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The effective size of the Scandinavian wolf population is too small for both short- and long-term conservation

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Abstract

The Scandinavian wolf population (Norway and Sweden) is intensively managed at a population size considered sustainable by managing authorities. As these authorities have decided to reduce the population to only 170 individuals, it is timely to evaluate this population size goal and to scrutinize underlying assumptions of recent simulation studies that inform population management. The effective size of a population determines the pace at which genetic diversity declines and inbreeding increases and plays a crucial role in short- and long-term extinction risks. Here we use the complete published pedigree of the Scandinavian wolf population to precisely calculate the effective size Ne since the founding of the population, per year. Our results indicate the Ne is unsustainably low. Moreover, we find that recent simulation studies commissioned by the managing authorities greatly overestimate the effective size of the Scandinavian wolf population, questioning their usefulness to inform population management.

Introduction

Wolf management policy in Scandinavia is based on balancing conservation interests with social, economic and cultural interests. Wolves are protected by the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, https://www.coe.int/en/web/bern-convention) (Norway and Sweden) and in Sweden also by the European Habitats Directive (COUNCIL DIRECTIVE 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora), and these agreements require that a favourable conservation status (FCS) be reached and maintained. Favourable Reference Values (FRVs) represent the minimum conditions needed for a species to be viable and maintain its natural population range and size on a long-term basis, which would imply FCS for the species.

Recent quantitative criteria to define FRV for wolf populations have been formulated for the European Commission (Linnell and Boitani 2025), which supersede earlier guidelines (Linnell et al. 2008). Sweden has a relatively long history of including genetic information to define a FRV for wolves under the EU Habitats Directive (Forslund 2008, Bruford 2015, Dussex 2024, Miller 2024). A central goal for the managing authorities (Swedish Environmental Protection Agency, SEPA) is to maintain a population size in which inbreeding is reduced below a certain threshold, while taking into account the mitigating effect of gene flow from the Russian and Finnish populations (Naturvårdsverket 2016). Since a change in the level of inbreeding is a direct consequence of the interaction between genetic drift (increasing inbreeding) and gene flow (decreasing inbreeding), simulations that address future population viability need to represent the local effective population size accurately.

After wolves were extirpated in the 1960s from the Scandinavian peninsula, the region was recolonized spontaneously by wolves from the Finnish-Karelian population in the 1980s (Vilà et al. 2003). After a slow initial growth phase, population size increased rapidly after 1991, when a third founder successfully reproduced (Vilà et al. 2003). The population further grew from 10 packs in the year 2000 to nearly 500

wolves in 2023 across 49 packs and 36 pairs (without reproduction), 90% of which occur in Sweden (Milleret et al. 2022, Svensson et al. 2023). At the beginning of 2025, the population consisted of 40 packs and 30 pairs, totaling circa 375 wolves, including pups of the year (Milleret et al. 2025b). These wolves all descend from three founders and four later immigrants from Finland and Russia (Åkesson et al. 2022, Miller 2024). Due to this founder effect, the population is highly inbred (Liberg et al. 2005, Kardos et al. 2018) with clear inbreeding depression and a high frequency of phenotypic anomalies (Räikkönen et al. 2013). In Sweden the population is subjected to a license hunt, which aims to keep the population above 300 wolves (Winter census, all ages combined), which is the current Favourable Reference Population size defined by SEPA. Although this population goal has been highly criticized from a scientific perspective (Laikre et al. 2022), SEPA recently explored through commissioned simulations (Dussex 2024, Miller 2024), whether a further reduction of the FRP to 170 wolves would compromise population viability, and has started to pursue this much reduced goal of 170 wolves through a gradual cull of the population (Swedish Government Decision L12025/01301). The European Commission disputed this goal as being sufficient for a favourable conservation status in a letter to the Ministry of Climate and Business (EC, 11/11/2025). The Swedish Government Decision was appealed in court by the Swedish Society for Nature Conservation, and on December 15th of 2025, the Administrative Court of Luleå issued a judgment (Case n° 2198-25) halting the licensed hunt for 2026 on the grounds that the authorities failed to demonstrate that the hunt would maintain the population in a favourable conservation status. Other regional courts followed, leading to a complete suspension of the licensed wolf hunt for winter 2026.

