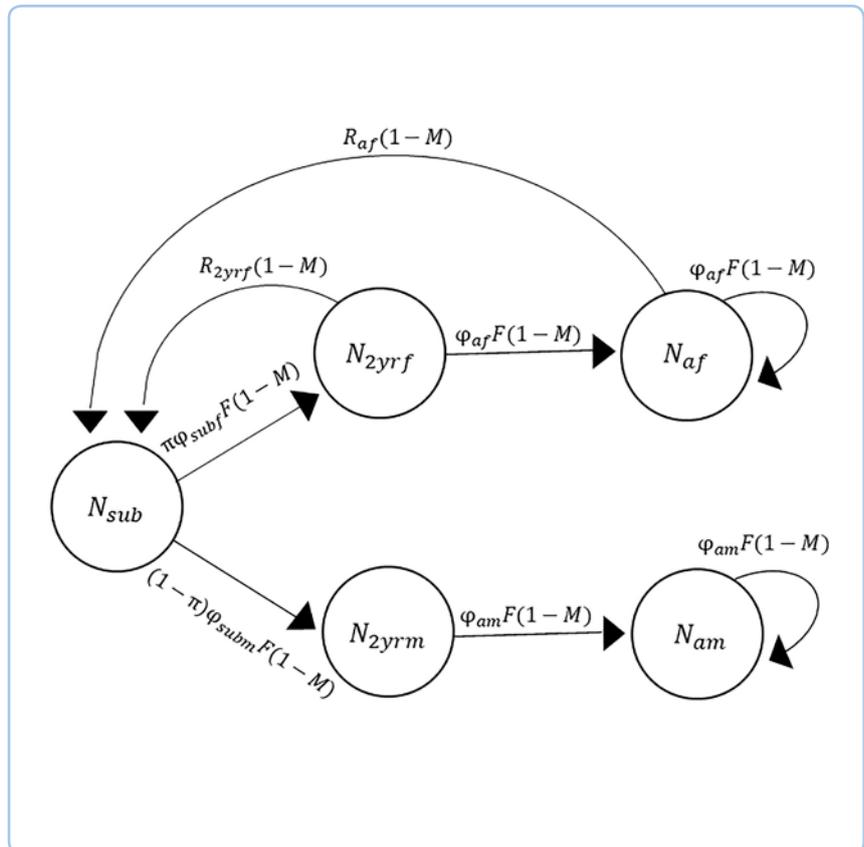


Bayesian Population Viability Analysis for Lynx and Wolverine in Scandinavia

L. SCOTT MILLS, MARK HEBBLEWHITE AND DANIEL R. EACKER

REPORT 6793 • NOVEMBER 2018



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L. Scott Mills, Mark Hebblewhite and Daniel R. Eacker

SWEDISH ENVIRONMENTAL
PROTECTION AGENCY

Order

Phone: + 46 (0)8-505 933 40

E-mail: natur@cm.se

Address: Arkitektkopia AB, Box 110 93, SE-161 11 Bromma, Sweden

Internet: www.naturvardsverket.se/publikationer

The Swedish Environmental Protection Agency

Phone: + 46 (0)10-698 10 00, Fax: + 46 (0)10-698 16 00

E-mail: registrator@naturvardsverket.se

Address: Naturvårdsverket, SE-106 48 Stockholm, Sweden

Internet: www.naturvardsverket.se

ISBN 978-91-620-6793-9

ISSN 0282-7298

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Print: Arkitektkopia AB, Bromma 2018

Cover photos: Wikimedia, Wiktionary



Preface

This report is written by professor L. Scott Mills (Principal Investigator of the project), professor Mark Hebblewhite (co-PI) and research-associate Daniel R. Eacker (programmer, statistician) at University of Montana (USA). The Swedish summary was written by Per Sjögren-Gulve at the Swedish Environmental Protection Agency (SEPA) and was translated into Northern Sami by Miliana Baer (Vájal Gielain AB). The report has been peer reviewed by Veronica Sahlén (Norwegian Environment Agency), Alexander Winiger (County Administrative Board of Norrbotten, Sweden), and two anonymous reviewers. It presents the results of population viability analyses of lynx and wolverine in Scandinavia and also of sensitivity analyses of the population models.

The SEPA and the report authors thank Per Sjögren-Gulve for coordinating the peer review and production of the report, and for guidance and oversight during development of these PVA models, providing data, and reports, as well as Henrike Hensel, and Peter Jaxgård, from the Wildlife Damage Centre of the Swedish University of Agricultural Sciences for assistance collating lynx harvest data. Comments from expert reviewers greatly helped improve the final version of this report. Photos of lynx and wolverine were reproduced here under the Creative Commons Attribution 3.0 Unported license and the Attribution-NonCommercial-NoDerivs 2.0 Generic, respectively.

The authors assume sole responsibility of the report and its conclusions. The SEPA thanks all who have taken part and contributed in the work.

Stockholm, November 2018

Maria Hörnell Willebrand
Head of Wildlife Analysis Unit,
The Swedish Environmental Protection Agency

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Sammanfattning

Rapporten redovisar en demografisk sårbarhets- och känslighetsanalys av lodjur och järv i Skandinavien. Naturvårdsverket önskade att analyser genomförs av effekterna på arternas populationsutveckling och -tillväxt av bland annat olika förvaltningsåtgärder kopplade till jakt i Sverige och Norge, samt effekter av spridning mellan länderna, inavelsdepression samt av täthetsberoende tillväxt. Känslighetsanalysen innebär man med modellsimuleringar undersöker vilka förändringar i individernas överlevnad, reproduktion och/eller spridning mellan länderna som påverkar populationens eller delbeståndens årliga ökningstakt mest.

Mills, Hebblewhite och Eacker gjorde översikter av publicerade vetenskapliga artiklar och rapporter, och utformade populationsmodellerna baserat på mer än 30 olika studier. De integrerade data från dokumenterade årliga resultat från skydds- respektive licensjakt i Sverige och Norge från åren 2011–2017, och använde även data från de årliga beräknade beståndsstorlekarna i de två länderna enskilt och tillsammans. Modellernas projektioner gjordes med fokus på de nästkommande 20 åren, vilket motsvarar cirka tre generationer av lodjur och järv demografiskt.

Baserat på de demografiska data för lodjur samt förvaltningen åren 2011–2017 blev det geometriska medelvärdet av den årliga populationstillväxten (λ_G) 1,03 i Sverige, dvs. under liknande förvaltning förväntas i genomsnitt en svag populationsökning med ca. 3% per år (konfidensintervall för $\lambda_G = 0,98$ – $1,08$). I Norge blev λ_G i genomsnitt 1,01 (med större konfidensintervall, 0,89–1,11). Givet samma överlevnad, reproduktion och förvaltning, och projicerat framåt, förväntas lodjuret öka något i Sverige med i genomsnitt cirka 5% per år och med cirka 6% per år i Norge. Givet ett modell-scenari med strikt skydd i Sverige förutspådde modellen att lodjuret ökar med i genomsnitt cirka 10% per år i både Sverige och Norge. Med dagens förvaltning indikerar modellens resultat att det är mycket sannolikt att det svenska lodjursbeståndet kommer att vara större än populationsreferensvärdet för gynnsam bevarandestatus (Favourable Reference Population ≥ 870 lodjur) i Sverige under de närmaste 20 åren. Modellen indikerade också att med större beskattning än 10% eller mer än 160 per år i Sverige under samma tidsperiod, ökar risken betydligt för att beståndet blir mindre än 870 lodjur.

I känslighetsanalysen sågs ingen mätbar effekt av inavelsdepression, troligen eftersom det svenska lodjursbeståndet är ganska stort och 20 år (ca. tre lodjursgenerationer) är en kort tidsperiod. Modelleringen indikerade att den gynnsamma bilden ovan starkt kan påverkas av täthetsberoende (resursbrist) som påverkar vuxna lodjurshonors överlevnad negativt. Resultaten indikerar potentiellt starkt negativa effekter på de skandinaviska lodjurens populationstillväxt av illegal jakt och av s.k. source-sink-dynamik där individer sprider sig till andra områden där dödligheten är betydligt högre, naturligt eller genom jakt. Starkast effekt sågs här av individers spridning från Sverige till Norge.

