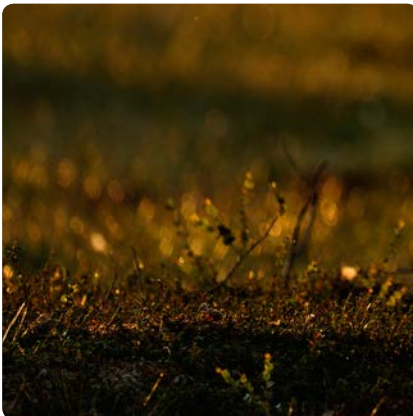


Complementary analyses of genetic Minimum Viable Population size of Scandinavian bears (*Ursus arctos*)

HELENA PURANEN-LI, CAROLINE SOLLEVI AND PER SJÖGREN-GULVE

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Förord

Med anledning av ett regeringsuppdrag 2012–2013 gav Naturvårdsverket Torbjörn Nilsson (fil. dr. i zoöekologi) i uppdrag att genomföra kvantitativa sårbarhetsanalyser för att bedöma minsta livskraftiga populationsstorlek (MVP, minimal viable population) för björn, järv och lo baserade på IUCN:s kriterium E. Dessa sårbarhetsanalyser utfördes med programmet VORTEX och omfattade även andra beräkningar som kunde underlätta Naturvårdsverkets fortsatta arbete med att bedöma arternas referensvärden för gynnsam bevarandestatus i Sverige.

I den vetenskapliga granskningen av Nilssons rapport blev modelleringen av björn kritiserad. Det påpekades att kompletterande simuleringar och genetiska MVP-analyser behövdes, då högre reproduktionsframgång hos björnhannarna än värdena som Nilsson använde dokumenterats i publicerad forskning. Denna rapport presenterar dessa kompletterande analyser som utförts av Helena Puranen-Li och Caroline Sollevi vid Stockholms universitet tillsammans med Per Sjögren-Gulve, Naturvårdsverket och docent i naturvårdsbiologi. Den sistnämnde var också projektledare för analyserna. Rapporten har genomgått extern granskning av utomstående expertis.

Författarna svarar själva för rapportens innehåll varför det inte kan åberopas som Naturvårdsverkets ståndpunkt. Naturvårdsverket framför ett varmt tack till de externa vetenskapliga granskarna för deras granskning och kommentarer.

Naturvårdsverket, december 2014

Eva Thörnelöf

Avdelningschef, Analys- & forskningsavdelningen

Sammanfattning

Den här rapporten är ett av de vetenskapliga underlagen rörande minsta livskraftiga populationsstorlek (Minimum Viable Population size; MVP) för Naturvårdsverkets bedömning av Sveriges referensnivå (Favourable Reference Population; FRP) för björn (*Ursus arctos*) i artikel-17-rapporteringen 2013. Här redovisas kompletterande analyser av den skandinaviska populationen av björn för att bedöma MVP i relation till två olika genetiska kriterier. Analyserna gjordes med datorsimuleringar, baserade på data från tidigare sårbarhetsanalyser (Nilsson 2013), med ny modellering av björnhannars reproduktionsframgång, och undersökte hur snabbt den skandinaviska björnstammen förlorar genetisk variation vid olika populationsstorlekar, utan mutation och utan invandring från östligare björnbestånd.

Den tidigare analysen (Nilsson 2013) använde resultaten från en analys av skillnad i genetisk variationsgrad (heterozygotigrad) mellan 22 björnar som först undersöktes och 127 björnar som undersöktes 14–16 år senare (Tallmon m.fl. 2004) för att beräkna hur många av björnhannarna som reproducerade sig per år. Beräkningen gav en siffra (3,3% per år) som var betydligt lägre än vad annan forskning om björnhannars reproduktionsframgång visat, både för den skandinaviska björnpopulationen (21,4% per år i södra skandinaviska studieområdet och 56,8% per år i norra studieområdet; Zedrosser m.fl. 2007), samt för grizzlybjörn (*Ursus arctos horribilis*; 49%, Craighead m.fl. 1995) och amerikansk svartbjörn (14% per år; Costello m.fl. 2009). Swenson och Kindberg, som var två av de vetenskapliga granskarna av Nilssons (2013) rapport, kritiserade Nilssons siffra och menade att den var för låg och att kompletterande MVP-analyser behövdes med data på reproduktionsframgången från Zedrosser m.fl.s undersökningar (2007).

