5

EV sampled from binomial distributions.

Population specific rates for SwedenNorway

  Percent of adult females breeding each year: =((Y%2)=0)*60
    with EV(SD): =((Y%2)=0)*10
  Percent of adult males in the pool of breeders: 75
  Normal distribution of brood size with mean: 5.3 with SD: 1.5

  Female annual mortality rates (as percents):
    Age 0 to 1:    18 with EV(SD): 1.5
    Age 1 to 2:    17.5 with EV(SD): 1.5
    Age 2 to 3:    16.3 with EV(SD): 1.5
    Age 3 to 4:    16.3 with EV(SD): 1.5
    After age 4:    =((MATE>-1)*13.4)+((MATE<0)*20) with EV(SD): 2

  Male annual mortality rates (as percents):
    Age 0 to 1:    18 with EV(SD): 1.5
    Age 1 to 2:    17.5 with EV(SD): 1.5
    Age 2 to 3:    16.3 with EV(SD): 1.5
    Age 3 to 4:    16.3 with EV(SD): 3
    After age 4:    =((MATE>-1)*13.4)+((MATE<0)*20) with EV(SD): 2
```

```
Catastrophe 1: Disease outbreak
    Local impact
    Frequency (%): 1
    Reproduction reduced by severity multiplier: 0
    Survival reduced by severity multiplier: 0.5

  Initial population size:
    Age   0  1  2  3  4  5  6  7  8  9  10  11  12  13  14  15  16  17  18  19  20  21  22  23  24  25  26    Females
0  0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
  Males   0  0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0

  Carrying capacity: 800
    with EV(SD):  0

  Harvest from year 1 through year 200 by increments of 2
    when =N>GS1
    of individuals that =(IS6=1)*(MK>(0.5*(1-(G/100))))
        Age         0      0
      Females       1      =((Y<12)*(0.15*(((N-GS1)/2))))+((Y>12)*(0.4*(((N-GS1)/2))))
                    2      0
                    3      =((Y<12)*(0.15*(((N-GS1)/2))))+((Y>12)*(0.3*(((N-GS1)/2))))
                    4      =((Y<12)*(0.15*(((N-GS1)/2))))+((Y>12)*(0.4*(((N-GS1)/2))))

      Males         1      =((Y<12)*(0.15*(((N-GS1)/2))))+((Y>12)*(0.4*(((N-GS1)/2))))
                    2      0
                    3      =((Y<12)*(0.15*(((N-GS1)/2))))+((Y>12)*(0.3*(((N-GS1)/2))))
                    4      =((Y<12)*(0.15*(((N-GS1)/2))))+((Y>12)*(0.4*(((N-GS1)/2))))


Population specific rates for FinlandRussia

  Percent of adult females breeding each year: =((Y%2)=0)*60
    with EV(SD): =((Y%2)=0)*10
  Percent of adult males in the pool of breeders: 75
  Normal distribution of brood size with mean: 5.3 with SD: 1.5
```

```
Female annual mortality rates (as percents):
    Age 0 to 1:    18 with EV(SD): 1.5
    Age 1 to 2:    17.5 with EV(SD): 1.5
    Age 2 to 3:    16.3 with EV(SD): 1.5
    Age 3 to 4:    16.3 with EV(SD): 1.5
    After age 4:    =((MATE>-1)*13.4)+((MATE<0)*20) with EV(SD): 2

  Male annual mortality rates (as percents):
    Age 0 to 1:    18 with EV(SD): 1.5
    Age 1 to 2:    17.5 with EV(SD): 1.5
    Age 2 to 3:    16.3 with EV(SD): 1.5
    Age 3 to 4:    16.3 with EV(SD): 3
    After age 4:    =((MATE>-1)*13.4)+((MATE<0)*20) with EV(SD): 2

  Catastrophe 1: Disease outbreak
    Local impact
    Frequency (%): 1
    Reproduction reduced by severity multiplier: 0
    Survival reduced by severity multiplier: 0.5

  Initial population size:
    Age   0  1  2  3  4  5  6  7  8  9  10  11  12  13  14  15  16  17  18  19  20  21  22  23  24  25  26
Females   0  90 0  60 0  33 0  23 0  16  0  12   0   7   0   3   0   3   0   2   0   0   0   1   0   0   0
  Males   0  90 0  60 0  33 0  23 0  16  0  12   0   7   0   3   0   3   0   2   0   0   0   1   0   0   0

  Carrying capacity: 800
    with EV(SD):  0

  Harvest from year 1 through year 200 by increments of 2
        Age      0               1                   2                   3                   4
    Females      0  =0.13*((PS2)/2)            0            =0.13*((PS3)/2)            =0.1*F
      Males      0  =0.15*((PS2)/2)            0            =0.15*((PS3)/2)            =0.1*M