I känslighetsanalyserna kopplade till överlevnad, reproduktion och spridning hos de svenska lodjuren (av båda könen), så hade ortstrohet – dvs. att lodjuren inte sprider sig från Sverige till Norge – störst och mycket stark effekt på beståndstillväxten. Därefter var de vuxna lodjurshonornas årliga överlevnad näst viktigast, och därefter överlevnaden av subadulta honor till vuxen ålder samt överlevnaden bland subadulta honor.

För järv blev den genomsnittliga årliga populationstillväxten (λ_G) 1,01 (konfidensintervall 0,94–1,07) i Sverige och negativ för det norska beståndet ($\lambda_G = 0,91$; intervall 0,83–0,98) under åren 2011–2017. Framåtprojektion under samma betingelser förutspår i genomsnitt ungefär oförändrad beståndsstorlek i både Sverige och Norge ($\lambda_G = 1,0$). Med strikt skydd i Sverige men inte i Norge, förutspås en ungefär 3-procentig beståndsökning i genomsnitt per år i båda länderna. Med liknande järvförvaltning som under 2011–2017 under de närmaste 20 åren förutspås en 60-procentig sannolikhet att beståndet i Sverige blir större än 600 järvar. Med strikt skydd i Sverige men oförändrad järvförvaltning i Norge blir den sannolikheten 80 %.

Liksom för lodjur indikerar känslighetsanalyserna att järvens populationstillväxt påverkas starkt av beskattningen i Norge samt av illegal jakt. Populationstillväxten påverkas främst av den årliga överlevnaden av unga honor till att bli vuxna, därefter av järvarna ortstrohet (att ej sprida sig från Sverige till Norge) samt av de vuxna honornas årliga överlevnad. Ungdjurens årliga överlevnad, liksom de vuxna hannarnas, hade endast liten påverkan.

Slutsatserna från analyserna är att livskraften (population viability) hos bestånden av lo och järv i Sverige mest påverkas av beskattningen (i båda länderna), spridningen till Norge och ”source-sink”-effekten som den innebär, samt av illegal jakt. Analyserna indikerade inte några betydande effekter av inavelsdepression under de närmaste 20 åren. Det behövs mer kunskap om eventuella effekter av täthetsberoende på populationstillväxten hos båda arterna.

För att uppnå och bibehålla gynnsam bevarandestatus – dvs. ha en beståndsstorlek som minst motsvarar referensvärdet FRP – för arterna i Sverige rekommenderar författarna att jakt sker endast när beståndet är större än referensvärdet samt är proportionell (% av aktuellt bestånd) eller en bestämd kvot (”fixed quota harvest”). Författarna betonar båda arternas känslighet för illegal jakt och att sådan tillsammans med legal beskattning även i modest omfattning kan få bestånden att minska. Givet den stora effekten på populationstillväxten av spridningen av lodjur liksom järv mellan Sverige och Norge, och vice versa, samt påverkan på den svenska beståndstillväxten av beskattningen i Norge, så rekommenderas fortsatta ansträngningar att integrera och samordna rovdjursförvaltningen länderna emellan och särskilt längs landsgränsen. Då alla simulerings- och modellresultat liksom förvaltningen beror av noggranna populationsberäkningar rekommenderar författarna fortsatt samarbete mellan Norge och Sverige för garanterat samordnad beståndsovervakning, särskilt i ländernas gränsområden.

Rörande analyserna, så användes s.k. ”Bayesian Integrated Population Models” (IPM) som är stadiebaserade, dvs. individerna i den skandinaviska populationen har för varje art delats upp i grupper efter kön och åldersstadium [t.ex. ungdjur (subadult), reproducerande vuxen, icke-reproducerande vuxen] i respektive land samt med överföring (spridande individer) mellan delbestånden i Sverige och Norge. Modellerna konstruerades i open-source-språket R (R Core Team 2016). Även en app baserad på R:s shiny-paket (Chang m.fl. 2017) finns tillgänglig ”open access” på Internet. Den årliga överlevnaden och fortplantningen av individerna i de olika stadierna och den årliga övergången (andel av individerna) från ett stadium till ett annat, liksom mellanårsvariationen i dessa parametrar, simuleras genom en populations-matrismodell som tillsammans med individerna som finns i de olika stadierna projiceras över de år som simuleras. De årliga överlevnads- och reproduktionstalen i modellen, liksom förflyttningen av individer mellan Sverige och Norge och vice versa, baseras på sammanställda publicerade data. Jakt påverkar överlevnaden hos de stadier som berörs, och i den utsträckning som könsmogna honor fälls så påverkar det även beståndets reproduktion. Beståndens sociala struktur medför att en hane kan fortplanta sig med flera honor under ett år och hannarna antas därför inte begränsa populationens reproduktion. Inavelsdepression tar sig uttryck som reducerad reproduktion eller minskad överlevnad i den modellerade populationen på grund av att den är inavlad och individerna är nära släkt med varann, och sänker den årliga populationstillväxten. Likaså kan resursbrist på grund av att det finns så många individer (täthetsberoende) påverka den lokala och/eller totala populationstillväxten.

Čoahkkáigeassu

Rapporta čilge demográfalaš rašes- ja hearkkesvuodaanalysa albasiin ja getkkiin Skandináviás. Luondogáhttendoaimmahat háliidii ahte analysat čadahuvvojedje váikkuhusain šlájaid populašvudnaovdáneamis ja – šaddamis earret iežá sierra hálddahušbijut čadnon bivdui Ruotas ja Norggas, ja maid váikkuhusat leavvamiin riikkaid gaskkas, deprešuvdna go lea sagaheapmi ealibiin mat leat ila lahka sogat ja maid valljodatsorjavaš (täthetsberoende) šaddan. Hearnkesvuodaanalysa mearkkaša ahte modeallastimuleremiiguin iskkat makkár rievdadusat indiviidaid birgemis, laskamis ja/ dahje leavvan riikkaid gaskkas váikkuha populašuvnna dahje oassemáddodaga jahkásaš lassánantávta eanemusat.

Mills, Hebblewhite ja Eacker ráhkadedje oppalašgeahčastaga almmuhuvvon diedalaš artiikkaliin ja raporttain, ja hábmejedje populašuvnamodeallaid vuodđuduvvon eanet go 30 sierra iskamiin. Sii integrerejedje dieđuid dokumenterejuvvon jahkásaš bohtosiin suodje- ja liseansabivdduin Ruotas ja Norggas jagiin 2011–2017, ja geavahedje maid dieđuid daid jahkásaš rehkenaston máddodatsturodagain daid guokte riikkain sierra ja ovtta. Modeallaid projekšuvnna dahkojedje deattuin daid boahte 20 jagiide, mii vástida sullii golbma albbas- ja geatkebuolvva demográfalaččat.

Vuodđuduvvon demográfalaš dieđuid vuodul albasiidda ja maid hálddahuš jagiin 2011–2017 geometralaš gaskamearalaš árvu dan jahkásaš populašvudnašaddadeapmái šattai (λ_G) 1,03 Ruotas, namalassii sullasaš hálddahušas vurdojuvvo gaskamearalaččat geahnohis populašvudnalassáneapmi sullii 3% jahkái (konfideansainterválla $\lambda_G = 0,98–1,08$). Norggas šattai λ_G gaskamearalaččat 1,01 (stuorit konfideansaintervállain, 0,89–1,11). Addon seamma birgema, laskama ja hálddahuš ja projiserejuvvon ovddusguvlui, vurdojuvvo albbas lassánit veaháš Ruotas gaskamearalaččat 5% jahkái ja sullii 6% jahkái Norggas. Jus addo modealla-scenario nanu sujiin Ruotas einnostedje modeallain ahte albbas lassána gaskamearalaččat sullii 10% jahkásaččat sihke Ruotas ja Norggas. Otná hálddahušain modealla boadus indikere ahte lea stuorra vejolašvuohta ahte ruota albbasmáddodat boahťá leat stuorit go populašvudnarefereansaárvu oiddolaš seailluhanštáhtusii (Favourable Reference Population ≥ 870 lodjur) Ruotas daid lagamus 20 jagiid. Modealla indikere maid ahte stuorit vearromáksin go 10% dahje eanet go 160 jahkái Ruotas seamma áigodagas, várra lassána sakka ahte máddodat šaddá unnit go 870 albasa.