Följaktligen genomfördes kompletterande analyser med den åldersspecifika reproduktionsframgång som Zedrosser m.fl. (2007) uppmätt i det södra studieområdet av den skandinaviska populationen. Den södra delens värden användes dels eftersom Nilssons (2013) analyser visade att MVP-värdena baserade på modellering och data från den södra populationsdelen i samtliga fall även var giltiga för den norra populationsdelen, och dels eftersom betydligt fler björnhannar undersökts i södra (44 st) än i det norra studieområdet (24 st). Den åldersspecifika modelleringen av björnhannarnas reproduktionsframgång var det enda som skilde från de input-data som Nilsson (2013) använde för VORTEX-simuleringarna av björn. Analyserna gjordes med respektive utan effekter av sällsynta katastrofer, precis som i Nilssons rapport (2013), och utan invandring av björnar från östligare populationer (Finland, Ryssland). Analyserna visade att det genetiska MVP-värdet motsvarande mindre än 5% förlust av genetisk variationsgrad på 100 år motsvarades av minst 400 björnar när sällsynta katastrofer fanns med, och minst 380 björnar om katastrofer ej fanns med. MVP-värdet motsvarande den genetiskt effektiva populationsstorleken (N_e) minst 500, blev minst 2350 när sällsynta katastrofer fanns med och minst 2250 om katastrofer ej kunde ske. Resultaten diskuteras bland annat i relation till huruvida den skandinaviska populationen är isolerad eller ej från östligare populationer, till de skandinaviska björnarnas genetiska särprägel, och till tänkbara FRP-värden.

Summary

This short report presents the results of analyses and assessment of genetic Minimum Viable Population size of Scandinavian bears (*Ursus arctos*) that complement the population viability analyses already performed by Torbjörn Nilsson (2013).

This is one of the scientific reports underpinning the Swedish Environmental Protection Agency's Article-17 reporting in 2013 of Favourable Reference Population size for the brown bear in Sweden. It presents complementary population viability analyses of the Scandinavian population with the VORTEX software to quantify minimum viable population size (MVP) estimates in relation to two criteria for genetic viability. The analyses were based on simulations without immigration and mutation, and using the same demographic data from empirical studies of the Scandinavian population as were used in a previous SEPA report (6549), except for the updated data on the reproductive success of males.

The genetic MVP corresponding to < 5% loss of genetic variability (i.e. heterozygosity) in 100 years was estimated at ≥ 380 bears when effects of catastrophes were not simulated, and at ≥ 400 bears when effects of rare catastrophes were included. The genetic MVP corresponding to an effective population size (N_e) of ≥ 500 was estimated at ≥ 2250 bears when effects of catastrophes were not simulated, and at ≥ 2350 bears when rare catastrophes were included. The study approach and results are discussed, for example, in relation to the two MVP criteria, FRP, and to the degree of genetic differentiation and isolation of the Scandinavian bear population.

Introduction

Population viability analyses of the Scandinavian populations of brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) were recently presented by Torbjörn Nilsson (Nilsson 2013). The analyses and scientific report were part of a government commission on Minimum Viable Population (MVP) estimates, and also intended to form support for further development of the management plans for the species in Sweden. The analyses included estimates of MVP based on empirical data and simulations.

The MVP estimates for the brown bear (Table 1) were questioned in the peer review of the report (Swenson & Kindberg 2013). The annual mating success value of 3.3% that Nilsson calculated from a reported change in heterozygosity between generations in the population quantified by repeated sampling by Tallmon et al. (2004) and applied to all adult males, was criticized for being too low. Swenson and Kindberg argued that analyses based on measured reproductive success (Zedrosser et al. 2007) should also have been performed to compare with Nilsson's results. Zedrosser et al. (2007) used genetic paternity analyses to determine which male bears of known age sired offspring that had survived to yearling age in both the southern and northern parts of the Scandinavian population and which ones did not. They found that, on average, 21.4% of the adult male bears (n = 44) produced young that became yearlings per year in the southern part and 56.8% in the northern (n = 24), i.e. much higher than the 3.3% estimated to have reproduced by Nilsson from Tallmon et al.'s (2004) results. The results of Zedrosser et al. (2007) are conservative, because they estimated the age-specific siring of young that survived to be yearlings. Their estimates would probably have been higher if they had been able to document the percentage of the males that sired young-of-the-year. Also other studies on reproduction success of male bears have demonstrated higher values: 49% of male grizzly bears (*Ursus arctos horribilis*) bred successfully (Craighead et al. 1995), and 14% of the males reproduced per year in a black bear (*Ursus americanus*) population (Costello et al. 2009).

Table 1. MinimumViable Population size estimates presented by Nilsson (2013) based on the southern brown bear population in Sweden.

	> 95 % of heterozygosity maintained in 100 years	Genetic Ne ≥ 500
Without catastrophes	≥ 1000	≥ 6838
With catastrophes	≥ 1100	–

Nilsson chose his approach based on the assumption that the reproduction rate of the sampled individuals in Zedrosser et al. (2007) was not representative for the entire male population. This conclusion was based on the finding that bears in Sweden were found in core and peripheral areas, with higher female density in the core areas and younger adult males primarily in the

periphery (Swenson et al. 1998). Thus these males would have much fewer opportunities to reproduce. However, comments by Swenson & Kindberg (2013) and personal communication (Swenson, Kindberg & Zedrosser, pers. comm.) regarding the distribution of the bear population yielded a clearer and updated picture of the current distribution. The female core areas have expanded and both males and females in lower density areas have larger home range sizes (Dahle & Swenson 2003), indicating that very few males currently reside in areas without females (Figure 1); consequently Swenson & Kindberg (pers. comm.) concluded that Zedrosser et al's data (2007) are representative for bears in Sweden today.