Genetics options:

  Initial population obtained from: ScandWolf_1Oct2022_Revised.txt
  Studbook population appended to any default initial population

  Genetic management for population: FinlandRussia
  Initial kinships set to: 0.1
```

Appendix III
Pedigree Input File (Founders and Living Animals Only: 1 October 2022)

(See Notes at the end of this listing for details on column headings)

ID*	**Sire**	**Dam**	**Sex**	**Alive**	**Age****	**Population**	**IS1*****
D-85-01	WILD	WILD	F	0	10	1	-1
G1-83	WILD	WILD	M	0	10	1	-1
G1-91	WILD	WILD	M	0	10	1	-1
M-09-03	WILD	WILD	M	0	10	1	-1
M-10-10	WILD	WILD	M	0	10	1	-1
G23-13	WILD	WILD	M	0	10	1	-1
G31-13	WILD	WILD	F	0	10	1	-1
G15-16	WILD	WILD	M	0	10	1	-1
G325-17	WILD	WILD	F	0	10	1	-1
G187-19	WILD	WILD	M	1	9	1	G120-21
G10-23	G159-17	G7-20	M	1	1	1	-1
G104-23	G104-11	G3-19	M	1	1	1	-1
G107-23	G11-17	G253-17	F	1	1	1	-1
G110-22	G34-20	G80-20	M	1	1	1	-1
G111-22	G160-16	G64-19	M	1	1	1	-1
G113-22	G64-19	G160-16	M	1	1	1	-1
G114-22	G64-19	G160-16	F	1	1	1	-1
G116-22	G64-19	G160-16	F	1	1	1	-1
G121-22	G11-17	G253-17	F	1	1	1	-1
G12-23	G114-21	G27-21	F	1	1	1	-1
G1-23	G159-17	G7-20	M	1	1	1	-1
G129-22	G86-17	G48-17	M	1	1	1	-1
G131-22	G139-21	G38-20	M	1	1	1	-1
G132-22	G139-21	G38-20	M	1	1	1	-1
G13-23	G239-19	G118-21	F	1	1	1	-1
G133-22	G139-21	G38-20	M	1	1	1	-1
G134-22	G139-21	G38-20	M	1	1	1	-1
G135-22	G139-21	G38-20	F	1	1	1	-1
G136-22	G86-17	G48-17	F	1	1	1	-1
G137-22	G11-17	G253-17	F	1	1	1	-1
G138-22	G226-19	G55-17	M	1	1	1	-1
G139-22	G226-19	G55-17	F	1	1	1	-1
G140-22	G199-19	G151-19	F	1	1	1	-1
G142-22	G85-22	G161-21	M	1	1	1	-1
G143-22	G85-22	G161-21	F	1	1	1	-1
G144-22	G85-22	G161-21	F	1	1	1	-1
G145-22	G24-20	G29-16	M	1	1	1	-1
G146-22	G68-17	G96-19	F	1	1	1	-1
G147-22	G139-21	G164-17	M	1	1	1	-1
G148-22	G139-21	G164-17	M	1	1	1	-1
G149-22	G112-20	G198-21	F	1	1	1	-1
G150-22	G112-20	G198-21	M	1	1	1	-1
G151-22	G22-14	G113-12	F	1	1	1	G96-22
G15-23	G11-17	G253-17	M	1	1	1	-1
G156-22	G71-18	G236-17	M	1	1	1	-1
G157-22	G71-18	G236-17	F	1	1	1	-1
G159-22	G71-18	G236-17	F	1	1	1	-1
G160-22	G71-18	G236-17	F	1	1	1	-1
G162-22	G71-18	G236-17	F	1	1	1	-1
G168-22	G54-21	G35-18	M	1	1	1	-1
G169-22	G54-21	G35-18	F	1	1	1	-1
G172-22	G226-19	G55-17	M	1	1	1	-1
G17-23	G226-19	G55-17	F	1	1	1	-1
G173-22	G78-20	G26-20	M	1	1	1	-1
G175-22	G68-20	G6-21	M	1	1	1	-1

ID	Sire	Dam	Sex	Alive	Age*	Population	IS1**
G176-22	G226-19	G55-17	M	1	1	1	-1
G177-22	G22-14	G113-12	F	1	1	1	-1
G179-22	G83-20	G13-20	F	1	1	1	-1
G180-22	G315-17	G51-16	F	1	1	1	-1
G181-22	G234-17	G15-18	M	1	1	1	-1
G182-22	G22-14	G113-12	F	1	1	1	-1
G18-23	G78-20	G26-20	F	1	1	1	-1
G183-22	G83-20	G13-20	M	1	1	1	-1