In Norway, where there also is license hunt, the goal is merely to have 3 reproduction events in Norway's wolf zone (covering barely 5% of mainland Norway) plus 2-6 reproduction events in packs shared with Sweden (Sandbekk and Gluva 2022). Outside of the Norwegian wolf zone, unfenced grazing of livestock and semi-domesticated reindeer are prioritized. Also in Sweden and Finland, the northern area is reserved for traditional reindeer herding. This creates a nearly 1000 km gap in the permanent wolf distribution between Scandinavian and Finnish or Russian wolves, and reduces survival of dispersing wolves in that area to nearly zero (Milleret et al. 2025a). Moreover, illegal killing is a contentious issue in southern Scandinavia, strongly impacting wolf population dynamics (Liberg et al. 2012).

The effective size of a population (N_e) reflects how much genetic drift and inbreeding impact the population. It is an important parameter in conservation biology, with two major thresholds for conservation: when Ne>50-100, the population is not considered at high short-term risk for serious inbreeding depression. When Ne>500-1000, it is assumed that it can maintain evolutionary potential in perpetuity (Frankham et al. 2014). Simulation and modelling studies have typically assumed that the ratio of the effective population size N_e to the total population size (all age classes included, N_{tot}) is 0.25 in Scandinavian wolves (e.g., Bruford 2015, Laikre et al. 2016, Dussex 2024), a value itself derived from simulations (Forslund 2008). We will further refer to N_e estimates derived from this N_e/N_{tot} ratio as "Forslund N_e". In a population with N_{tot}=510 wolves, which equals the number of Scandinavian wolves in 2021 (Milleret et al. 2025b), this yields a contemporary estimate of Forslund N_e=128 (assuming N_e/N_{tot}=

0.25), which would suggest that the population is not at substantial short-term risk of loss of fitness due to inbreeding depression.

To verify whether the generally applied Forslund N_e/N_{tot} ratio of 0.25 is realistic, we calculated N_e from the complete Scandinavian wolf pedigree from 1983 to 2022 (Åkesson et al. 2023) for each year since its founding and compare the results to published values of N_c and N_{tot}. We specifically focus on mean and variance in lifetime reproductive output (LRO: the number of offspring an individual has produced that survived to adulthood and established a territory) to calculate N_e and the mean N_e/N_{tot} ratio.

Methods

The Scandinavian wolf population has been monitored in great detail since its establishment in the 1980s, with annual census and genetic monitoring. As a result, a complete pedigree of the population is known. Appendix 1 of Åkesson et al. (2023) provides a complete overview of all 389 Scandinavian wolf pairs that reproduced between 1983 and 2022. The overview presents the unique name of all reproducing pairs, the inbreeding coefficient *F* of their offspring (assuming initially *F*=0 in the founders), the year of first reproduction of the pair, and the genotype codes of Sires and Dams in the Scandinavian wolf database and their pack origins. Over time some packs have dissociated, and new Sire-Dam combinations were formed, giving rise to a new pack name in the database. For each individual, the pack of origin is known, and this can be counted as a successful reproduction for its parents; i.e., that one of its offspring reached adulthood and was recognized as a pack founder. In this manner, we can calculate lifetime reproductive output (LRO) per pack, and by linking packs to pack founders, we get LRO per individual. We consider the first year of reproduction of an individual as that individual's cohort year.

Annual estimates of total population size, number of family groups and average inbreeding coefficients of the population were extracted from the annual wolf monitoring reports of the Scandinavian authorities (https://www.slu.se/centrumbildningar-och-projekt/viltskadecenter/publikationer/inventeringsrapporter/inventeringsrapporter-varg/), most of which is provided in Svensson et al. (2023). Total population size data prior to 1998 were taken from Wabakken et al. (2001).