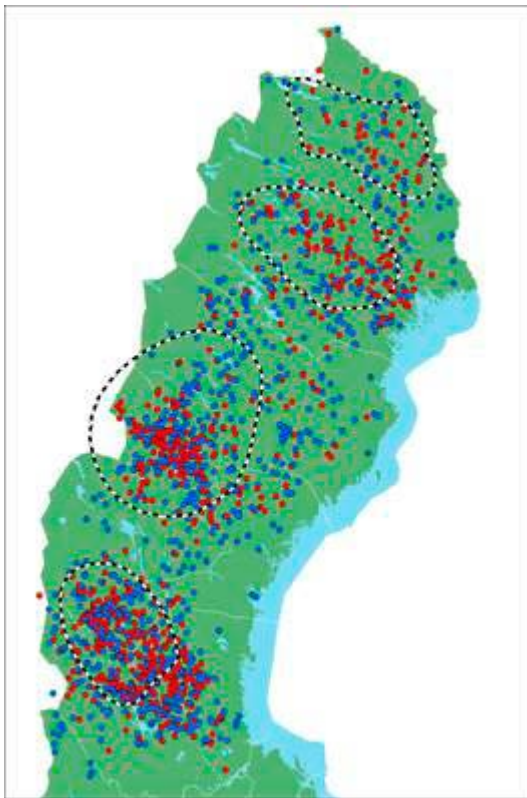


Figure 1. The distribution range of bears in Sweden has changed since 1998. The dotted lines show the core areas as they were shown in Swenson et al. (1998). The spots represent females (red spots) and males (blue spots) shot by hunters between 1981 and 2010. The female core areas have expanded resulting in very few males residing in areas without females (Kindberg et al. 2009, Swenson & Kindberg, pers. comm. 2013).

The Swedish Environmental Protection Agency initiated further analyses to deal with these comments. This report presents genetic MVP values for the Scandinavian bear population using demographic data from its southern part (“southern bear population”) and VORTEX simulations with the same data set as Nilsson (2013), but with the age-specific yearly reproductive success values (YRS) presented by Zedrosser et al. (2007), instead of 3.3%. We chose to focus on the southern bear population, because Nilsson’s (2013) results consistently showed higher MVP values with demographic data from the southern part of the population than with data from the northern part, i.e. the MVP values based on data from the southern part were consistently valid also for the northern demographic scenarios. Furthermore, Zedrosser et al.’s (2007) YRS values from the southern study area were based on a greater number of male bears than in the northern area and were lower, thus yielding MVP estimates which would err on the conservative side, i.e. also apply, in the northern part of the population.

Nilsson (2013) carried out sensitivity tests of the VORTEX models for all three species and input scenarios. Regarding effects on heterozygosity loss, he found that increased catastrophe severity and reduced proportion of males breeding had the strongest effects on heterozygosity loss. Thus we anticipated that changing the annual percentage of males breeding (a nearly seven-fold increase) would affect the MVP estimates.

The genetic MVP criteria used were: (A) the population size at or above which the population’s genetic effective size (N_e) is ≥ 500 (Franklin 1980; long-term MVP in Nilsson 2013). At this effective population size, the loss of overall heterozygosity – and to the same extent quantitative genetic variation in polygenic characters – is expected to be counterbalanced by the heterozygosity created by mutations, i.e. the level of overall polygenic variability is maintained in the long term; and (B) the population size at or above which the simulated population loses less than 5% of its heterozygosity in 100 years (Allendorf & Ryman 2002; short-term genetic MVP in Nilsson 2013).

Methods

All simulations were performed with the program VORTEX version 9.99c (Lacy et al. 2005), which is available at <http://www.vortex9.org/vortex.html>. The program is described in detail by Miller & Lacy (2005).

MVP values were estimated based on two different criteria: (A) the minimum population size fulfilling a genetic effective population size $N_e \geq 500$ (long-term MVP), and (B) the minimum population size at which 95 % or more of the initial heterozygosity remains after 100 years (short-term MVP). VORTEX does not include mutation in its simulations. Thus, to find the population size meeting the criterion of $N_e \geq 500$, we calculated the expected heterozygosity after 100 years according to:

$$\frac{H_t}{H_0} = \left(1 - \left(\frac{1}{2N_e}\right)\right)^t$$

Equation 1. H_t/H_0 describes the remaining proportion of heterozygosity after t generations, N_e = the (harmonic mean) effective population size, t = number of generations.

Nilsson (2013) showed that the generation time of the bears in the southern subpopulation was 10.97 years, yielding that 100 years equal 9.116 generations ($t = 9.116$). Thus, equation 1 predicts that when $N_e = 500$, the proportion of remaining heterozygosity after 100 years [i.e. $(1 - 1/1000)^{9.116}$] is expected to be 0.991. We subsequently used VORTEX simulations to find the minimum population size at which such a proportion of the initial heterozygosity remained, on average, after 100 years and which would correspond to $N_e = 500$.