G185-22	G112-20	G198-21	M	1	1	1	-1
G187-22	G139-21	G164-17	F	1	1	1	-1
G188-22	G139-21	G164-17	F	1	1	1	-1
G189-22	G108-19	G110-19	F	1	1	1	-1
G191-22	G55-16	G56-16	F	1	1	1	-1
G192-22	G129-21	G58-21	M	1	1	1	-1
G19-23	G78-20	G26-20	F	1	1	1	-1
G193-22	G68-17	G96-19	M	1	1	1	-1
G194-22	G68-17	G96-19	M	1	1	1	-1
G195-22	G226-19	G55-17	F	1	1	1	-1
G196-22	G165-17	G24-19	F	1	1	1	-1
G198-22	G12-19	G25-18	M	1	1	1	-1
G199-22	G92-16	G113-16	F	1	1	1	-1
G200-22	G92-16	G113-16	M	1	1	1	-1
G201-22	G112-20	G198-21	M	1	1	1	-1
G202-22	G234-17	G15-18	M	1	1	1	-1
G20-23	G24-20	G29-16	F	1	1	1	-1
G203-22	G55-16	G56-16	M	1	1	1	-1
G204-22	G79-18	G62-20	M	1	1	1	-1
G205-22	G79-18	G62-20	M	1	1	1	-1
G207-22	G226-19	G55-17	M	1	1	1	-1
G208-22	G132-21	G84-18	F	1	1	1	-1
G211-22	G54-21	G35-18	F	1	1	1	-1
G212-22	G54-21	G35-18	M	1	1	1	-1
G21-23	G24-20	G29-16	M	1	1	1	-1
G213-22	G315-17	G51-16	F	1	1	1	-1
G214-22	G159-17	G7-20	M	1	1	1	-1
G215-22	G124-16	G37-16	F	1	1	1	-1
G217-22	G108-21	G233-19	M	1	1	1	-1
G218-22	G108-19	G110-19	M	1	1	1	-1
G219-22	G315-17	G51-16	F	1	1	1	-1
G220-22	G132-21	G84-18	M	1	1	1	-1
G221-22	G165-17	G24-19	F	1	1	1	-1
G222-22	G69-21	G5-21	F	1	1	1	-1
G2-23	G7-21	G218-19	F	1	1	1	-1
G223-22	G226-19	G55-17	M	1	1	1	-1
G224-22	G159-17	G7-20	M	1	1	1	-1
G225-22	G95-21	G97-21	F	1	1	1	-1
G226-22	G89-16	G64-17	F	1	1	1	-1
G227-22	G12-19	G25-18	M	1	1	1	-1
G231-22	G89-16	G64-17	F	1	1	1	-1
G232-22	G165-17	G24-19	M	1	1	1	-1
G23-23	G74-21	G82-21	F	1	1	1	-1
G233-22	G104-11	G3-19	F	1	1	1	-1
G234-22	G234-17	G15-18	F	1	1	1	-1
G235-22	G79-19	G250-17	M	1	1	1	-1
G236-22	G74-21	G82-21	M	1	1	1	-1
G24-23	G12-19	G25-18	M	1	1	1	-1
G26-23	G34-20	G80-20	M	1	1	1	-1
G27-23	G24-20	G29-16	M	1	1	1	-1
G28-23	G24-20	G29-16	M	1	1	1	-1
G29-23	G69-21	G5-21	F	1	1	1	-1
G30-23	G69-21	G5-21	M	1	1	1	-1
G32-23	G50-20	G194-19	M	1	1	1	-1

ID	Sire	Dam	Sex	Alive	Age*	Population	IS1**
G3-23	G34-20	G80-20	F	1	1	1	-1
G33-23	G50-20	G194-19	M	1	1	1	-1
G35-23	G34-19	G100-20	F	1	1	1	-1
G36-23	G55-16	G56-16	F	1	1	1	-1
G37-23	G10-20	G88-21	F	1	1	1	-1
G38-23	G24-20	G29-16	F	1	1	1	-1
G41-23	G234-17	G15-18	M	1	1	1	-1
G42-23	G55-16	G56-16	M	1	1	1	-1
G4-23	G239-19	G118-21	M	1	1	1	-1
G44-23	G11-16	G251-19	M	1	1	1	-1
G45-23	G34-19	G100-20	M	1	1	1	-1
G46-23	G55-16	G56-16	F	1	1	1	-1
G47-23	G222-17	G4-20	M	1	1	1	-1
G48-23	G222-17	G4-20	M	1	1	1	-1
G50-23	G139-21	G164-17	F	1	1	1	-1
G52-23	G11-17	G253-17	F	1	1	1	-1
G5-23	G91-21	G29-21	M	1	1	1	-1
G56-23	G104-11	G3-19	M	1	1	1	-1
G57-23	G68-20	G6-21	M	1	1	1	-1
G58-23	G139-21	G164-17	F	1	1	1	-1
G59-23	G159-17	G7-20	M	1	1	1	-1
G62-23	G12-19	G25-18	M	1	1	1	-1
G63-23	G108-16	G68-13	F	1	1	1	-1