Hearnkesvuodaanalysas ii oidnon mihtideaddji váikkuhus deprešuvnna go ila lahka sogat sagahit, jáhkehahti danne go ruota albbasmáddodat lea oalle stuora ja 20 jagi (sullii golbma albbasbuolvva) lea oanehis áigeáigodat. Modelleren indikerii ahte dat oiddolaš govva bajil garrasit sáhtta váikkuhuvvot valljodatsorjavašvuodas (resursavátni) mii sakka váikkuha ráves albasciikkuid birgema heittot.

Boadus indikere vejolaš garra negatiiva váikkuhusaid daid skandinávalaš albasiid populašvudnašaddamii lobihis bivddus ja n.g. source-sink-dynamik gos indiviida leavvá iežá guovlluide gos jápmin lea ollu alibut, lunddolaš dahje bivddu bokte. Stuurimus váikkuhus oidnui dás go indiviidat levvet Ruotas Norgii.

Hearnkesvuodaanalysat čadnon birgemii, laskamii ja leavvamii ruota albasiin (goappaš sohkebalelit), de báikebissun – namalassii ahte albasat eai leava Ruotas Norgii – lea stuurimus ja oalle stuorra váikkuhus máddodatšaddamii. Dan maññil leai ráves

albasciikkuid jahkásaš birgen nubbin deháleamos, ja dan maññil birgen subadulta ciikkuin ráves ahká ja maid birgen subadulta ciikkuin.

Geatkái gaskamearalaš jahkásaš populašuvdnašaddan (λ_G) 1,01 (konfidensintervála 0,94–1,07) Ruotas ja negatiiva norgga máddodahkii ($\lambda_G = 0,91$; intervála 0,83–0,98) jagiid 2011–2017. Einnosteapmi ovddusguvlui oaidná gaskamearalaččat sullii rievdatkehtes máddodaga sihke Ruotas ja Norggas ($\lambda_G = 1,0$). Go lea nanu suodji Ruotas muhto i Norggas, einnostuvvo sullii 3-proseantta máddodatlaskan gaskamearalaččat jahkái goappaš riikkain. Sullasaš geatkehálddahusain dego jagiid 2011–2017 daid lagamus 20 jagiid einnostuvvo 60-proseanta vejolašvuolta ahte máddodat Ruotas šaddá eanet go 600 geatkki. Muhto nanu sujiin Ruotas ja rievdatkehtes geatkehálddahus Norggas šaddá jáhkehahtti 80%.

Dego albasiidda hearckesvuodaanalysa indikere ahte geatkki populašuvdnalaskan váikkuhuvvo sakka vearromáksimis Norggas ja maid lobihis bivddus. Populašuvdnalaskan váikkuhuvvo eanemusat dan jahkásaš birgemis nuorra ciikkuin ja dan maññil geatkki báikebissumii (ahte eai vuolgge Ruotas Norgii) ja maid ráves ciikkuid jahkásaš birgen. Nuorra ealibiid jahkásaš birgen, dego ráves rávjáid, váikkuhii dušše veaháš.

Loahppaboadus analysain lea ahte eallinfápmu (population viability) albasiid ja getkkiid máddodagas eanemus váikkuhuvvo vearromáksimis (goappaš riikkain), leavvan Norgii ja "source-sink"-váikkuhusas maid dat máksá, ja maid lobihis bivddus. Analysat eai indikere makkárge mearkašahtti váikkuhusaid deprešuvnnas go ila lahka sogat sagahit daid lagamus 20 jagiin. Lea dárbu eanet dieđuide vejolaš váikkuhusain sorjjavašvuhtii galle ealibat leat ovttá guovllus ja populašuvnnašaddamis goappaš šlájain.

Jus galgá ollašuttit ja doalahit oiddolaš seailluhanstáhtusa – namalassii doallat máddodatsturodaga mii unnimusat vástida referánsaárvvu FRP – šlájaid Ruotas čállit ávžžuhit ahte galgá dušše bivdit go máddodat lea stuorit go refereansaárvvu ja lea proporšunála (% áigequovdilis máddodagas) dahje mearriduvvo eari mielde ("fixed quota harvest"). Čállit deattuhit ahte šlájaid hearckesvuolta lobihis bivdui ja dakkár bivdu ovttas lágalaš vearromáksiimiin oalle unna logut sáhttet dagahit njeaidima máddodagain. Go lea ožžon dan stuorra váikkuhusa populašuvnnašaddamii albasiid ja getkkiid leavvamis Ruota ja Norgga gaskkas, ja nuppos, ja maid váikkuhus dan Ruota máddodahkii go lea vearromáksin Norggas, de ávžžuhuvvo ahte joatkašuhtti rahčamušat integreret ja ovttastahttit meahcceallehálddáhusa riikkaid gaskal ja erenoamážit riikarájiid mielde. Go visot simuleren- ja modeallabohtosat ja maid hálddahus leat čadnon dárkilis populašuvnnaárvvostallamiidda ávžžuhit čállit ahte ovttasbargu Norgga ja Ruota gaskkas joatká dáhkidan dihte ovttastuvvon máddodatbearráigeahču, erenoamážit riikkaid rádjeguovlluin.

Mii guoská analysa geavahuvvui ng. "Bayesian Integrated Population Models" (IPM) mii lea vuodđuduvvon muttuid mielde (stadiebaserad), namalassii indiviidat dan skandináválaš populašuvnnas leat juohke šlájii juhkkjuvvon joavkkuide, sohkabeali ja ahkedási mielde [omd.), nuorraealibat (subadult), reproduserejeaddji ráves ealit, ráves ealit mii ii reprodusere] iešguđet riikkain ja maid sirdin (indiviiddat mat levvet) gaskal oassemáddodagas Ruotas ja Norggas. Modeallat leat ráhkaduvvon open-source-gillii R (R Core Team 2016). Ja maid App vuodđuduvvon R:s shiny-báhkke (Chang ja earát 2017) lea vejolaš "open access" Internehtas. Dat jahkásaš birgen ja laskan indiviidain dain sierra muttuin ja jahkásaš rasten (oassi indiviidain) ovttá muttus nubbái, dego rievdadusat jagiid gaskkas daid paramehtariin, simulerejuvvo populašuvdna-matrismodeallas mii

ovttas indiviiddaiguin mat leat daid sierra muttuin projiserejuvvojit dan jagi miehtá mii simulerejuvvo. Dat jahkásaš birgen- ja laskanlogut modeallas, dego sirdimat indiviiddain Ruota ja Norgga gaskkas ja nuppos, leat vuodđuduvvon čohkkehuvvon almmuhuvvon dieđuid vuodul.

Bivdu váikkuha birgema dain muittuin mat váikkuhuvvot, ja nu guhkás go ciikkut mat leat álgán gieibmit goddojuvvo de dat maid váikkuha máddodaga laskama. Máddodagaid sosiála struktuvra mielddisbuktá ahte rávjá sáhtta laskat máŋga ciikkuiguin ovttá jagis ja rávjját eat danne oaivvilduvvot ráddjet populašuvnna laskama. Deprešuvdna go ıla lahka sogat sagahit boahtá oidnosii go lea binnun laskan dahje unnun birgen modellerejuvvon populašuvnnas dan siva dihte go indiviidat leat ıla lahka sogat guhte guimmiiguin, ja dáinna vuolidit dan jahkásaš populašuvnnašaddadeami. Maid váilevaš návccat go lea ıla ollu indiviidat (valljodatsorjavašvuohta) váikkuha báikkálaš ja/dahje ollislaš populašuvnnašaddama.