We modelled two different scenarios, with and without catastrophes. In the catastrophe scenario the probability of catastrophes was set at 1 % per year, so on average there was one catastrophe per simulation run of 100 years, similar as was done in Nilsson (2013). During a catastrophe year, the individual survival of all bears was reduced by half and all reproduction failed.

Instead of using a mean reproduction rate for all males (3.3%; Nilsson 2013), we used age-specific reproduction data collected for males whose ages were known, based on the results of a genetic paternity analysis (Figure 2; Zedrosser et al. 2007). To assess if the results were applicable despite some young males residing outside the study area, which could produce uncertainty in the reproductive rates of younger males (age 3–5), we also performed simulations with reduced reproduction by 25% and 50% for these three age classes. Except for the values of age-specific %Males Successfully Producing Offspring (function used in VORTEX¹) gathered from Zedrosser et al. (2007), we used the same input values as in Nilsson's (2013) Base scenario (Table 2). For more detailed information, see Nilsson (2013).

¹ Function used in Vortex as age-specific percentage of males successfully siring offspring (A = age):
=((A=3)*4.8)+((A=4)*11.4)+((A=5)*15.2)+((A=6)*15.6)+((A=7)*29.6)+((A=8)*30.4)+((A=9)*27.3)+
(((A=10)OR(A=11)OR(A=12)OR(A=13)OR(A=14))*23)+((A>=15)*34.9)

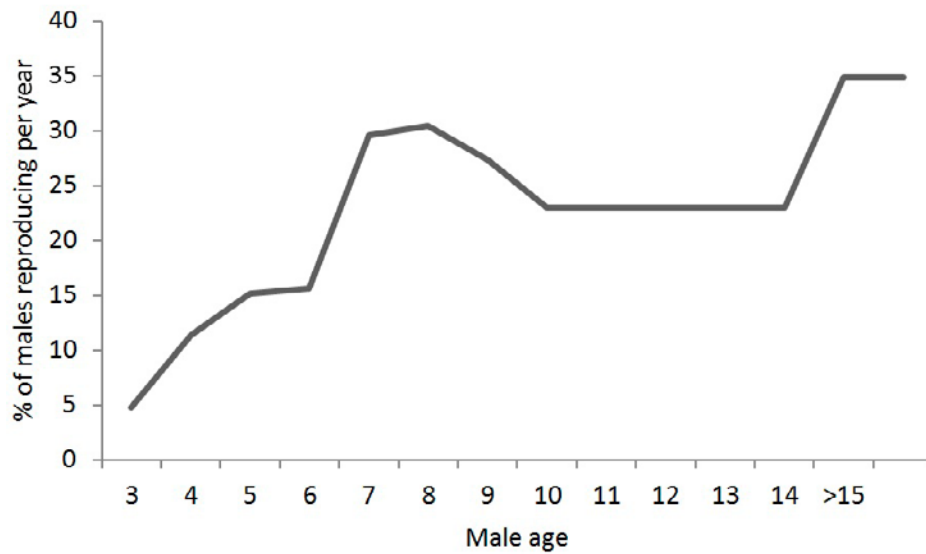


Figure 2. Annual percentage of male brown bears successfully siring offspring that lived to become yearlings at different ages in the southern study area documented by Zedrosser et al. (2007) using genetic paternity analysis.

Inbreeding depression is measured in terms of lethal equivalents (LE), which represents the quantity of deleterious recessive alleles in the population. Similar to Nilsson's (2013) Base Scenario simulations, LE was set to 6.5.

We ran 2500 or 10000 simulations with various initial population sizes $N_0 = K$ (carrying capacity, maximum population size), similar to Nilsson (2013), to find the population size meeting the respective MVP criteria. The initial population size (N_0) in the search of the short-term MVP was set in intervals of 10 animals, whereas the simulations for the long-term MVP were done with N_0 -intervals of 50 animals.

Table 2. Demographic input data used in simulations of the southern bear population. Table copied from Nilsson (2013) with bold values showing the modified age-specific reproduction success among males used in this study.