G64-23	G34-19	G100-20	M	1	1	1	-1
G65-23	G7-21	G218-19	M	1	1	1	-1
G66-23	G10-20	G88-21	M	1	1	1	-1
G67-23	G199-19	G151-19	F	1	1	1	-1
G68-23	G226-19	G55-17	F	1	1	1	-1
G70-23	G132-21	G84-18	M	1	1	1	-1
G71-23	G201-21	G152-15	F	1	1	1	-1
G7-23	G55-16	G56-16	F	1	1	1	-1
G75-23	G187-19	G120-21	F	1	1	1	-1
G76-23	G187-19	G120-21	M	1	1	1	-1
G77-23	G79-18	G62-20	M	1	1	1	-1
G78-23	G201-21	G152-15	F	1	1	1	-1
G79-23	G201-21	G152-15	M	1	1	1	-1
G80-23	G201-21	G152-15	F	1	1	1	-1
G81-23	G201-21	G152-15	F	1	1	1	-1
G82-23	G201-21	G152-15	F	1	1	1	-1
G8-23	G78-20	G26-20	M	1	1	1	-1
G83-23	G201-21	G152-15	M	1	1	1	-1
G84-23	G211-19	G33-21	F	1	1	1	-1
G85-23	G62-20	G79-18	F	1	1	1	-1
G87-23	G211-19	G33-21	F	1	1	1	-1
G88-23	G211-19	G33-21	M	1	1	1	-1
G89-23	G211-19	G33-21	F	1	1	1	-1
G90-23	G201-21	G152-15	F	1	1	1	-1
G9-23	G78-20	G26-20	F	1	1	1	-1
G93-23	G187-19	G120-21	M	1	1	1	-1
G94-23	G187-19	G120-21	M	1	1	1	-1
G95-23	G199-19	G74-19	F	1	1	1	-1
G96-23	G124-16	G37-16	F	1	1	1	-1
G97-23	G25-18	G12-19	F	1	1	1	-1
JuWo01	G34-20	G80-20	F	1	1	1	-1
JuWo02	G79-18	G62-20	M	1	1	1	-1
JuWo03	G91-21	G29-21	M	1	1	1	-1
JuWo04	G86-17	G48-17	F	1	1	1	-1
JuWo05	G83-20	G13-20	M	1	1	1	-1
JuWo06	G89-16	G64-17	M	1	1	1	-1
JuWo07	G95-21	G97-21	M	1	1	1	-1
JuWo08	G159-17	G7-20	M	1	1	1	-1
JuWo09	G74-21	G82-21	F	1	1	1	-1

ID	**Sire**	**Dam**	**Sex**	**Alive**	**Age***	**Population**	**IS1****
JuWo10	G315-17	G51-16	M	1	1	1	-1
JuWo11	G69-21	G5-21	F	1	1	1	-1
JuWo12	G226-19	G55-17	M	1	1	1	-1
JuWo13	G139-21	G164-17	M	1	1	1	-1
JuWo14	G108-19	G110-19	F	1	1	1	-1
JuWo15	G95-21	G97-21	M	1	1	1	-1
JuWo16	G79-18	G62-20	F	1	1	1	-1
G100-22	G68-19	G35-18	M	1	3	1	-1
G101-22	G68-19	G35-18	F	1	3	1	-1
G104-22	G154-15	G37-18	F	1	3	1	G37-22
G105-22	G71-18	G236-17	M	1	3	1	G191-21
G106-22	G234-17	G15-18	F	1	3	1	-1
G108-22	G244-19	G36-20	M	1	3	1	-1
G112-22	G64-19	G160-16	F	1	3	1	-1
G118-22	G86-17	G48-17	F	1	3	1	-1
G119-22	G244-19	G36-20	F	1	3	1	-1
G120-22	G22-14	G113-12	F	1	3	1	G92-23
G1-22	G168-17	G124-13	M	1	3	1	G101-19
G12-22	G159-17	G7-20	F	1	3	1	G22-23
G122-22	G241-19	G40-20	F	1	3	1	G240-19
G123-22	G244-19	G36-20	F	1	3	1	-1
G126-22	G68-17	G96-19	M	1	3	1	-1
G130-22	G315-17	G51-16	M	1	3	1	-1
G138-21	G234-17	G15-18	F	1	3	1	G108-20
G140-21	G86-17	G48-17	F	1	3	1	-1
G141-21	G86-17	G48-17	F	1	3	1	-1
G141-22	G315-17	G51-16	F	1	3	1	-1
G14-23	G165-17	G24-19	F	1	3	1	-1
G148-21	G124-16	G37-16	F	1	3	1	-1
G150-21	G79-18	G62-20	M	1	3	1	-1
G153-21	G58-19	G151-17	F	1	3	1	G46-21
G160-21	G264-17	G259-17	M	1	3	1	G173-21
G161-21	G264-17	G259-17	F	1	3	1	G85-22
G16-22	G28-16	G12-20	F	1	3	1	-1
G162-21	G264-17	G259-17	F	1	3	1	-1
