

Joint Statement on the Results and Implications of Analyses Informing the Designation of
Favorable Reference Value for the Wolf (*Canis lupus*) Population in Sweden

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Introduction – Setting the Context for the Analysis

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 reference value for the wolf (*Canis lupus*) regarding population size, as defined for favourable conservation status according to the European Union’s Habitats Directive, could be in the interval between 170 and 270 individuals as stated in the parliament proposition from 2012 (prop. 2012/13:191).

We conducted independent analyses using different simulation tools (Miller: Vortex (Lacy and Pollak, 2022); Dussex: SLiM (Haller and Messer 2019)) to explore the demographic and genetic characteristic defining wolf population viability in Scandinavia. Comparing the results from our independent simulations facilitates an assessment of the congruence and robustness of our results which will then be used by SEPA to develop recommendations for wolf population management in Sweden.

Before discussing specific aspects of these analyses, we believe it is important to highlight key underlying concepts and their definitions as presented in the European Union’s guidance document on this broad topic (DG Environment 2023) in the context of the commission to SEPA and our associated work as described in this joint statement and in our separate reports. 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 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.”

We therefore treat our contribution to this SEPA commission as addressing the identification of a minimum viable population size for wolves in Scandinavia. Translation of this MVP value to a population abundance incorporating larger-scale ecosystem functionality and representation – the favourable reference population (FRP) value – requires a process of “upscaling” as described in the guidance document (DG Environment 2023). Furthermore, we understand that this “upscaling” to a larger population abundance value representing the FRP value is outside the scope of the work described by our PVA efforts and is instead to be conducted by SEPA once our work is complete and fully documented.

Another important issue influencing the interpretation of our analyses concerns the ambiguity in the Habitats Directive and supporting documents (e.g., DG Environment 2023) around the explicit definition of population viability. 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, we saw it as our task to agree on an operational definition of viability that could ultimately be adopted by SEPA and other management authorities as appropriate to guide wolf management in Sweden. Specifically, we include both demographic and genetic components in our general definition by defining viability as (A) the probability of population extinction of less than 10% over 100 years, and (B) the retention of at least 95% of current estimated genetic diversity over that same time period. Adopting a different set of criteria may lead to some modifications to our general conclusions, but we use here a consistent definition of viability to frame the results and their implications.

Key Features of the Analytical Methods

The simulation models we used to perform this analysis share important similarities that facilitate meaningful comparison of their results. For example, both Vortex and SLiM are individual-based models which track the fates of individual animals and their genetic variants over time. In addition, both models use age- and sex-specific demographic rates derived from detailed analysis of field data including annual rates of reproductive success and, depending on the specific model, survival or mortality. Immigration and/or emigration at a user-specified rate can be included in both models, and the two models allow for population abundance regulation through multiple mechanisms. Genetic processes including loss of genetic variation through inbreeding and genetic drift are also featured in both models, with simulation of inbreeding depression accomplished in SLiM through the accumulation of deleterious mutations and in Vortex through the specification of the number of lethal equivalents in the wolf population genome. In all, the two models used here are effective and flexible tools for evaluating both general demographic and genetic components of population viability in the context of our specific assignment.

Accompanying these similarities are also some features that differ between the two models. SLiM features more complex mechanics compared to Vortex for simulating population genetic parameters. These mechanics include the specification of both wolf-specific deleterious and neutral mutation rates across chromosomes, identification of selection and dominance coefficients for mutations, detailed specification of both masked and realized genetic load (the assemblage of genes responsible for inbreeding depression) and recombination of chromosomes across generations. While Vortex does not feature this level of detail when simulating population genetic processes, it uses the full pedigree for the Scandinavian wolf population since its founding in 1983 (Åkesson et al. 2023) to initialize the genetic structure (relatedness, inbreeding, etc.) of the population with a high degree of realism and accuracy. In terms of population demographic processes, SLiM uses a relatively more simplified treatment of parameters such as breeding system and catastrophic variation in annual mortality rate while Vortex allows the user to explicitly define these demographic characteristics in as

much detail as the data allow. In basic terms, we can conclude that the SLiM model is focused most heavily on detailed population genetic processes, with Vortex focused more heavily on detailed demographic processes with a higher-level treatment of genetic components of viability.