Reproduction	Southern area, Base scenarios	Values taken from or calculated from data in
Age of 1st offspring for females	4	Zedrosser et al. 2009, table 1 & 3
Age of 1st offspring for males	3	Zedrosser et al. 2007
Maximum age of reproduction	27	Zedrosser et al. 2007
Max litter size	4	Zedrosser et al. 2009
Mean litter size	2.289	Zedrosser et al. 2009, table 2
SD litter size	0.884	Zedrosser et al. 2009, table 2
Sex ratio at birth, % males	50	Jon Swenson, pers.comm.
% adult females breeding	57.5	Zedrosser et al. 2009, table 2
SD _{EV} in # breeding females	17.8	Nilsson (2013)
% of males breeding a certain year		
From age 3 to 4	4.8	Zedrosser et al. 2007
From age 4 to 5	11.4	Zedrosser et al. 2007
From age 5 to 6	15.2	Zedrosser et al. 2007
From age 6 to 7	15.6	Zedrosser et al. 2007
From age 7 to 8	29.6	Zedrosser et al. 2007
From age 8 to 9	30.4	Zedrosser et al. 2007
From age 9 to 10	27.3	Zedrosser et al. 2007
From age 10 to 14	23	Zedrosser et al. 2007
From age 15 to 27	34.9	Zedrosser et al. 2007
Mortality rates (%)		
Female mortality from age 0 to 1	35	Swenson et al. 2001
SD _{EV} in 0 to 1 female mortality	27.6	Nilsson (2013)
Female mortality from age 1 to 2	17.7	Bischof et al. 2009, table 2
SD _{EV} in 1 to 2 female mortality	13.5	Nilsson (2013)
Female mortality from age 2 to 3	6	Bischof et al. 2009, table 2
SD _{EV} in 2 to 3 female mortality	2.2	Nilsson (2013)
Female mortality from age 3 to 4	6	Bischof et al. 2009, table 2
SD _{EV} in 3 to 4 female mortality	1.1	Nilsson (2013)
Female mortality from age 4 to 5	6	Bischof et al. 2009, table 2
SD _{EV} in 4 to 5 female mortality	0.54	Nilsson (2013)
Female annual mortality after age 5	6.6	Bischof et al. 2009, table 2
SD _{EV} in female mortality after age 5	0.59	Nilsson (2013)
Male mortality from age 0 to 1	35	Swenson et al. 2001
SD _{EV} in 0 to 1 male mortality	27.6	Nilsson (2013)
Male mortality from age 1 to 2	8.6	Bischof et al. 2009, table 2
SD _{EV} in 1 to 2 male mortality	6.5	Nilsson (2013)
Male mortality from age 2 to 3	18.3	Bischof et al. 2009, table 2
SD _{EV} in 2 to 3 male mortality	6.6	Nilsson (2013)
Male mortality from age 3 to 4	18.3	Bischof et al. 2009, table 2
SD _{EV} in 3 to 4 male mortality	3.3	Nilsson (2013)
Male mortality from age 4 to 5	18.3	Bischof et al. 2009, table 2
SD _{EV} in 4 to 5 male mortality	1.6	Nilsson (2013)
Male annual mortality after age 5	10.7	Bischof et al. 2009, table 2
SD _{EV} in male mortality after age 5	0.96	Nilsson (2013)
Expected annual growth rate (λ) based on the data above	1.145	

Results

The criterion $N_e \geq 500$ yielded MVP estimates of 2250 and 2350, without (Figure 3) and with catastrophes, respectively (Table 3). The population size required to maintain > 95% heterozygosity in 100 years was estimated to be 380 without catastrophes and 400 with catastrophes (Figure 4; Table 3). These MVP-values did not change when simulations were performed with reduced reproduction rates for 3–5 year-old males. Extinction did not occur in any of the simulations.

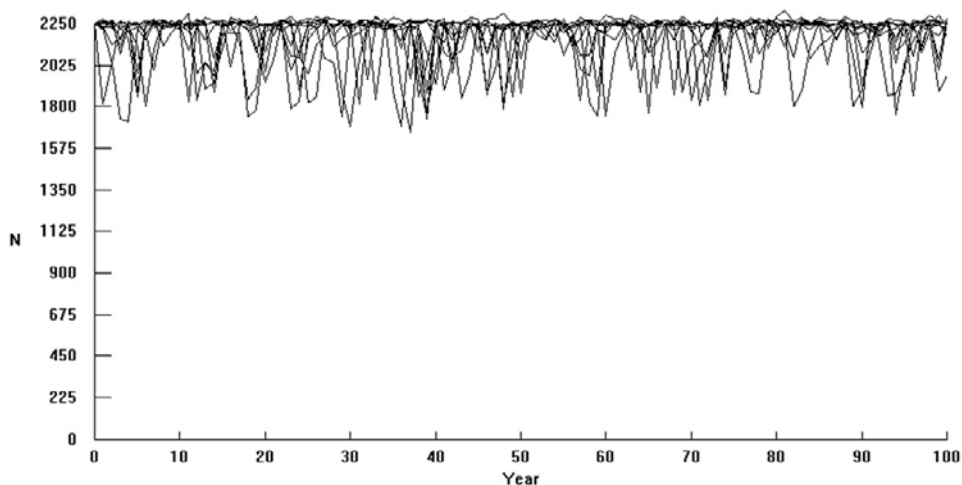


Figure 3. A demonstration of how population size (N) may fluctuate over 100 years in the simulations without catastrophes.