G16-23	G315-17	G51-16	F	1	3	1	-1
G164-22	G55-16	G56-16	F	1	3	1	-1
G166-21	G234-17	G15-18	M	1	3	1	G38-20
G166-22	G205-17	G70-19	M	1	3	1	G8-21
G167-21	G234-17	G15-18	M	1	3	1	-1
G169-21	G104-11	G3-19	M	1	3	1	-1
G170-21	G68-19	G35-18	F	1	3	1	-1
G170-22	G40-19	G133-19	F	1	3	1	-1
G173-21	G175-19	G9-18	F	1	3	1	G160-21
G174-22	G69-21	G5-21	M	1	3	1	G106-21
G175-21	G11-16	G251-19	F	1	3	1	-1
G178-22	G124-16	G37-16	F	1	3	1	-1
G180-21	G108-16	G68-13	M	1	3	1	G39-20
G181-21	G108-16	G68-13	M	1	3	1	-1
G182-21	G50-20	G194-19	F	1	3	1	-1
G183-21	G50-20	G194-19	M	1	3	1	G197-19
G184-21	G108-16	G68-13	F	1	3	1	-1
G184-22	G55-16	G56-16	F	1	3	1	-1
G186-22	G28-16	G12-20	M	1	3	1	-1
G190-22	G108-19	G110-19	F	1	3	1	G25-19
G192-21	G222-17	G4-20	F	1	3	1	-1
G193-21	G222-17	G4-20	F	1	3	1	-1
G197-22	G165-17	G24-19	M	1	3	1	-1
G206-22	G172-19	G48-18	F	1	3	1	-1
G209-22	G68-17	G96-19	F	1	3	1	-1
G210-22	G315-17	G51-16	F	1	3	1	G125-17
G21-22	G79-18	G62-20	F	1	3	1	-1

ID	**Sire**	**Dam**	**Sex**	**Alive**	**Age***	**Population**	**IS1****
G213-21	G187-19	G168-16	M	1	3	1	-1
G214-21	G187-19	G168-16	F	1	3	1	-1
G216-22	G11-17	G253-17	M	1	3	1	G65-22
G220-21	G315-17	G51-16	F	1	3	1	-1
G22-22	G125-17	G140-13	F	1	3	1	G238-21
G222-21	G264-17	G259-17	F	1	3	1	-1
G22-23	G11-17	G253-17	M	1	3	1	G12-22
G224-21	G12-19	G25-18	F	1	3	1	-1
G225-21	G108-19	G110-19	M	1	3	1	-1
G227-21	G168-17	G124-13	F	1	3	1	-1
G228-22	G58-19	G151-17	F	1	3	1	G92-20
G229-21	G159-17	G7-20	M	1	3	1	-1
G229-22	G55-16	G56-16	M	1	3	1	-1
G230-22	G11-16	G251-19	M	1	3	1	-1
G23-22	G12-19	G25-18	M	1	3	1	-1
G233-21	G168-17	G124-13	M	1	3	1	-1
G237-21	G124-16	G37-16	F	1	3	1	-1
G238-21	G226-19	G55-17	M	1	3	1	G22-22
G239-21	G79-19	G250-17	M	1	3	1	-1
G240-21	G68-17	G96-19	F	1	3	1	-1
G242-21	G12-19	G25-18	M	1	3	1	-1
G243-21	G104-11	G3-19	M	1	3	1	-1
G244-21	G104-11	G3-19	M	1	3	1	G243-19
G249-21	G24-20	G29-16	F	1	3	1	-1
G252-21	G24-20	G29-16	M	1	3	1	-1
G25-23	G9-20	G10-15	M	1	3	1	-1
G254-21	G92-16	G113-16	M	1	3	1	G55-23
G255-21	G79-19	G250-17	M	1	3	1	-1
G259-21	G79-18	G62-20	M	1	3	1	G165-22
G31-23	G88-17	G188-17	M	1	3	1	-1
G34-23	G226-19	G55-17	M	1	3	1	-1
G37-22	G12-19	G25-18	M	1	3	1	G104-22
G39-23	G108-16	G68-13	F	1	3	1	-1
G40-23	G104-11	G3-19	M	1	3	1	G6-21
G4-22	G89-16	G64-17	F	1	3	1	-1
G43-23	G172-19	G48-18	F	1	3	1	-1
G44-22	G71-18	G236-17	M	1	3	1	G1-21
G49-23	G104-11	G3-19	M	1	3	1	G115-21
G51-23	G199-19	G74-19	M	1	3	1	-1
G53-22	G124-17	G239-17	M	1	3	1	-1
G53-23	G315-17	G51-16	M	1	3	1	-1
G54-23	G68-17	G96-19	F	1	3	1	-1
G55-22	G64-19	G160-16	M	1	3	1	-1
G55-23	G11-17	G253-17	F	1	3	1	G254-21
G59-22	G71-18	G236-17	M	1	3	1	-1
G60-23	G79-19	G250-17	M	1	3	1	-1