Summary

This project was motivated by a Swedish Environmental Protection Agency (SEPA) wish to evaluate population viability and effects of management actions on lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) in Sweden. Given concerns about potential risk of further decline for these species, and that the lynx declined significantly from 2011 to 2014 and the wolverine from 2012 to 2016, SEPA wanted a demographically-explicit model that could evaluate the effect of management-related actions (including human-caused mortality) on population dynamics and viability. Ultimately, the goal is to contribute to these species being maintained in favorable conservation status in Sweden as required under the European Union (EU) Habitats Directive. Specifically, we were tasked by SEPA to conduct a demographic population viability analysis (PVA), including inbreeding depression, for both lynx and wolverine in the main Scandinavian peninsula with a focus on Sweden.

We developed a flexible Bayesian integrated population model (IPM) to model lynx and wolverine population dynamics using a sex-specific model with 5 stage classes. Bayesian models lend themselves well to conducting population viability analyses (PVAs) as they are flexible, can integrate different data types, account for demographic and environmental stochasticity, and provide results in the form of posterior probabilities of key quantities such as abundance and probability of extinction. We conducted a literature review of published scientific papers and government reports to construct prior distributions for the model, drawing on over 30 studies to obtain parameter estimates for sex- and stage-structured vital rates for Norway and Sweden. We also integrated information from known/reported legal and protective harvest for both lynx and wolverine from the period of 2011–2017 in databases provided by SEPA to understand population trends in a retrospective sense immediately prior to 2017. To anchor population projections both retrospectively and under future scenarios, we used previously published population estimates from the Large Carnivore Initiative for Europe (LCIE) documents for the year 2011. We developed the Bayesian IPM to accommodate different types of harvest, as well as cryptic poaching, potential classic ‘negative’ density-dependence, inbreeding depression, and source-sink dynamics between Norway and Sweden. Our Bayesian IPM was developed in the open-source programming language R (R Core Team 2016), and we developed an easy-to-use Application Program Interface (API) based on the shiny package in R (Chang et al. 2017). Our API not only facilitates our modeling for this project, it also allows flexible and user-friendly modeling of other future scenarios.

We then evaluated the consequences of over 40 different management and ecological scenarios on lynx and wolverine population viability. In addition to tracking abundance under different scenarios, we estimated the probability of the population remaining at or above a specified management-relevant abundance threshold (“quasi-persistence probability”). For example, the

relevant management thresholds we used to track quasi-persistence in Sweden were 870 for lynx and 600 for wolverines, numbers based on previous government publications. In our API, these thresholds can easily be changed as management objectives are updated. We separately considered the following scenarios from a harvest perspective for both lynx and wolverines: 1) status quo with estimates of harvest from literature studies and harvest databases; 2) complete protection for both species in Sweden; 3) varying levels of a constant proportional harvest; 3) varying levels of a fixed quota system of harvest; and 4) threshold harvest with no harvest below the management threshold and either fixed quota or proportional harvest scenarios above the threshold. We then combined the status quo scenarios with: a) inbreeding depression; b) density-dependence in vital rates; c) source-sink dynamics; and d) cryptic poaching with varying levels of unreported and undetected illegal harvest. We used a Monte Carlo Markov Chain (MCMC) sampling algorithm to simulate posterior distributions of parameters given our input parameters (and variances) for each scenario, and report for each scenario the geometric mean population growth rate, abundance, and probability of exceeding the management thresholds (i.e. quasi-persistence probability) in both Sweden and Norway for the next 20 years.

Focusing first on lynx, during the retrospective time period of 2011–2017, the geometric annual population growth rate, λ_G , for lynx was 1.03 (95% Bayesian Confidence Interval, BCI of 0.98–1.08) in Sweden, and lower at 1.01 (95% BCI 0.89–1.11) in Norway, likely because of differential harvest which was higher in Norway. Given status quo vital rates, projecting into the future, Sweden lynx are predicted to experience modest population growth of $\lambda_G = 1.05$ (on average 5% per year; 95% BCI 0.99–1.09) as well as Norway, 1.06 (95% BCI 1.02–1.11). Under the scenario of complete protection, λ_G of lynx are projected to increase to 1.10 (1.04–1.14) in both Sweden and Norway (1.10, 95% BCI 1.05–1.14). Abundances of lynx under complete protection and under exponential growth became unrealistically large in 20 years, highlighting the importance of understanding density dependence in vital rates in the future. Under status quo conditions in Sweden, the probability of there being more lynx than the management threshold of 870 was always near 1.0 over all years (2011–2037).

Considering the harvest scenarios, without a threshold below which harvest is set to zero, only the lowest harvest quota of 80–160 lynx or the lowest proportional harvest scenarios of 0.05–0.10 harvest rate led to stationary or increasing population growth and maintained a high and increasing probability of exceeding the management threshold of 870 lynx. For any proportional harvest > 0.10 or quota > 160 lynx in Sweden, λ_G and abundance decreased, and probability of falling below the management threshold increased. If harvest is eliminated below the threshold of 870, λ_G , abundance, and quasi-persistence probability all stayed stationary or increasing

Next, we report effects of non-harvest factors on population viability of lynx. There were no measurable effects of inbreeding depression on recruitment

rate under a range of scenarios, because abundances were relatively large and the projection interval (20 years) relatively short. Although empirical evidence is lacking from the field, we next modeled 4 different levels of negative density dependence on adult female survival. Only under no density dependence did the population keep increasing in size, where λ_G stayed $\gg 1.0$ and probabilities of quasi-persistence were high.

We found strong effects of source-sink dynamics and cryptic poaching on viability of Sweden's lynx. The viability of Swedish lynx with a quasi-persistence threshold of 870 was strongly influenced by the different modeled scenarios of dispersal rates to and from Norway/Sweden, but was more influenced by increasing dispersal rates from Sweden to Norway. The simulations of increased dispersal from Norway to Sweden had little overall effect on the abundance and quasi-persistence probability for lynx in Norway, but higher immigration from Sweden greatly improved the probability of meeting the management objective for Norway. In the face of even modest levels of additional cryptic poaching (> 0.10 additional harvest rate) in Sweden in addition to status quo levels of harvest, lynx experienced decreased abundance, λ_G and probability of quasi-persistence above 870. This emphasizes the key role of understanding cryptic poaching on lynx and wolverine viability in Sweden.

We also conducted a Bayesian-based, life-stage simulation analysis to investigate sensitivity of λ_G to different vital rates in Sweden. The vital rate that had the highest impact on λ_G was fidelity (1 – probability of emigrating from Sweden to Norway), which had a slope (β) of close to 1 (0.90), and $R^2 = 0.42$ indicating essentially additive effects of emigration from Sweden to Norway on Sweden population growth rate. The next 3 most important vital rates were adult female survival ($\beta = 0.69$, $R^2 = 0.26$), the recruitment rate for adult female lynx ($\beta = 0.19$, $R^2 = 0.20$), and the survival of subadult females ($\beta = 0.24$, $R^2 = 0.07$).

Next, we summarize results for wolverine. Wolverine λ_G was stable or slightly declining between 2011–2017, with $\lambda_G = 1.01$ (95% BCI = 0.94–1.07) in Sweden, but declining in Norway with $\lambda_G = 0.91$ (95% BCI = 0.83–0.98) during the same time period. Projecting into the future showed similar growth rates in Sweden of $\lambda_G = 1.00$ (95% BCI = 0.95–1.06) and in Norway with $\lambda_G = 1.01$ (95% BCI = 0.96–1.02). Under complete protection in Sweden, but not Norway, λ_G in Sweden would be expected to increase to 1.03 (95% BCI = 0.97–1.09), and increase in Norway to 1.03 (95% BCI = 0.97–1.08). Under the status quo management scenario, the probability of exceeding the threshold of 600 wolverines in Sweden was always > 0.60 over the next 20 years, and increases to 0.80 under complete protection in Sweden. Because of the lower threshold, Norway always has a probability of exceeding its threshold of ~ 1.0 . Similar to the lynx harvest scenarios, without a lower threshold, only modest amounts of proportional harvest rates (0.03) or a modest quota (18) maintains $\lambda_G > 1.0$ and a high probability of exceeding 600 wolverines. Again, similarly to lynx, introducing a threshold of no harvest when $N < 600$ stabilizes population growth rates, size, and persistence probabilities. Also

similar to lynx, there were no strong effects of inbreeding depression nor realistic effects of density dependence on wolverine population dynamics and persistence.