Since we have the full pedigree of the entire population since its founding, we can calculate the precise value for N_e at each time step, without sampling error. We calculated N_e across annually moving windows of 4 years (cohorts), which fits an average generation time estimate of 3.6-4.5 years calculated from a dataset of 641 reproducing wolves in Scandinavia over a period of 35 years (using the weighted mean age of breeders; Flagstad et al. unpublished). Average K (LRO) and V_K (the variance in K) were calculated per period across all adults from the pedigree data. We used Equation S1 and the method of Waples (2024) to calculate N_e from variance in LRO in populations with overlapping generations. This is a modification of the age-structured method of Hill (1972, 1979), and accounts for deviations from =2, rescaling V_K to its expected value in a population of constant size (with =2). Here

we calculate the N_e per cohort per sex, and use the sex ratio formula to calculate overall .(Kimura and Crow 1963).

In addition, inbreeding increases the variance of a trait (Crow and Kimura 1970), and with sexual reproduction this happens by increasing the variance in reproductive success of the grandparents' (and earlier ancestors') genome sections in the parent generation, and therefore also reduces the effective size, such that $N_e=N/(1+F)$, with F the inbreeding coefficient (Pollak 1987). We therefore corrected the N_e estimate based on and V_K with the average inbreeding coefficient across each cohort, which is based on the complete pedigree (Åkesson et al. 2023). This also integrates the realized effect of gene flow in the population from the Karelian/Finnish wolf population, as gene flow reduces inbreeding.

The N_c used here to calculate and V_K only includes individuals that have started reproductive activity, not pairs of wolves that might breed in the next year or years. Including non-reproductive individuals would not matter, as the increase in N_c would result in a decrease in and an increase in V_K to produce exactly the same N_e (Waples 2024). For cohorts younger than 2016-2019 the data on lifetime reproductive output are not complete for the entire cohort, since some parents are still alive and haven't realized their full LRO yet. We used the and V_K of earlier cohorts (since 2003) to estimate N_e in the most recent cohorts. We used the conversion in Waples (2002) to rescale K to 2 in this cohort and calculated the corresponding V_K, which should provide a good approximation.

Results

Table 1 presents the summary of the N_e values per year across the development of the Scandinavian wolf population (with and without considering inbreeding) and compares the realized N_e (with and without taking inbreeding into account) to the total population size (Forslund 2008, Laikre et al. 2016). Overall, we see estimates of contemporary N_e increase from 2 in the 1983-1986 cohort to a maximum of 77 (not considering inbreeding) or 59 (with inbreeding) in the 2016-2019 cohort. Figure 1 shows the trajectory of the pedigree-based N_e (with and without considering inbreeding), and the change in the Forslund N_e, calculated by multiplying the yearly total census size N_{tot} with the Forslund N_e/N_{tot} =0.25.

Although in initial generations the difference between the Forslund N_e and the pedigree-based N_e is small, this quickly changes to a twofold difference as the population grows. Even without taking inbreeding into account, the Forslund N_e is still on average 1.7 times larger than calculated from the pedigree. When corrected for =2, the variance in reproductive success V_{K2} has been stable around a value of 5.2 (SD 1.04) in males and 5.6 (SD 1.13) in females since 1998. This yields an average N_e/N_{packs} ratio of 1.17 across cohorts, and a N_e/N_{tot} ratio of 0.12 (Table 1).

Discussion

Estimating the effective size of populations is of high relevance for policy and management, as N_e affects short- and long-term population viability. As such, effective size forms an essential part of conservation criteria for large carnivores in Europe (Linnell and Boitani 2025).

Detailed and complete population data that allow the calculation of exact parameter values are publicly available for the Scandinavian wolf population, which make a nearly exact calculation of N_e feasible: our only source of bias is in the generation time. Our results indicate that the current N_e of the Scandinavian wolf population is well below 100; for the 2016-2019 cohort, we find a value of 59. The current total population size (Winter 2024-2025 census) is estimated at 375 individuals (95% CI 354-400) with a total of 40 packs (Milleret et al. 2025b, Svensson et al. 2025). Applying the N_e/N_{tot} conversion of 0.12, this yields an expected N_e=45, which is far below the threshold of 100 to avoid inbreeding depression in the short term (Frankham et al. 2014).