G61-23	G92-16	G113-16	M	1	3	1	-1
G6-23	G226-19	G55-17	M	1	3	1	-1
G65-22	G11-17	G253-17	F	1	3	1	G216-22
G66-22	G165-17	G24-19	M	1	3	1	-1
G69-22	G165-17	G24-19	M	1	3	1	-1
G72-22	G199-19	G74-19	F	1	3	1	-1
G72-23	G89-16	G64-17	M	1	3	1	-1
G75-22	G88-17	G188-17	F	1	3	1	-1
G77-22	G2-20	G35-20	M	1	3	1	-1
G86-22	G55-16	G56-16	M	1	3	1	-1
G89-22	G12-19	G25-18	M	1	3	1	-1
G9-22	G226-19	G55-17	M	1	3	1	-1
G92-22	G125-17	G140-13	M	1	3	1	-1
G92-23	G50-20	G194-19	M	1	3	1	G120-22
G94-22	G68-19	G35-18	M	1	3	1	-1
G95-22	G159-17	G7-20	M	1	3	1	-1

ID	**Sire**	**Dam**	**Sex**	**Alive**	**Age***	**Population**	**IS1****
G96-22	G124-16	G37-16	M	1	3	1	G151-22
G97-22	G145-19	G223-17	M	1	3	1	G34-21
G20-22	G199-19	G74-19	M	1	3	1	-1
G194-21	G222-17	G4-20	F	1	3	1	-1
G60-22	G71-18	G236-17	F	1	3	1	-1
G212-21	G187-19	G168-16	M	1	3	1	-1
G54-22	G124-17	G239-17	M	1	3	1	-1
G91-23	G124-17	G239-17	F	1	3	1	-1
G71-22	G86-17	G48-17	M	1	3	1	-1
YeWo01	G11-16	G251-19	M	1	3	1	-1
YeWo02	G11-16	G251-19	M	1	3	1	-1
YeWo03	G79-18	G62-20	M	1	3	1	-1
YeWo04	G205-17	G70-19	M	1	3	1	-1
YeWo05	G68-19	G35-18	M	1	3	1	-1
YeWo06	G68-19	G35-18	F	1	3	1	-1
YeWo07	G124-16	G37-16	M	1	3	1	-1
YeWo08	G159-17	G7-20	F	1	3	1	-1
YeWo09	G199-19	G74-19	M	1	3	1	-1
YeWo10	G124-17	G239-17	M	1	3	1	-1
YeWo11	G108-16	G68-13	F	1	3	1	-1
YeWo12	G241-19	G40-20	F	1	3	1	-1
YeWo13	G68-17	G96-19	F	1	3	1	-1
YeWo14	G124-16	G37-16	M	1	3	1	-1
G101-21	G92-16	G113-16	M	1	5	1	-1
G106-21	G92-16	G113-16	F	1	5	1	G174-22
G108-20	G165-17	G24-19	M	1	5	1	G138-21
G108-21	G11-17	G253-17	M	1	5	1	G233-19
G110-21	G11-17	G253-17	M	1	5	1	-1
G111-21	G11-17	G253-17	F	1	5	1	G13-22
G112-20	G68-19	G35-18	M	1	5	1	G198-21
G113-20	G159-17	G169-16	F	1	5	1	G100-15
G114-20	G159-17	G169-16	F	1	5	1	G146-21
G114-21	G58-17	G31-19	M	1	5	1	G27-21
G115-21	G11-17	G253-17	F	1	5	1	G49-23
G117-22	G124-16	G37-16	F	1	5	1	-1
G118-21	G92-16	G113-16	F	1	5	1	G239-19
G120-21	G2-19	G213-17	F	1	5	1	G187-19
G1-21	G205-17	G77-17	F	1	5	1	G44-22
G13-22	G92-16	G113-16	M	1	5	1	G111-21
G132-21	G40-19	G133-19	M	1	5	1	-1
G144-21	G43-17	G135-16	F	1	5	1	G78-22
G146-21	G11-17	G253-17	M	1	5	1	G114-20
G165-21	G315-17	G51-16	F	1	5	1	G2-22
G165-22	G22-14	G113-12	F	1	5	1	G259-21
G191-21	G22-14	G113-12	F	1	5	1	G105-22
G198-21	G58-19	G151-17	F	1	5	1	G112-20
G201-21	G22-14	G113-12	M	1	5	1	G152-15
G2-22	G168-17	G124-13	M	1	5	1	G165-21
G226-21	G168-17	G124-13	M	1	5	1	-1
G27-21	G124-17	G239-17	F	1	5	1	G114-21
G29-21	G154-15	G37-18	F	1	5	1	G91-21
G33-21	G154-15	G37-18	F	1	5	1	G211-19
G34-21	G154-15	G37-18	F	1	5	1	G97-22
G41-22	G205-17	G70-19	F	1	5	1	G88-17
G44-21	G2-19	G213-17	M	1	5	1	G251-19