As with lynx, population viability of wolverine in Sweden was very sensitive to harvest in Norway and cryptic poaching. Population growth rate of wolverine in Sweden were most sensitive, in rank order, to: recruitment rate of adult females ($\beta = 0.28$, $R^2 = 0.43$), fidelity ($\beta = 0.94$, $R^2 = 0.31$), adult female survival ($\beta = 0.84$, $R^2 = 0.27$), whereas male and female subadult survival, as well as adult male survival had little effect on population growth rate.

In conclusion, we found that the main drivers of the viability of lynx and wolverine in Sweden were the choice of harvest strategy, dispersal rates with neighboring Norway and the resultant potential for source-sink dynamics, and the amount of underreported and unknown cryptic poaching. Given current abundances of lynx and wolverine in Sweden, at approximately 1 650 and 550, there is minimal concern for short-term (20-year) effects of inbreeding depression. And given the dearth of empirical evidence, we do not recommend considering density-dependence in current scenarios. Nonetheless, our results highlight the important need for a better understanding of how vital rates of lynx or wolverine are affected by density in the future given projected positive population growth under, for example, status quo scenarios in Sweden.

In terms of recommendations, the best harvest strategy in Sweden to maintain the minimum threshold abundance seems to be either proportional or a fixed quota harvest that occurs only above this management threshold. We also highlight the sensitivity of Swedish lynx and wolverine population growth to the level of unreported, or cryptic, poaching. Even modest levels of additive cryptic poaching can drive Swedish lynx and wolverine populations to decline under status quo harvest rates. Given the importance of movement between Sweden and Norway to population viability of Swedish lynx and wolverine populations, and the dependence of Swedish population growth rate on Norway harvest scenarios, we recommend continued efforts to integrate carnivore management especially along the long border between Sweden and Norway. Finally, all of our simulations depend on accurate population estimates, especially given this transboundary movement, to inform future management. We recommend continued joint collaboration between Norway and Sweden to ensure that, again, especially in the border regions of both countries, lynx and wolverine population estimates are coordinated.

1. Background and motivation of population analyses

This project was motivated by a wish from the Swedish Environmental Protection Agency (SEPA) to evaluate population viability and effects of management actions on lynx (*Lynx lynx*) and wolverines (*Gulo gulo*) in Sweden. Given concerns about potential further declines for these species, and that the lynx declined significantly from 2011 to 2014 and the wolverine from 2012 to 2016, SEPA asked for a demographically-explicit model that could evaluate various scenarios in a population viability context, and the role of various management-related actions (including hunter-caused mortality) in affecting population dynamics. Ultimately, the goal was to contribute to these species being maintained in favorable conservation status in Sweden as required by the EU Habitats Directive (92/43/EEG).

Specifically, we were tasked by SEPA to conduct a demographic population viability analysis (PVA), including inbreeding depression and sensitivity analyses, for both lynx and wolverine in the main Scandinavian peninsula with a focus on Sweden, but given the importance of potential immigration/emigration with Norway, to consider Norway as well. In addition to understanding the general population viability under current/historic conditions, we were asked to evaluate the effects of different management scenarios, including different harvest strategies, on the population viability of these two carnivores. Furthermore, we were asked to conduct a sensitivity analysis of which demographic, inbreeding, age structure, or other factors have the strongest effect on population growth rate, risk of decline, as well as highlight data gaps and key parameters for which data were deficient in the scientific literature. Lastly, we were asked to address potential population monitoring strategies, given the implications of our PVA and sensitivity analyses, to SEPA. Our work complements recent PVA analyses conducted for large carnivores in Sweden by other authors (e.g., Nilsson 2013, Puranen-Li et al. 2014, Bruford 2015).

In this report, we describe a Bayesian integrated population model (IPM) that we developed to perform these analyses for wolverines and lynx in Sweden. Our model is developed in the open-source R statistical programming environment (R Core Team 2016). This model features a user-friendly ‘front end’ (e.g., an Application Program Interface or API) that facilitates a sex- and stage-structured demographic PVA (including the potential to incorporate stochasticity, inbreeding depression, density dependence, connectivity with Norway, and harvest). Such a model can be used to evaluate which factors most affect population dynamics and persistence.

Our report contains the following components: a) overview of the population viability analysis concepts underlying our approach; b) background on the ecological, genetic and management-relevant components included in the model; c) management outcomes and scenarios evaluated in the two species models; d) general methods underlying our modeling framework; e) input

parameters and results for lynx; f) input parameters and results for wolverine; f) results; g) discussion/conclusions, and h) appendices (Note: source R code for the basic Bayesian IPM for two species is included in appendices). We also provide a revised version of the software to run the program following feedback from the SEPA review.

2. Overview of population viability approaches and concepts¹

Here we give a general overview of key concepts related to Population Viability Analysis (PVA) that underlie our approach. PVA can be defined as “the application of data and models to estimate likelihoods of a population crossing thresholds of viability within various time spans, and to give insights into factors that constitute the biggest threats” (Mills 2013:227).

Although many approaches to quantitative population viability analysis (PVA) exist, two main classes can be distinguished. The first projects time series of population counts. The mean stochastic population trend and its process variance are first calculated from the time series of abundance (or abundance index) estimates. Then, in its simplest form, the trend and variance estimates are used in a random walk or diffusion process to estimate the probability that a population will stochastically decline to a threshold size of concern (quasi-extinction or persistence threshold) in a specified time (e.g., Dennis et al. 1991, Boyce 1992, Morris and Doak 2002). Viability (or population persistence) is driven by the mean and variance of the stochastic growth rate. If the mean growth rate is large, and the variance in growth rate relatively small, then even quite small populations will be likely to persist far into the future. Conversely, regardless of mean growth rate or abundance, populations with large variance in growth rate will have higher risk of extinction. Typically, mechanistic-based drivers of population dynamics (e.g., inbreeding depression, management actions, anthropogenic stressors) are not easily incorporated in these time series-based approaches, nor do they lend themselves to demographic sensitivity analyses. Another major complication are challenges in obtaining accurate estimates of abundance over time, where survey methods often provide only raw counts, not true population estimates, and field survey methods often change, obscuring the true population process because of substantial sampling variation.

The second major class of PVA models is often called “demographically explicit” to capture the fact that births, deaths, age structure, stressors, and immigration/emigration can be accounted for. Within this framework, mechanistic factors that affect population dynamics through age-specific vital rates (birth and death rates) can be explicitly modeled. These factors include, for example, density dependence, harvest, and genetic factors such as inbreeding depression. This ability to model inbreeding depression is especially important because for over 20 years it has been known that demographic and genetic effects *interact* to increase vulnerability to extinction in remnant or small populations (Mills and Smouse 1994). That is, in small populations, deterministic stressors (e.g., overharvest, disease, invasive species) decrease

¹ Parts of this section are adapted from the Final Report to SEPA by the PI on a synthesis of science-based criteria for “Favorable Reference Population” of the Scandinavian wolf (August 31, 2015).

vital rates, that in turn decreases the census and effective abundances, which exacerbates the effects of stochastic fluctuations and inbreeding depression, further decreasing vital rates, and so on. This process is captured by the “extinction vortex” (Figure 1).

These processes interacting in the extinction vortex to alter a population’s probability of persistence (Figure 1) are precisely the dynamics accounted for by demographically explicit PVAs.

For many reasons, PVAs should be interpreted more as an arbiter of the relative effects of different management actions than as a reliable predictor of exact population outcomes. For example, density dependence – including both the specified carrying capacity (K) and the functional form used to describe density dependence (e.g. ceiling, logistic, Allee) can vastly affect the outcomes of PVA predictions, causing different PVA models to have widely divergent predictions even when the input data (e.g. vital rates and their variances, abundances and age structure, etc.) are identical for the different models (Mills et al. 1996).