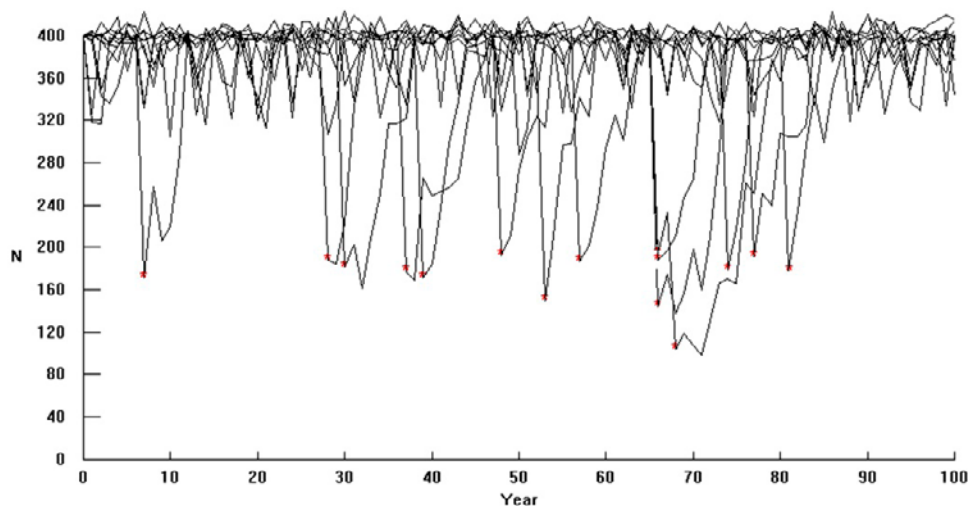


Figure 4. VORTEX simulation showing how a Scandinavian brown bear population with $N_0 = 400$ can fluctuate during 100 years when affected by catastrophes. Stars (*) indicate when a catastrophe has occurred.

Table 3. Population sizes required to meet the Minimum Viable Population (MVP) criteria $N_e \geq 500$ and > 95% remaining heterozygosity in 100 years, respectively, with and without catastrophes. In the final simulations, we ran 10000 replicates to assess the MVP with > 95% heterozygosity retained in 100 years, and 2500 replicates to assess $N_e \geq 500$. SD is the standard deviation in the remaining heterozygosity (H) after 100 years among the replicates. Population extinction did not occur in any of the simulations ($P_{ext} < 0.0005$ during 100 years).

	> 95 % of H in 100 years	$N_e \geq 500$
Without catastrophes	≥ 380 (Average remaining $H_{100} \pm SD = 0.9500 \pm 0.0088$)	≥ 2250 (Average remaining $H_{100} \pm SD = 0.9911 \pm 0.0007$)
With catastrophes	≥ 400 (Average remaining $H_{100} \pm SD = 0.9504 \pm 0.0091$)	≥ 2350 (Average remaining $H_{100} \pm SD = 0.9911 \pm 0.0008$)

Discussion

From a genetic perspective, a well-established goal for long-term population viability is an effective population size (N_e) of ≥ 500 (Franklin 1980). Our analyses indicated that a minimum population size of 2350 was required to meet this criterion with the demographic rates for the southern brown bear population with catastrophes. To retain more than 95% of the heterozygosity in 100 years, on the other hand, the Scandinavian bear population must have a minimum of 400 individuals. Both MVP values assume an approximately stable age distribution in the population.

The noticeable difference between our bear MVP estimates (2350 and 400) and those in Nilsson's (2013) report (6838 and 1100, respectively) is explained by the change of one particular parameter, male reproductive success, as predicted e.g. by the model sensitivity analyses by Nilsson (2013). This illustrates the impact of male reproductive success on the MVP estimates. The expected annual population growth rate (λ) was estimated at 1.142 in Nilsson's report ("Base scenario") and 1.145 using our data. No population extinction occurred at the population levels for the genetic MVP estimates, either in his simulations or in ours.

The reproductive success estimated by Nilsson originates from an empirically measured change in genetic variation (Tallmon et al. 2004). This change might have been unrepresentative due to sampling error. In the study population of approximately 700 bears, Tallmon et al.'s sample in the first generation ($n_1 = 22$) was not large and may have suffered from sampling bias to a much greater extent than the second sample ($n_2 = 127$), taken 14–16 years later. We cannot exclude the possibility that the heterozygosity of the 22 sampled bears may have been biased high. Tallmon et al.'s (2004) study would have produced more reliable results if the first genetic sample also had included in the order of 100 individuals and not merely 22.

Our supplementary analyses with reduced reproduction rate (25% and 50%) for young males (age 3–5) did not have a noticeable effect on the MVP values. This indicates that despite the fact that some males might have resided outside the study area, which might yield an over-estimated reproductive rate for young males (3–5 years old), such young males' reproduction did not have a strong effect on the genetic MVP estimates.

Immigration – gene flow

The results of Manel et al. (2007; their Fig. 6b) indicate that long-range dispersal by some individual bears may occur within Scandinavia, but Kopatz et al. (2014; their Fig. 4b) found no bears with Finnish or Russian genetic characteristics (putative migrants) in Scandinavia ($n = 181$). We thus modeled the Scandinavian bear population as having no immigration from more eastern populations.