While acknowledging these similarities and differences in basic model structure, it is worth noting here that the two modeling approaches differ markedly in the initial population conditions and the means by which the wolf population is regulated moving forward in time. The SLiM model begins retrospectively with the initiation of the wolf population in Sweden through immigration from Finland/Karelia in the early 1980s and accounts for specific known immigration events between 1990 and 2021. Moving forward in time beginning in 2022, the population abundance is regulated by the use of a traditional carrying capacity (K) value that restricts reproduction and survival to prevent the simulated population from exceeding the specified value and thus does not explicitly model yearly culling. The values of K used in the SLiM model included the range of abundance values (170 – 270) specified in the commission to SEPA. In contrast, the Vortex model is initiated with the known abundance of wolves in Scandinavia as of 1 October 2022 (N = 463: Milleret et al. (2023)) and the full pedigree of those individuals, establishing the genetic structure of the population based on past immigration events and breeding histories. Because the Vortex model was initialized with an abundance that already exceeded the range of favorable reference population values outlined in the SEPA commission (N = 170 – 270), a process of gradually reducing this current population to those FRP values was employed to simulate controlled hunting. Once the simulated population reached the desired test abundance, ongoing regulation of population abundance is achieved through continued culling. In this way, population management effectively becomes a carrying capacity of sorts that controls future population growth. While the precise methods of population regulation may differ between the two modeling approaches, neither of them explicitly simulate intrinsic ecological limits to population growth but are instead effectively simulating abundance ceilings imposed by population management practices.

Finally, we note that specific demographic inputs to the two models are largely concordant. Inspection of Table 1 in the SLiM simulation report of Dussex and of Table 1 in Miller's Vortex modeling report shows very similar values for a range of parameters governing mean annual rates of reproduction and survival. One demographic rate that differs slightly between the two models is pup mortality, with Dussex using 30.0% and Miller using 32.3% (citing the annual report on wolf population abundance and dynamics published by Milleret et al. 2023). This difference may be attributed to a slightly different definition of the time period over which mortality is imposed within the annual cycle, although this possible explanation is not confirmed.

Results of the Simulation Models: Consensus Findings and Model-Specific Insights

Despite the differences in the two modeling approaches noted above, the general similarities across the two models in both structure and biological input led to consistent results from the analyses. Specifically, the results showed that population viability – as we have provisionally defined it for this analysis – can be achieved with a total wolf population in Scandinavia (as estimated through the census date of 1 October) within the range of 170 to 270 wolves if the following conditions are achieved:

- Demographic performance of the population leads to a long-term expectation of positive population growth through time. Viability cannot be achieved if the population declines in abundance over time through low reproductive success and/or unsustainable mortality; and
- Immigration occurs according to the following specifications:
 - SLiM model:
The average effective immigration rate (wolves that disperse and reproduce) into Scandinavia from the original source population in Finland/Karelia(Russia) is no less than one to three individuals per decade, or approximately one individual per 1.5 generations;

- Vortex model:
The average demographic immigration rate (acknowledging that some immigrants may die before reproducing) is no less than three individuals per decade, or approximately one individual per generation, based on the assumed generation length of three to four years (Wikenros et al. 2021).

If these conditions are met, our models show a low probability of population extinction – less than 0.02 over the next 100 years – and a retention of at least 95% of the current genetic diversity present in the Scandinavian population as well as less than 5% increase in inbreeding over that same time horizon. Because a portion of the Scandinavian wolf population resides in Norway, the total population abundance would need to be downscaled appropriately to derive a suitable viable population abundance estimate for the Sweden component of the population. The detailed analysis of Milleret et al. (2023) indicates that the wolf population in Norway constitutes about 15% of the total population in Scandinavia.

As the preferred population abundance threshold (minimum viable population size) increases or decreases across the range specified in this analysis, the demographic conditions needed to achieve viability likewise change. Specifically, maintaining the population at a smaller abundance such as 170 or 200 individuals requires higher levels of immigration from northern sources in order to offset the more rapid rate of loss of gene diversity through more pronounced inbreeding and genetic drift. Our model results explicitly show this phenomenon, which is a fundamental observation in the management of small and isolated wildlife populations subject to the genetics impacts of isolation and inbreeding. In light of this situation, it would generally be advisable (and supported by the quantitative analyses summarized here) that the preferred viable population abundance be set near the high end of the proposed range. This larger abundance means comparatively higher levels of genetic viability can be achieved with relatively lower rates of immigration from an external source.