G46-21	G27-19	G85-19	M	1	5	1	G153-21
G5-21	G104-11	G3-19	F	1	5	1	-1
G54-21	G22-14	G113-12	M	1	5	1	G35-18
G55-21	G104-11	G3-19	M	1	5	1	-1
G58-21	G89-16	G64-17	F	1	5	1	-1
G6-21	G104-11	G3-19	F	1	5	1	G40-23
G62-21	G88-17	G188-17	F	1	5	1	-1

ID	Sire	Dam	Sex	Alive	Age*	Population	IS1**
G69-21	G28-16	G12-20	M	1	5	1	G216-19
G7-21	G22-14	G113-12	M	1	5	1	G218-19
G74-21	G168-17	G124-13	M	1	5	1	G82-21
G78-20	G156-16	G135-17	M	1	5	1	G26-20
G78-22	G281-17	G9-18	M	1	5	1	G144-21
G80-20	G315-17	G51-16	F	1	5	1	-1
G81-21	G88-17	G188-17	M	1	5	1	-1
G8-21	G22-14	G113-12	F	1	5	1	G166-22
G82-21	G108-16	G68-13	F	1	5	1	G74-21
G83-20	G159-17	G169-16	M	1	5	1	G13-20
G88-21	G123-14	G31-13	F	1	5	1	G10-20
G90-20	G68-17	G96-19	M	1	5	1	-1
G91-21	G177-19	G223-17	M	1	5	1	G29-21
G92-20	G43-17	G135-16	M	1	5	1	G228-22
G93-21	G2-19	G213-17	F	1	5	1	G297-17
G95-21	G165-17	G24-19	M	1	5	1	G97-21
G97-20	G104-15	G88-16	F	1	5	1	-1
G97-21	G165-17	G24-19	F	1	5	1	G95-21
G98-21	G92-16	G113-16	F	1	5	1	-1
G100-20	G156-16	G135-17	F	1	5	1	G34-19
G67-21	G22-14	G113-12	F	1	5	1	-1
G101-19	G159-17	G169-16	F	1	7	1	G1-22
G107-21	G58-17	G31-19	M	1	7	1	G57-21
G108-19	G166-14	G97-15	M	1	7	1	G110-19
G110-19	G166-14	G97-15	F	1	7	1	G108-19
G13-20	G92-16	G113-16	F	1	7	1	G83-20
G139-21	G156-16	G135-17	M	1	7	1	G164-17
G194-19	G168-17	G124-13	F	1	7	1	G50-20
G197-19	G168-17	G124-13	F	1	7	1	G183-21
G211-19	G176-16	G87-17	M	1	7	1	G33-21
G216-19	G23-16	G14-19	F	1	7	1	G69-21
G2-20	G45-19	G147-15	M	1	7	1	G35-20
G226-19	G45-19	G147-15	M	1	7	1	G55-17
G229-19	G315-17	G51-16	F	1	7	1	-1
G233-19	G92-16	G113-16	F	1	7	1	G108-21
G239-19	G92-16	G113-16	M	1	7	1	G118-21
G240-19	G11-17	G253-17	M	1	7	1	G122-22
G243-19	G123-14	G31-13	F	1	7	1	G244-21
G244-19	G89-16	G64-17	M	1	7	1	G36-20
G251-19	G11-16	G132-16	F	1	7	1	G44-21
G258-19	G169-17	G136-17	M	1	7	1	G262-17
G34-20	G123-14	G31-13	M	1	7	1	-1
G35-20	G125-17	G259-17	F	1	7	1	G2-20
G36-20	G159-17	G169-16	F	1	7	1	G244-19
G38-20	G123-14	G31-13	F	1	7	1	G166-21
G39-20	G237-17	G10-15	F	1	7	1	G180-21
G4-20	G222-17	G7-18	F	1	7	1	G222-17
G57-21	G90-17	G272-17	F	1	7	1	G107-21
G62-20	G34-18	G129-17	F	1	7	1	G79-18
G7-20	G159-17	G169-16	F	1	7	1	G159-17
G85-22	G125-17	G140-13	M	1	7	1	G161-21
G218-19	G96-12	G26-15	F	1	7	1	G7-21
G50-20	G35-16	G80-17	M	1	7	1	G194-19
G10-20	G43-17	G135-16	M	1	9	1	G88-21
G12-19	G22-14	G113-12	M	1	9	1	G25-18
G12-20	G83-14	G147-15	F	1	9	1	G28-16
G172-19	G6-12	G77-14	M	1	9	1	G48-18
G25-19	G43-17	G135-16	M	1	9	1	G190-22
G26-20	G156-14	G53-16	F	1	9	1	G78-20
G3-19	G123-14	G31-13	F	1	9	1	-1
G34-19	G97-17	G168-16	M	1	9	1	G100-20
G64-19	G86-16	G166-16	M	1	9	1	G160-16