Using 12 microsatellite markers, Schregel et al. (2012) reported that bears from Västerbotten (Sweden) had lower heterozygosity ($\bar{H}_{obs} = 0.69$) than conspecifics from Troms (0.74), Pasvik (0.80) and Karelia (0.78). The F_{ST} -values (averaged over loci) among the bear populations in their study were $0.091^{**} \leq F_{ST} \leq 0.12^{**}$ suggesting moderate genetic connectivity. But Schregel et al.'s

Bayesian analysis (BayesAss), on the other hand, indicated ongoing limits to gene flow towards the west, and the existence of barriers to migration between the eastern and western brown bear populations of Northern Europe. F_{ST} values require many generations to approach an equilibrium situation and also exhibit great sampling error. Whitlock & McCauley (1999; their Fig. 3) showed that at effective population sizes of 100–1000 and a migration rate $0.001 \leq m \leq 0.01$ (i.e. combinations ranging from 0.1 to 10 genetically effective migrants per generation; cf. Mills & Allendorf 1996), from 100 to more than 1000 generations is required for equilibrium. And the generation time of the Scandinavian bears is 11 years (Nilsson 2013). Thus, we think the above F_{ST} values should be interpreted with caution and are likely to reflect the past, rather than the present, situation.

A similar study on the North-European lynx (*Lynx lynx*; Hellborg et al. 2002) demonstrated slightly higher F_{ST} values ($0.136^{***} \leq F_{ST} \leq 0.291^{***}$) and also that clustering based on Nei's genetic distance D classified the Scandinavian and the Finnish-Baltic lynxes as two distinct groups. Schregel et al. (2012) did not present any neighbor-joining analysis but their Figure 3 (PCA) and Table 5 (Bayesian analysis) indicated a similar overall pattern as in Hellborg et al. (2002). Therefore, we believe it is more cautious to view the Scandinavian bears as not being coherent with the more eastern North European populations at present. Thus, we view our modeling results as applying to the Scandinavian rather than to a Fennoscandian or pan-North-European population.

Demographic vs. genetic MVP estimates

Regarding the choice of MVP value in relation to criteria for assessment of Favourable Reference Population (FRP; Evans & Arvela 2011, Laikre et al. 2009) for the Scandinavian bears, it is important to consider that 100 years cover only 9 bear generations. Thus, using a MVP that quantifies loss of heterozygosity during 100 years is not enough to evaluate long-term viability. For the Scandinavian bears, we therefore consider the $N_e \geq 500$ criterion is more appropriate for the FRP assessment. This will also help conserve the genetic characteristics of the population to a larger extent (cf. Schregel et al. 2012).

The large difference between the estimated MVP values presented in this report compared to those presented by Nilsson (2013) demonstrates that accurate knowledge about male reproductive success may also be important when estimating genetic MVPs. For this assessment of the Scandinavian bears, we chose a precautionary approach, using the demographic data from the southern part of the population, which had lower average male reproductive success (Zedrosser et al. 2007) and the MVP-values of which also applied to the bears in the northern part (Nilsson 2013). Future research – e.g. within the Scandinavian Bear Project – might investigate this issue further. The analyses and results in this report are based on the best information currently available.

Acknowledgements

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Appendix: Peer-review statements

Dr Sean Hoban (National Institute for Mathematical & Biological Synthesis, University of Tennessee, USA):

The “Complementary analyses of genetic Minimum Viable Population size of Scandinavian bears (*Ursus arctos*)” by Puranen-Li et al. provides a valuable addendum to the full PVA analysis performed by Nilsson. Puranen-Li et al. contribute insightful commentary as well as an additional simulation of viability using different assumptions than those used by Nilsson. This additional simulation results in a revised (downward) estimate of MVP (minimum viable population) size that should be considered along with the main PVA report. The complementary analyses are well-explained, concise, and well-written.

The authors have nicely addressed the critiques from my peer review of the document. Foremost, in response to my principal consideration, the authors included better explanations of parameter choice and more references from other bear reproduction studies. Thus I am more or less convinced that the higher proportion of male reproductive success is plausible and even probable. The analysis of Puranen-Li et al is now very suitable due to these explanations and references.

It is also good that the authors are quite clear about exactly the parameter that was changed (age 3–5 year old males). I think the parameterization is innovative and useful. It is a pity that, regarding my third suggestion, the authors cannot provide a temporal map of the range. But I understand the time constraint, and the Figure is not necessary. It is also a pity that the authors do not perform more modeling of possible catastrophes e.g. from climate-induced fire, disease, or food shortage. It would be highly interesting and important to explore sensitivity of the population to catastrophes. Though I understand this is probably outside the study scope.

I think the section on migration is also quite good, clear and a useful summary, and I appreciate the sentences on research needs, e.g. more accurate estimates via the Scandinavian Brown Bear Project, mentioned in the closing paragraph. A very good conclusion. Overall I’m quite pleased with the result and support final publication of this report. I would categorize it as “very good.”

Dr Torbjörn Nilsson (County Administrative Board of Värmland, Sweden):

This is a well-performed and well-written study. It complements my study (Nilsson 2013) by assessing MVP values for bear in Scandinavia, according to long-term and short-term genetic MVP criteria, in a way that I might have preferred to do it unless an empirical measurement of the rate of heterozygosity loss had been available for one of the subpopulations within Scandinavia.