Metapopulation connectivity

To be considered safe from a genetical point of view, (meta)populations should have a minimum effective size of at least 500 (Franklin 1980, Jamieson and Allendorf 2012, Hoban et al. 2020) or even 1000 (Frankham et al. 2014), which is an order of magnitude larger than the current Scandinavian wolf population. This threshold value is mirrored in recent guidelines on large carnivore conservation (Linnell and Boitani 2025) and in headline indicator A.4 of the Kunming Montréal Global Biodiversity Framework of the Convention on Biological Diversity (https://www.cbd.int/gbf). We do not imply that the Scandinavian population by itself should have an effective size larger than 500 (~500 packs; Mergeay et al. (2024)), but that it should be part of a functionally connected metapopulation of at least this size.

Functional connectivity among subpopulations requires multidirectional gene flow of at least one effective migrant per generation (Mills and Allendorf 1996). It follows logically from Wright's Island Model (Wright 1931) that one effective migrant per generation is a tipping point in metapopulation connectivity: below this threshold value, subpopulations experience genetic drift that is largely independent from each other, whereas above this value subpopulations increasingly experience correlated genetic drift (indicating functioning as a connected metapopulation), and at migration-drift equilibrium the realized inbreeding effective size of well-connected subpopulations approaches that of the metapopulation (Ryman et al. 2019). Since 1991 (across seven wolf generations), only four immigrants have contributed genetically (Åkesson et al. 2022). The northern half of Fennoscandia has a zero tolerance policy towards wolf establishment (Boitani et al. 2022), creating a large gap in permanent wolf distribution between Scandinavian and S-Finnish or Russian wolves. Wolves dispersing across this vast area can be legally killed: across the past 4 years more than 160 dispersing wolves have been shot in N-Finland before they could reach Sweden or Norway (Harri Norberg, Finnish Wildlife Agency, pers. comm.), reducing survival of wolves attempting to disperse from Finland or Russia into Sweden to nearly zero (Milleret et al. 2025a).

Note that the one migrant per generation threshold assumes next to migration-drift equilibrium an island model of gene flow, receiving immigrants from and sending out emigrants to all directions. In contrast, the Scandinavian peninsula is rather an endpoint in a linear stepping stone model of gene flow. As a result, functional connectivity requires up to four times more exchange than under a typical island model of gene flow (Wright 1931, Crow and Aoki 1984, Levin 1988). Moreover, the Scandinavian peninsula seems at present a sink of immigrants, likely with even more limited levels of emigration.

At present, we cannot consider the Scandinavian wolf population to be functionally connected to other wolf populations. Even when assuming ample connectivity with Finland (30 packs), Karelia (30 packs) and Murmansk (10 packs) (Boitani et al. 2022, Poyarkov et al. 2022), the current metapopulation N_e would still fall very short of the well-established threshold of 500 (Laikre et al. 2016, Mergeay et al. 2024). Reducing the culling in northern Fennoscandia could probably boost gene flow into the Scandinavian wolf population, but this is a contentious issue, linked to reindeer herding practices by the Saami people. Connectivity with the Baltic population, across Finland and Russia, is at present unknown, but is likely to be low and decreasing due to recently erected border fences between the Baltic states and Russia, and between Poland and Belarus.

Increasing connectivity (defined by the effective number of migrants, N_em) is not only a matter of ecological permeability of the landscape matrix (which is at present very limited because of culling), but also of the population size. Gene flow could increase if source populations would be allowed to grow. However, population sizes in adjacent source populations are not likely to increase due to the recent lowering of the protection of wolves across Europe (in both the Bern Convention https://search.coe.int/directorate_of_communications?i=0900001680b4ad28 and the Habitats Directive https://www.europarl.europa.eu/doceo/document/TA-10-2025-0100_EN.html).