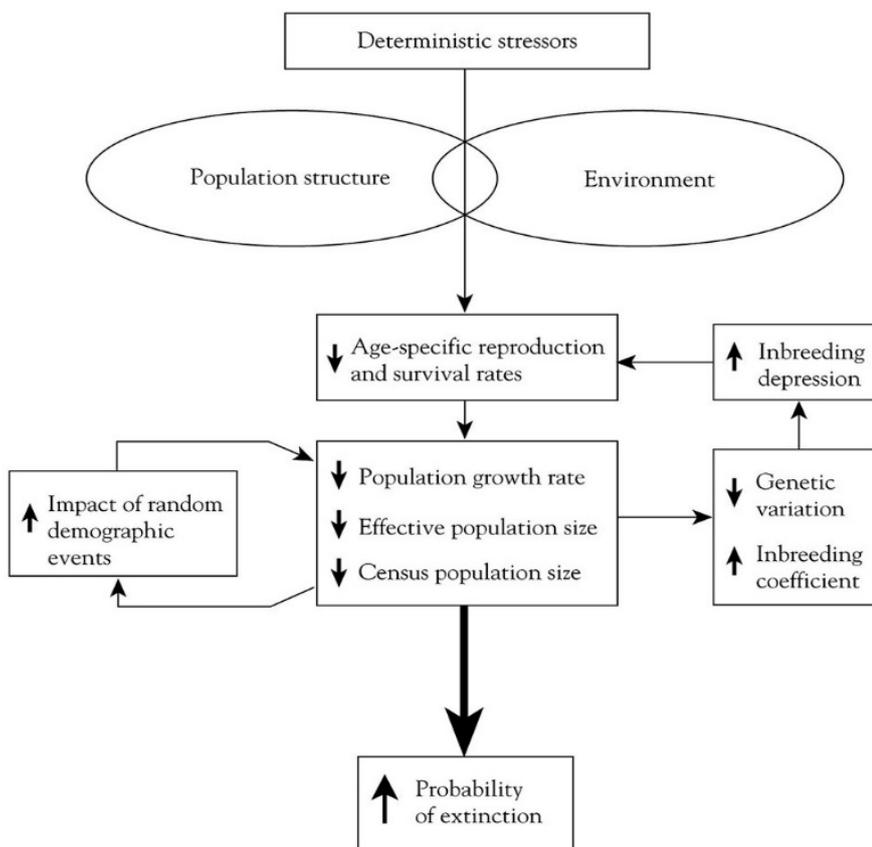


Figure 1. From Mills 2013, modified from Soulé and Mills (1998). A simplified representation of the extinction vortex. The effects of deterministic stressors are filtered by the population’s environment (habitat as well as variable extrinsic factors such as weather, competition, predators, and food abundance) and by its structure (including age structure, sex ratio, behavior, density dependence, physiological status, and intrinsic birth and death rates). Each turn of the feedback cycle increases extinction probability. The extinction vortex model formalizes the fact that extinction probability arises from an interaction of genetic and nongenetic factors.

A demographically explicit PVA model also directly accommodates analysis of the relative ‘importance’ of different vital rates and management actions. Broadly speaking, ‘sensitivity analysis’ refers to how changes in vital rates – due to either a natural change or through management – may change population growth or persistence (Mills and Johnson 2013). Such sensitivity analyses facilitate an assessment of the relative effects of different management actions for meeting population goals. Although matrix-based calculation of analytical ‘elasticities’ and ‘sensitivities’ (based on eigenanalysis of the mean matrix) were an early form of ‘sensitivity analysis’, other approaches currently exist to more realistically accommodate real-world changes to vital rates through management actions (Mills 2013). Here we emphasize sensitivity analyses accomplished through manual perturbation and life-state simulation analysis (LSA).

Manual perturbations simply use the PVA modeling framework to ask “what if” scenarios. For example, if survival changed by 5%, what would the effects be on abundance, viability, etc? This flexible and powerful approach allows the user to perturb vital rate and management possibilities in sensible and transparent ways to assess future growth rate, abundance, or persistence. Different vital rates can be perturbed by any amounts simultaneously, as would occur under real-world management actions.

Life-stage simulation analysis (LSA) standardizes the manual perturbation method to provide insights into the relative effects of various management actions including harvest or other forms of mortality (Wisdom and Mills 1997; Wisdom et al. 2000, Hoekman et al. 2002, Gerber et al. 2004, Johnson et al. 2010a, Taylor et al. 2012). In brief, the LSA approach builds thousands of plausible matrices from the specified means and variances of stage-specific vital rates. Population growth rate (asymptotic or non-asymptotic λ) are calculated for each matrix. Baseline scenarios can be compared to various management alternatives with a variety of metrics (e.g., probability of positive population growth, R^2 between λ and different vital rates). Eacker et al. (2017) recently extended the LSA approach to Bayesian IPMs, showing that Bayesian population analysis could be used to derive analytical sensitivity parameters (i.e., based on eigenvectors and eigenvalues) and generate simulated values for LSA within an IPM. Thus, Bayesian IPMs provide a flexible tool to estimate demographic rates, conduct population viability analysis, and understand population dynamics through broad scale sensitivity analyses to provide the most precise information to managers that are tasked with making challenging conservation decisions.

3. Ecological, genetic and management-relevant components included in our models

We used Bayesian methods to forecast Eurasian lynx and wolverine population dynamics in Sweden in a PVA framework that includes sensitivity analyses. The use of Bayesian integrated population models (IPMs) has become more common in assessing population dynamics because of their ability to overcome many of the limitations imposed by traditional analyses (see Schaub and Abadi 2011). In contrast to traditional methods, Bayesian IPMs estimate demographic parameters in a single, comprehensive, stage-based model to exploit all available information (e.g., harvest, count, capture-mark-recapture data) about population processes (Johnson et al. 2010b, Schaub and Abadi 2011). The benefits of this approach are that parameter estimates become more precise due to joint estimation, process and sampling mechanisms are specifically accounted for, estimates for years with missing data can be inferred, and covariates (e.g., inbreeding depression, density dependence) can be simultaneously modeled. Bayesian methods are also often easier to implement than classic frequentist approaches. Bayesian IPMs can be customized for population viability analyses to evaluate the probability of a population being below a quasi-persistence threshold of either N or λ (Kéry and Schaub 2012; Bauer et al. 2015). For instance, persistence probabilities are easily derived from the posterior distributions of parameters (e.g., Bauer et al. 2015). This allows easy calculation of the probability that a population will be above or below some threshold N or λ in given year. Further, scenarios evaluating the relative importance of various management actions on population growth (e.g. sensitivity analyses) are easily incorporated.

Next, we briefly describe some of the ecological, genetic, and management-based concepts included in our Bayesian PVA and sensitivity analysis. The specific modeling of these factors are described in Section 4.0, Population Viability Analysis Methods, and the particular values for each model species in Section 5.0 – Lynx and Section 6.0 – Wolverine.

3.1 Stage and Age Structure

Animal population ecologists and managers are often interested in the dynamics of specific age classes or stage classes. First, different stressors and management actions affect different stages of animals in different ways. Second, stage classes and stage-specific vital rates are not equal in their effects on population growth, so that management actions that target different stage classes will not be equal in their effectiveness. Third, different stages may have different values to the public (especially in animals where males of different stages are harvested).

One useful way to account for age or stage structure is through matrix models (Mills and Smouse 1994, Mills 2013, Caswell 2001). A population matrix model provides a convenient accounting system to track stage-specific vital rates and abundances through time to determine how different vital rates and stages affect dynamics. The sex- and stage-specific model we developed for lynx and wolverine accounts for four stages: a) subadults (or yearlings) of both sexes; b) 2-year old females; c) adult females; and d) adult males, with accompanying vital rates. These stages are projected through a 4×4 matrix model (see section 5.2 below).