To my knowledge, the present study may be the first Vortex-based PVA where the annual probability of reproducing in males is modeled as a function of age. This is interesting as a demonstration of the increased flexibility of the more recent versions of the PVA package Vortex. Comparing the results between the present study and mine is interesting because the difference clearly illustrates how strong effect the proportion of males taking part in reproduction may have on the rate of loss of heterozygosity, and hence also on the N_e/N ratio and on genetic MVP values. This supports and reinforces one of the conclusions from the sensitivity analyses in my study. I agree with the general conclusion in the present report that knowledge about how reproductive success is distributed among males may be important when estimating genetic MVPs.

At the same time, **I disagree with the claim that the results of the present report would be based on the best information currently available.** The present modeling study disregards the empirical results found by Tallmon et al. (2004), and I think the arguments for this disregarding are weak. The authors of the present study argue that the first sample analyzed by Tallmon et al. was small ($n = 22$). However, the uncertainty caused by small sample sizes is described by estimating confidence intervals (CI). The upper 95 % CI for N_e presented by Tallmon et al. were 73.2 or 117.2, if the time between the genetic samples was one or two generation times, respectively. Interpolating between these values and calculating in the same way as in Table 7 of Nilsson (2013) yields $N_e = 87$, $N_e/N = 0.1243$, and long-term MVP = 4023. Hence, the MVP values estimated in the present study are not only far lower than those stemming from the estimates of Tallmon et al., but also much lower than the lowest MVP that can be calculated from the confidence intervals presented by Tallmon et al.

There are several biological reasons to suspect that the present study may underestimate the rate of heterozygosity loss, and therefore also may underestimate the genetic MVP values:

- The proportion of males taking part in reproduction was here taken from data collected within core areas where sex ratio is approximately even, without accounting for the fact that a certain fraction of male bears reside in peripheral areas where few females are found.
- A male bear reproducing in one year probably has a higher chance of reproducing also the following year, and then over a series of years the proportion of males taking part in reproduction will be lower than if mating success in one year were random with regard to mating success in previous years.
- Among male bears within core areas, and also among those actually taking part in reproduction a certain year, the distribution of reproductive success may be more than randomly uneven, e.g. due to a correlation with body size (cf. Zedrosser et al. 2007).

For these reasons, I think my MVP estimates based on the available empirical measurement of heterozygosity change are still the MVPs that best reflect the information currently available.

In this statement, I assume that the genetical and statistical methodology applied by Tallmon et al. were correct. Neither the authors of the present study, nor Swenson & Kindberg (2013) who previously criticized my approach, have demonstrated that there would be anything erroneous in the genetical or statistical procedures used by Tallmon et al. The best way to resolve this issue would probably be to repeat the study of Tallmon et al. with a new and larger sample from the same subpopulation.

Prof. Jon Swenson (Norwegian University of Life Sciences) & Dr Jonas Kindberg (Swedish University of Agricultural Sciences):

We are pleased that the Swedish Environmental Protection Agency followed our advice and repeated the Minimum Viable Population (MVP) Analysis in a supplementary report by Puranen-Li et al. (2014), using the paternity rates published in Zedrosser et al. (2007, *J. Anim. Ecol.*) and the additional information we provided. We note that following our recommendations changed the long- and short-term Minimum Viable Populations, as defined in the original report by Nilsson (2013), dramatically.

We do not have any specific comments on the report by Puranen-Li et al. (2014), other than we feel much more confident about using the best available empirical data and knowledge about the distribution of bears in Sweden to estimate MVPs, which Puranen-Li et al. (2014) did in their report.

Complementary analyses of genetic Minimum Viable Population size of Scandinavian bears (*Ursus arctos*)

REPORT 6644

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The authors assume sole responsibility for the contents of this report, which therefore cannot be cited as representing the views of the Swedish EPA.

Denna rapport är ett av de vetenskapliga underlagen inom Naturvårdsverkets bedömning av referensnivån (FRP) för björn i artikel-17-rapporteringen 2013. Rapporten är skriven på engelska och redovisar kompletterande analyser av den skandinaviska populationen av björn för att bedöma minsta livskraftiga populationsstorlek i relation till två olika genetiska kriterier.

Analyserna gjordes med datorsimuleringar baserade på data från tidigare sårbarhetsanalyser (Rapport 6549) och med ny modellering av björnhannars reproduktionsframgång, och undersökte hur snabbt den skandinaviska björnstammen förlorar genetisk variation vid olika populationsstorlekar och utan invandring från östligare björnbestånd.

This is one of the scientific reports underpinning the Swedish Environmental Protection Agency's Article-17 reporting in 2013 of Favourable Reference Population for the brown bear in Sweden. It presents complementary population viability analyses of the Scandinavian population of brown bear (*Ursus arctos*) to quantify minimum viable population size (MVP) estimates in relation to two criteria for genetic viability.

The analyses were based on simulations without immigration, using demographic data from empirical studies of the Scandinavian population also used in a previous SEPA report (6549), but with updated scientific data on the reproductive success of male bears.