Theoretical and simulation-based versus empirically estimated N_e

So far, the N_e of the Scandinavian wolf populations has been modeled and simulated (Forslund 2008, Bruford 2015), but rarely accurately measured. Bensch et al. (2006) estimated N_e to be 45.6 (95% CI: 20.4 – 181.2) from a cohort sampled in 2002 on the basis of linkage disequilibrium at 31 microsatellite markers. Since N_e estimated with LD is that of the parents of the sampled cohort (born on average 4 years earlier), these estimates reflect the effective size of a population that had a total population size of N_{tot}=70 (62-78) wolves (Table 1) (Wabakken et al. 1999). The value we calculated for the 1998-2001 cohort is well below that value. Perez-Sorribes et al. (2024) used whole genome sequencing data to calculate for the 1999-2006 cohort N_e=12 (95% CI: 10-13), when the average N_{tot} was 110 wolves and 11 packs. Their estimates for the 2007-2014 cohort was N_e=26 (95% CI: 25-27). This corresponds well with the pedigree-based estimates of K and V_K for those same periods, and with the mean number of packs (Table 1).

Recent individual based modelling and simulation studies have assessed whether reducing the population to 170-270 individuals would endanger the Scandinavian wolf population, while allowing for

various levels of gene flow from a “large and continuous population” (Dussex 2024, Miller 2024). Before that, Bruford (2015) used a similar approach, but with a carrying capacity of 700 wolves, and using input parameter values provided by SEPA, based on Forslund (2009). To check the validity of these simulations and their underlying assumptions, we estimated N_e from the reported changes in gene diversity H_e and compared these to the pedigree-based values for corresponding population sizes. For example, Dussex (2024) reports a change in nucleotide diversity of 10% across 33 generations for a simulated population of N_{tot}=310 wolves. As a population loses $1/(2N_e)$ of its nucleotide diversity or gene diversity per generation, This corresponds to N_e=157, which is larger than the typical number of adults in the population for such a total population size (see supplementary material for details). This implies reproductive variance is even smaller than in an ideal Fisher-Wright population. This value is in stark contrast with our exact measurement of N_e from the full pedigree (Table 1): at Nc=307 (the mean value of the 2007-2010 cohort), the population had an effective size N_e=46.5 and N_{eF}=36.1. Across all simulation studies commissioned by SEPA, the simulation results for closed populations reflect populations with effective sizes that are 1.5 to 4.2 times larger than the corresponding values emanating from the entire pedigree (supplementary material). Underlying reasons for this discrepancy are discussed in the supplementary material, and tend to reflect unrealistic parameter settings for the simulations. For example, the variance in reproductive success extracted from the entire pedigree across each time step is up to ten times larger than the values emanating from the simulations by Dussex (2024). This discrepancy suggests that these simulations do not reflect the biological reality of the population and provide a poor basis for a population management plan.

Our N_e calculations for the Scandinavian population are based on the exact lifetime reproductive output data from the entire pedigree and correspond very closely with observations in other European populations that the number of packs is an excellent proxy of the effective size (Mergeay et al. 2024). Recent population genomic estimates of the N_e of the Scandinavian wolf population corroborate this further (Pérez-Sorribes et al. 2024). At present (Winter 2024-2025 census) the population’s estimated effective size has fallen below 50. Lowering the population size to 170 individuals would yield an even smaller effective population size of only 20. This is well below short term conservation thresholds to minimize adverse effects of inbreeding depression (Frankham et al. 2014).

Recent simulation studies have focus largely on avoiding extinction (Dussex 2024, Miller 2024), but a favourable conservation status, as defined by the Habitats Directive, needs much more than not going extinct; it requires robust and thriving populations that maintain themselves in the long term (Linnell & Boitaini 2025). With a management goal of 170-270 individuals, this population would depend levels of gene flow to permanently rescue the severely inbred population that are currently not attained (Dussex 2024), and which are unlikely to be met with a zero tolerance policy towards wolves dispersing from adjacent populations. In spite of complex modelling efforts to forward simulate the trajectory of this population under a range of scenarios, the Scandinavian wolf population cannot be considered robust. It would not be the first wolf population to collapse under the burden of inbreeding depression (Hedrick et al. 2019).