The difference observed in the threshold immigration rate between the two models reported above most likely results from the more fine-scale treatment of population genetic mechanics in the SLiM model compared to the simpler Vortex-based analysis. Higher rates of immigration as simulated in SLiM also led to the potential introduction of a larger number of deleterious genetic variants (i.e., genetic load) into the Scandinavian wolf population, which could lead to more inbreeding depression as the introduced load is expressed through time via inbreeding. A reduced threshold for immigration of one immigrant per decade as a mechanism for maintaining population viability follows from this analytical result.

Another characteristic that is different in the two models is the estimation of relatedness between the Scandinavia and Finland/Karelia populations. The SLiM model aims to recreate the historical process of founding the Scandinavia population through immigration of individuals from the Finland/Karelia population, thereby creating a kinship between the new population and its source. In contrast, the Vortex model assumes that the Scandinavia and Finland/Karelia populations are unrelated, or at least as unrelated to each other as the individual founders of the Scandinavia population are to one another on a relative scale. This is a pronounced simplification in the Vortex-based approach, as there is clearly a defined ancestral relationship between these two populations. Despite this simplification, both models lead to similar conclusions regarding the value of sustained connectivity between the populations as a mechanism for reducing inbreeding and introducing new genetic variation to sustain prolonged population viability of the Scandinavia wolf population. Results such as these highlight the value of this simulation approach for quantifying the relative change in key population genetic parameters over time, even while the capacity for accurate prediction of absolute population metrics is impractical owing to persistent gaps in our full understanding of genetic and demographic processes in these wolf populations (and wildlife populations in general). This is a key requisite for understanding the true value of population viability analysis as a decision-support tool (e.g., Morris and Doak 2002; McCarthy et al. 2003; Lotts et al. 2004).

For populations at the lower end of the 170-270 threshold, our simulations indicate that migration may represent a risk of introducing new deleterious variation, which could lead to a reduction in fitness if inbreeding remains high. While temporary, this reduction in fitness will induce a purging effect which is relevant to the long-term health of the population. Nevertheless, it is possible that the negative effects of this genetic load may be counter-balanced by a genetic rescue effect where beneficial genetic variation increases fitness. This underlines the need to monitor both changes in genetic load as well as overall fitness following reproduction by immigrants.

Conclusions

That these two independent simulation modeling approaches generate quite similar results as described in the previous section, even in the presence of identified differences in model structure and/or function, should increase confidence among management authorities in the utility of this exercise. Each model has strengths and weaknesses that become apparent when judging their realism against our understanding of the biology of wolves in Scandinavia. Taken together, they provide useful information for broad policy and management decisions regarding wolf conservation in Sweden. At the same time, each individual model can be studied in more detail to provide additional insight into specific population dynamics questions for which they are particularly well-suited. Those insights can be found in each of the two full modeling reports accompanying this joint statement.

We end this statement with a final reminder of our understanding of the scope of this analysis. As argued in the Introduction, our intent with these two PVA efforts is to explore the demographic conditions that are necessary to promote viability of the wolf population in Sweden as embodied in the general concept of minimum viable population (MVP) size and as described in the Habitats Directive guidance on using model-based approaches to determine MVP (DG Environment 2023). The time horizon for this evaluation is 100 years from today, which is considered by many to constitute a “long-term” projection of population performance (e.g., IUCN 2012). However, in keeping with the recommended use of ecological functionality in the estimation of favourable reference population values, the time horizon on which to determine a favorable reference population (FRP) value could extend beyond 100 years. The actual population size required to achieve that favorable status, moreover, will be larger than the estimated minimum viable population size. The Habitats Directive guidance document (DG Environment 2023) includes suggested protocols on upscaling MVP value or range to a corresponding FRP.

Additional analyses beyond the scope of the present demographic/genetic modeling efforts are required to implement this upscaling. These added analyses will likely include habitat suitability modeling, and considerations of landscape-level genetic, geographical and climatological factors that would influence the capacity of wolves to serve their proper ecological role in Sweden over the next century and beyond. To fulfill this role, the population of wolves in Sweden will need to be part of a functioning metapopulation with genetic connectivity to the Finland/Karelia population and perhaps elsewhere. The value of this connectivity for maintaining wolf population viability should not be discounted. Whenever possible, functional connectivity of Scandinavian habitats and those farther to the northeast should be encouraged and maintained to the fullest extent possible. The sociopolitical complexities of such a recommendation are not to be taken lightly, but the biological needs of wolf populations in the region as described in these analyses provide a scientific basis for productive species conservation planning. Considerations on metapopulation conservation of wolves in Fennoscandia by Bruford (2015) and Laikre et al. (2016) are particularly relevant in this regard.

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