Importantly, the fact that different stage classes will differentially affect population growth means that the number of animals in each stage class can have substantial effects on population growth. Under constant conditions any initial stage distribution will converge on an asymptotic stable stage distribution (SSD) and asymptotic growth rate (λ_{SSD}) characteristic to the particular vital rates in the matrix (Mills 2013, Caswell 2001). However, if the initial stage distribution is not in SSD then transient dynamics (or population inertia) will occur that will cause population growth to be greater or less than λ_{SSD} depending on the reproductive values of the stages in the initial population vector (Caswell 2001, Koons et al. 2006). Practically speaking, this means that a deterministic population projection initiated with 100 animals and an expected asymptotic growth rate at SSD of 10% per year ($= 1.1$) would have 110 animals after 1 year if the initial population is distributed at SSD, but could have much fewer (perhaps 95) or much more (perhaps 115) if the initial stage distribution is far from SSD (see examples in Mills 2013, Chapter 6).

Despite the importance of initial age distribution, there is little known about age distribution of large carnivores such as lynx and wolverine in Sweden. Therefore, we used the default of distributing the initial distribution of initial abundances for both species in our model according to the SSD given our vital rates. However, we also allow the user interface of our model for user input of any alternative initial stage distribution. In the case of starting at SSD, the population will grow asymptotically without any fluctuations due to transient dynamics in stage distribution (Mills 2013, Caswell 2001). If the user enters any other initial stage distribution, they should know that population growth will – for several years – be more or less than λ_{SSD} purely due to transient dynamics until asymptotic convergence to SSD. Also, variation in retrospective harvest rates will cause population growth rates to bounce around initially, but the population will return to constant growth once harvest is kept constant. Finally, we did not explicitly account for senescence by truncating fecundity or survival above some fixed age, or according to some function (Caswell 2001), in part because of the lack of empirical evidence for senescence in large carnivores such as lynx and wolverine.

3.2 Stochasticity

Two main forms of stochasticity, or variation, affecting vital rates can be distinguished that should be included in any population projection model. First *demographic stochasticity* arises from random deviations that arise in a deterministic (non-varying) environment simply because whole animals experience probabilistic, often binomially distributed (0, 1) vital rates (e.g. an animal with a 70% survival cannot 70% survive; either it lives with 70% probability or dies with 30% probability). Demographic stochasticity is analogous to coin-flipping (i.e., Bernoulli) variation around an expected mean of 50:50, where the expectation is driven by the vital rate mean. The effect of demographic stochasticity disappears as abundance exceeds about 100 and the expected mean converges on the actual mean (Morris and Doak 2002).

While demographic stochasticity occurs even in totally deterministic, constant conditions, *environmental stochasticity* incorporates variability in the mean vital rate over time as environmental conditions change. Weather often drives environmental stochasticity (e.g. wet versus dry years), as do unpredictable disease outbreaks or changes in predator abundance. Notably, environmental stochasticity affects growth rates at any size of population (unlike demographic stochasticity). As an aside, we note that ‘genetic stochasticity’ – the random variation in allele frequencies (and associated fitness costs of inbreeding) at small populations is described below in a section on “Inbreeding Depression”.

3.3 Density Dependence

Density dependence arises when a population’s density or abundance affects the vital rates of individuals in the population, which in turn can affect the population growth rate. Classic, or negative density-dependence occurs when factors such as parasitism, predation, or intraspecific competition for resources lead to a reduction in vital rates as populations increase in size. Negative density dependence tends to be regulatory, as it reduces population growth at high abundance and increases it at low abundance. This regulation leads to stable fluctuations around a long-term mean abundance where population growth rate is stationary at carrying capacity (K) (Mills 2013). At K, births = deaths, and the population stabilizes, dependent on the degree of environmental stochasticity. Although the simplest and most common way of modeling negative density dependence is the logistic (or discrete-time form, the Ricker), this assumes that all density dependence is negative, in a linear fashion from 0 to carrying capacity, and that the carrying capacity can be quantified from field data. Another form of pseudo density dependence is the ‘ceiling model’, whereby population growth is exponential to K, but can never increase above K. A ceiling type model is unrealistic for most species, with possible exceptions being those with very strong territoriality or a strict limiting resource such as nest boxes or overwinter spots.

To our knowledge, none of these assumptions can be evaluated based on field studies of density-dependence in wolverines and lynx. Only 1 study in the literature reports evidence for density-dependence in a single vital rate, adult survival, for wolverine in one study area in southern Sweden (Brøseth et al. 2010). While this provided some evidence for density-dependence in a single vital rate, it has not been demonstrated that this translated to density dependence in population growth rate around a carrying capacity. There might be compensation amongst vital rates as adult survival declined at higher densities, for example, with increased recruitment or fecundity. And for lynx, there were no studies demonstrating density-dependence anywhere in Scandinavia. One difficulty in applying the results of Brøseth et al. (2010) is that the abundances from which density dependence estimates were derived ranged from 70–120, far lower than the population sizes of wolverine or lynx in either Sweden or Norway that were modeled in the PVA. Despite this considerable uncertainty in how density dependence would operate at these larger spatial scales and population sizes, and without any evidence for lynx, we included it in our PVA using the same form as found by Brøseth et al. 2010, whereby adult survival declined as density increased. Therefore, our default scenarios did not include density-dependence but we evaluated sensitivity of results to differing strength of density-dependence in PVA analyses for both wolverine and lynx.

In addition to negative density dependence, at small population sizes, wild populations might experience “Allee effects” or positive density dependence, whereby vital rates correlate positively with density, especially at low densities (Mills 2013). Mechanisms driving positive density dependence include cooperative defense, foraging efficiency, mate finding, and rearing of offspring (Kramer et al. 2009, Gregory et al. 2010). When these mechanisms occur, a decreasing abundance leads to decreased vital rates and population growth rate. We found no scientific literature on which to parameterize positive density dependence for our focal species; therefore, the current model contains no positive density dependence. (Parenthetically, some would consider inbreeding depression to be a form of positive density dependence, as vital rates are decremented as abundance declines; we do include inbreeding depression in our model [see next section]).

3.4 Inbreeding Depression

Inbreeding depression arises in cases when a loss of heterozygosity due to inbreeding translates into a decrease in one or more vital rates (e.g. survival, reproduction, Allendorf et al. 2013, Mills 2013). In essence, inbreeding can occur through two mechanisms: a) preferential non-random mating with relatives (denoted by F_{is}); and b) genetic drift arising from random mating in small populations (denoted by F_{st}). Inbreeding via preferential mating can usually be dismissed in most wild vertebrates, so that ‘inbreeding’ (F) in small populations of conservation concern arises from genetic drift (e.g. $F = F_{st}$).

This form of inbreeding quantifies the loss of heterozygosity based on the genetic effective population size (N_e) over time (See Box 1). Juvenile survival is often considered to be the vital rate most affected by inbreeding, because inbreeding depression in this stage would purge deleterious alleles from being expressed in later stages. However, arguments have been made for including inbreeding depression in other vital rates, which would increase the overall effect of inbreeding depression on population dynamics (Allendorf et al. 2013, O’Grady et al. 2006).

Although inbreeding depression can absolutely drive population declines and increased extinction risk, it should not be considered axiomatic that inbreeding depression will *always* have these negative population-level effects. For example, Johnson et al. (2011) show that endangered Sierra Nevada big-horn sheep suffered statistically significant inbreeding depression on fecundity. However, incorporating these costs of inbreeding into a matrix projection model showed that the inbreeding depression on sheep fecundity would have minimal effect on short-term population growth, implying that other management actions would be more effective at short-term recovery than would genetic rescue to address inbreeding depression. In general, inclusion of inbreeding depression in a PVA is appropriate to evaluate its potential effect on viability.