Conclusion

The Scandinavian wolf population is genetically depleted and inbred, and its effective size is already below any scientifically accepted safe conservation threshold. Lowering the total population size to just 170 individuals while continuing to impede gene flow is likely to exacerbate genetic drift, inbreeding and inbreeding depression. Recent simulation studies strongly underestimate the rate of genetic drift the population experiences and cannot, therefore, be considered as realistic representations of the Scandinavian wolf population.

Declarations

Conflict of Interest

The authors declare no conflict of interest.

Data availability statement

All source data were drawn from Appendix 1 of https://www.slu.se/globalassets/ew/org/centrb/vsc/vsc-dokument/vsc-publikationer/rapporter/2022/slakttrad-skand-varg-2021-version1-1.pdf.

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Table

Table 1. N_e estimates and summary statistics of population variables in the Scandinavian wolf population since its founding, for a generation interval of 4 years. N_{ef}, female effective size. N_{em}, male effective size. F: average population-level inbreeding coefficient. N_e: age-structured effective size for overlapping generations. N_e (F): N_e corrected for inbreeding. Packs: number of packs. N_{tot}: the total population size (including juveniles and yearlings). F is the average across the four years of the inbreeding coefficient in each calendar year (from Åkesson et al. 2023).

Cohort	N_{ef}	N_{em}	N_e	F	N_e (F)	Packs	N_{tot}
1983-1986	1.3	1.1	2.4	0.00	2.4	1	3
1984-1987	1.3	1.7	3.0	0.25	2.4	1	5
1985-1988	1.3	1.7	3.0	0.25	2.4	1	6
1986-1989	1.3	1.7	3.0	0.25	2.4	1	10
1987-1990	1.3	1.7	3.0	0.25	2.4	1	8
1988-1991	1.2	2.0	3.0	0.23	2.4	2	8
1989-1992	2.4	2.0	4.4	0.22	3.6	2	17
1990-1993	2.8	2.9	5.6	0.20	4.7	3	20
1991-1994	4.1	4.2	8.4	0.19	7.0	3	28
1992-1995	3.0	2.8	5.8	0.19	4.9	3	34
1993-1996	2.2	2.8	5.0	0.18	4.2	3	39
1994-1997	4.5	4.5	9.0	0.19	7.6	6	49
1995-1998	4.1	4.2	8.3	0.19	7.0	6	70
1996-1999	4.1	3.6	7.7	0.20	6.4	7	74
1997-2000	5.9	6.0	11.9	0.23	9.6	12	92
1998-2001	5.6	5.7	11.3	0.26	9.0	11	106
1999-2002	6.5	5.6	12.1	0.28	9.5	8	92
2000-2003	8.2	7.3	15.4	0.28	12.0	11	111
2001-2004	12.9	10.7	23.4	0.29	18.2	14	144
2002-2005	13.5	11.9	25.3	0.29	19.6	15	151
2003-2006	13.3	13.3	26.6	0.29	20.6	17	153
2004-2007	16.1	14.6	30.6	0.30	23.6	20	188
2005-2008	18.9	17.3	36.1	0.30	27.9	29	233
2006-2009	17.8	14.6	32.0	0.30	24.7	28	272
2007-2010	24.7	22.0	46.5	0.29	36.1	31	307
2008-2011	24.2	20.6	44.5	0.28	34.8	33	295
2009-2012	23.7	23.5	47.2	0.27	37.1	38	380
2010-2013	29.7	28.4	58.1	0.26	46.0	43	400

2011-2014	26.2	24.3	50.4	0.25	40.3	49	460
2012-2015	32.8	33.7	66.5	0.25	53.4	41	430
2013-2016	35.9	34.2	70.0	0.24	56.5	46	430
2014-2017	33.4	33.8	67.2	0.23	54.4	41	410
2015-2018	40.9	35.5	76.1	0.24	61.4	40	380
2016-2019	44.6	34.2	77.4	0.24	58.8	45	450