ID	Sire	Dam	Sex	Alive	Age*	Population	IS1**
G71-18	G132-11	G74-11	M	1	9	1	G236-17
G74-19	G29-15	G173-16	F	1	9	1	-1
G79-18	G124-17	G172-14	M	1	9	1	G62-20
G79-19	G58-17	G175-17	M	1	9	1	G250-17
G84-18	G18-15	G89-15	F	1	9	1	-1
G15-18	G123-14	G31-13	F	1	11	1	G234-17
G164-17	G123-14	G31-13	F	1	11	1	G139-21
G165-17	G123-14	G31-13	M	1	11	1	-1
G168-17	G12-16	G66-12	M	1	11	1	G124-13
G222-17	G6-12	G77-14	M	1	11	1	G4-20
G234-17	G123-14	G31-13	M	1	11	1	G15-18
G236-17	G6-12	G77-14	F	1	11	1	G71-18
G239-17	G13-16	G56-11	F	1	11	1	G124-17
G25-18	G47-10	G18-10	F	1	11	1	G12-19
G253-17	G26-16	G123-16	F	1	11	1	-1
G262-17	G47-16	G48-17	F	1	11	1	G258-19
G266-17	G123-14	G31-13	M	1	11	1	-1
G297-17	G72-16	G152-15	M	1	11	1	G93-21
G315-17	G104-15	G88-16	M	1	11	1	G51-16
G35-18	G122-14	G110-14	F	1	11	1	G54-21
G125-17	G155-14	G139-14	M	1	13	1	G210-22
G159-17	G90-15	G80-13	M	1	13	1	G7-20
G250-17	G68-15	G10-15	F	1	13	1	G79-19
G48-18	G156-14	G53-16	F	1	13	1	G172-19
G55-17	G89-16	G64-17	F	1	13	1	G226-19
G68-17	G96-12	G26-15	M	1	13	1	G96-19
G96-19	G151-15	G99-16	F	1	13	1	G68-17
G108-16	G95-10	G16-12	M	1	15	1	G68-13
G113-16	G108-14	G1-14	F	1	15	1	-1
G124-17	G63-15	G64-15	M	1	15	1	G239-17
G152-15	G86-11	G144-14	F	1	15	1	G201-21
G28-16	G104-11	G13-15	M	1	15	1	G12-20
G51-16	M-09-03	G68-13	F	1	15	1	G315-17
G56-16	G84-11	G12-12	F	1	15	1	G55-16
G86-17	G164-13	G113-12	M	1	15	1	G48-17
G88-17	G61-14	G66-12	M	1	15	1	G41-22
G100-15	G37-10	G85-13	M	1	17	1	G113-20
G160-16	G24-12	G86-15	F	1	17	1	G64-19
G48-17	G11-13	G49-12	F	1	17	1	G86-17
G55-16	G39-11	G12-09	M	1	17	1	G56-16
G64-17	G133-13	M-10-08	F	1	17	1	G89-16
G67-16	G39-11	G12-09	F	1	17	1	-1
G89-16	G24-12	G86-15	M	1	17	1	G64-17
G68-13	G22-12	G12-10	F	1	21	1	G108-16
G124-13	G7-10	D-11-17	F	1	25	1	G168-17

Notes:

* Individuals beginning with JuWoXX and YeWoXX are juveniles and yearlings, respectively, added to the population in order to bring the total abundance up to the desired value as determined by recent census methodologies.

** Age is defined here in the context of two 6-month timesteps per calendar year. Because the model begins on 1 October, assumed to be six months after the production of pups the previous spring, the youngest individuals in this initial population are one timestep in age. It follows that the age of all individuals is expressed in odd numbers, corresponding to the odd-numbered timesteps in which the population census is taken.

*** IS1 = Individual State Variable 1 = the ID of the mate of the given individual assigned at the beginning of the simulation. Mate assignments are symmetrical, so that the mate of X is Y and the mate of Y is X.