Figures

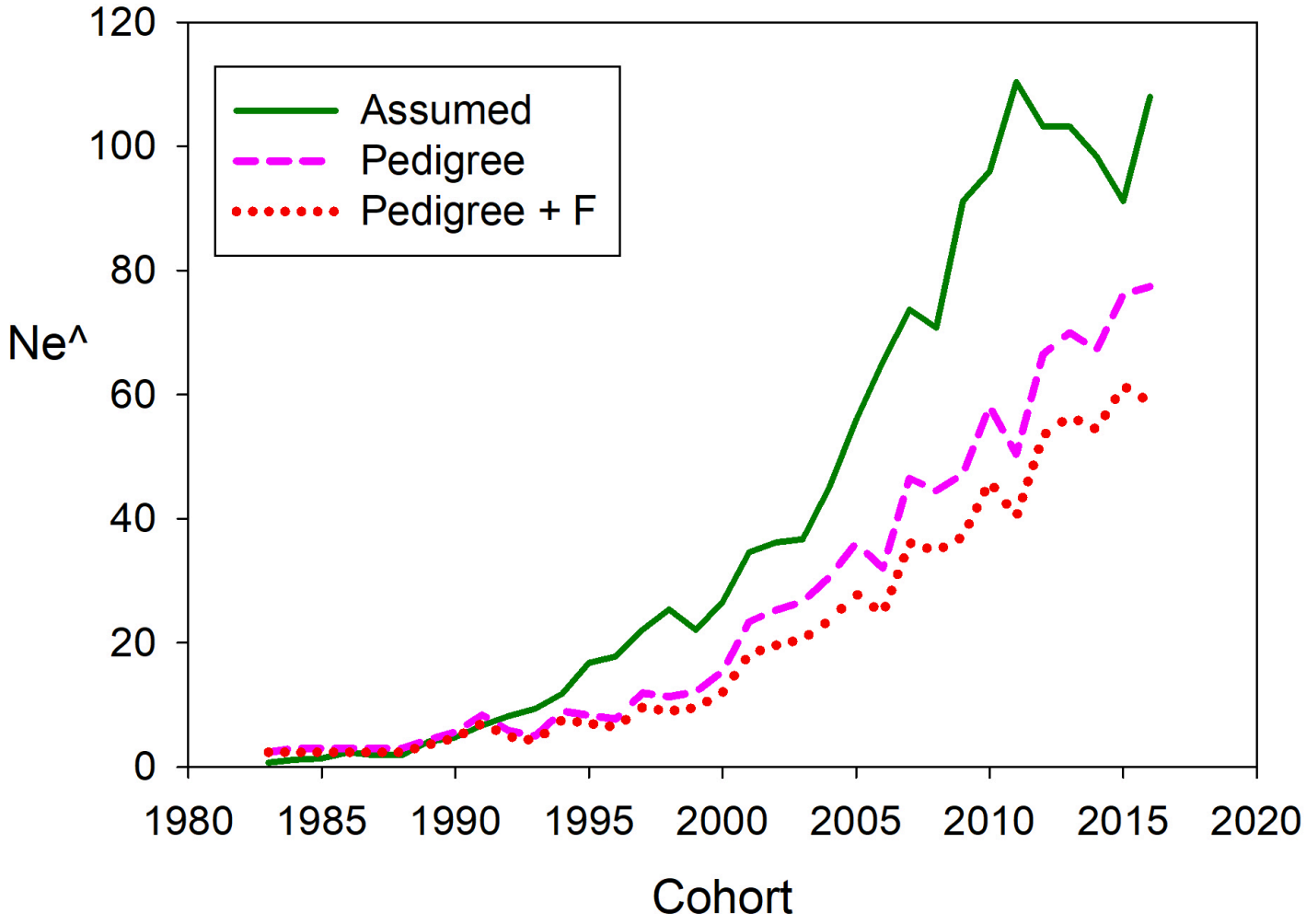

Figure 1

The change in the effective size of the Scandinavian wolf population since its founding, assuming 4 year cohorts along a 1 year moving window. The full green line represents the "Forslund N_e", the N_e typically

assumed by multiplying the total population size N_{tot} with the default N_e/N ratio of 0.25. The magenta dashed line represents the N_e calculated from the variance in reproductive success using the entire pedigree. The red dotted line further includes the effect of inbreeding. There are no error bars since these are exact calculations from the entire pedigree, thus having no sampling error.

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