PVA models often account for inbreeding depression by decrementing vital rates based on inbreeding coefficient (due to drift) at that time step and the specified cost of inbreeding. The ‘inbreeding load’ (or ‘lethal equivalents per gamete’), commonly denoted as B , can be calculated empirically as the rate at which survival (or other fitness attributes) declines with increased inbreeding (Morton et al. 1956, Hedrick and Kalinowski 2000). Because species-specific estimates of inbreeding depression are often lacking for species of conservation concern, PVA models often evaluate ‘what if’ scenarios based on reasonable ranges of inbreeding depression derived from the literature. In the most classic paper quantifying lethal equivalents, Ralls et al. (1988) estimated 1.57 lethal equivalents per gamete (= 3.57/diploid genome) as the median B for juvenile survival in 40 non-domestic mammal species in captivity. This median value is the default value for incorporating inbreeding depression in the PVA Program “VORTEX” (Lacy and Pollak 2014). Subsequent reviews have generally supported $B = 1.57$ as a reasonable rule of thumb for inbreeding load on juvenile survival (Keller and Waller 2002, Crnokrak and Roff 1999). However, these reviews and others (e.g., Fox and Reed 2010) have noted that the captive conditions of Ralls et al. (1988) may have biased low estimates of inbreeding because the higher stress conditions in the wild substantially increases the cost of inbreeding compared to the more benign captive conditions. For these reasons, in a PVA for Scandinavian wolves, Nilsson (2013) used higher lethal equivalents (B from 6.5–10.5) and found strong effects of inbreeding on the viability of the relatively small Scandinavian wolf (*Canis lupus*) population.

Given a specified cost of inbreeding (B), the proportionate reduction in fitness at a particular inbreeding coefficient (F) is: $G = 1 - e^{(-BF)}$ (Morton et al. 1956, Keller and Waller 2002; See FOOTNOTE 2 BELOW). Therefore, in a matrix model the non-inbred survival rate (S_0) for a given cohort in a given

time step is decremented by the cost of inbreeding to give the survival under inbreeding (S_F) as (Mills and Smouse 1994)²: $S_F = S_0 * (e^{-BF})$.

For our lynx and wolverine PVA models, we set $F=0$ for the beginning of each simulation. The model then increments F at time step t by the classic formula based on effective population size (N_e): $F(t) = 1 - (1 - 1/[2 N_e])^t \sim 1 - e^{-t/[2N_e]}$. The genetic effective size (N_e) is the size of an ideal population that would lose heterozygosity due to genetic drift at the same rate as the actual population in question; thus, N_e provides a standardized baseline to estimate the expected loss of genetic variation due to genetic drift. Practically speaking, N_e is always smaller than the population head count, or census size (N). How much smaller N_e is than N varies widely according to mating system and life history. For monogamous or mildly polygynous mammals, ratios of N_e/N tend to be in the range of 0.3 to 0.5. There are few published estimates for N_e/N ratios for Eurasian lynx and wolverines, so we used a range of ratios of 0.3 to 0.5.

For the wolverine and lynx models, empirical estimates of the cost of inbreeding (B) do not exist. In the absence of any estimates of inbreeding depression for any wild lynx or wolverines, we used a range of values of $B = 6.5-10.5$ following from the Nillson (2013) PVA and imposed the effect on recruitment rate. This was equivalent to imposing an effect on juvenile survival since recruitment rate (the number of offspring surviving to age 1 per breeding adult female) is the product of juvenile survival, litter size, and proportion of females that breed. Although these values of B are at the upper end of estimated values (see reviews above), we are not modeling inbreeding depression on other vital rates such as subadult or adult survival. Further iterations of this model could easily incorporate inbreeding depression on other vital rates.

3.5 Human-caused Mortality

Relevant deterministic stressors are an essential component of PVA models. Although stressors often include habitat loss, predation, disease, and climate change, for the target species evaluated here the biggest perceived stressor is human-caused mortality (Kaczensky et al. 2012, Chapron et al. 2015). This may include legal harvest, management removals, or poaching. Harvest can be considered along a spectrum from completely additive mortality, where every removal subtracts from total abundance, or completely compensatory, where every removal is replaced without a decline in abundance by a new recruit (Mills 2013). This represents the scenario where mortality from one source (e.g., harvest) offsets mortality from other sources (e.g., starvation).

² Note: This formulation assumes multiplicative fitness costs across loci; Mills and Smouse (1994) note the strong evidence for synergistic formulations that yield nonlinear results for higher values of F . Simply put, this can be modeled by replacing F with $[G = F/(1-F)]$; we use this approach for this model, a somewhat conservative approach as F remained small for the relatively large N_e of wolverine and lynx.

In reality, the degree to which harvest falls on this continuous spectrum from completely additive to completely density dependence varies on species life-history, density-dependence (i.e., most harvest tends to be compensatory at higher densities approaching carrying capacity), and other factors such as weather.

For large carnivores, in general, there is conflicting evidence for strong compensatory mortality, and more evidence in general that harvest by humans tends to be additive (but see Murray et al. 2010). Nevertheless, in the case of our two-focal species, lynx and wolverine, there was little direct evidence for human-caused mortality being additive or compensatory. Thus, we adopted the approach of modeling a range of additive harvest rates from zero to very high levels, that could conceptually represent varying degrees of compensatory harvest. For example, if we modeled a total additive harvest of 0.10, this could be considered equivalent to a partially compensatory harvest rate of 0.20 if managers felt that indeed, compensatory mortality was justified for lynx and wolverine.

Two general classes of harvest strategies include a fixed quota harvest (removing a fixed number of individuals each time step), and fixed-effort harvesting (where a constant proportion is harvested so that fewer individuals are harvested when the population is small) (Lande et al. 1997, Saether et al. 2010, Mills 2013). Often, wildlife managers use a combination of methods combined with a threshold denoting break points of different management strategies; for species of concern, there may be no harvest below the threshold. Finally, there can be cryptic poaching where some additional amount of harvest is illegal, undetected, or unreported (Liberg et al. 2012). Usually, the only way to estimate such cryptic poaching is via tracking of marked animals, for example, through radiotelemetry. As an example, McLellan et al. (1999) showed that reported harvest of grizzly bears (*Ursus arctos*) from legal harvest underestimated total mortality (which included poaching) by 50%. However, recent studies suggest that cryptic poaching may be still underestimated even when using radiotelemetry (Liberg et al. 2012). Similar to other effects on vital rates, harvest or cryptic poaching can be incorporated as a deterministic parameter in PVA models. For example, a fixed-harvest rate can be set that reduces abundance at the next time step, or, harvest can be integrated directly from field estimates that already account for harvest mortality. In addition, 'extra' cryptic poaching can also be deterministically added. And in the context of Bayesian PVA, these deterministic harvest rates are then incorporated into stochastic simulations of vital rates and abundance to explore consequences to population viability.

3.6 Connectivity Among Multiple Population

The framework of single-population PVAs can be extended (if sufficient input data exists) to multiple populations. The general principles to emerge from theory and practice with multiple population PVAs is that persistence of both

individual populations and the greater metapopulation are highly affected by connectivity (both demographic migration and gene flow) and by the degree of correlation in population dynamics among the individual populations. In the context of understanding population viability of the main Sweden populations of lynx and wolverine, it is important to understand the potential impacts of potential source-sink dynamics between Sweden and adjacent Norway. These two countries share a long, permeable border, and there is abundant evidence of movements, immigration and emigration across this border by Scandinavian carnivore populations including bears (Bischof et al. 2015), wolves (Kojola et al. 2009), lynx (Linnell et al. 2001), and wolverine (Gervasi et al. 2015). Here, we considered basic source-sink dynamics between populations of lynx and wolverine in Sweden and Norway, respectively, based on a previous studies that measured dispersal in wolverine (Gervasi et al. 2015). We considered that all non-juvenile age classes could migrate between adjacent countries, and provide more species-specific details below in Section 5.0 and 6.0. In general, harvest-related mortality was higher for both lynx and wolverines in Norway compared to Sweden. We considered a variety of differential harvest scenarios to help inform the consequences of harvest in Norway to the viability of lynx and wolverine in Sweden.

3.7 Outputs of PVA: projection intervals, quasi-extinction thresholds, and probability distributions

PVA outcomes are fundamentally defined by the projection interval, or time span over which projections are made (Frankel and Soulé 1981). As with any other prediction (e.g., weather, stock market), the assumptions (and therefore predictions) of PVA will be less and less reliable further into the future. Scott et al. (1995) proposed that when PVA is used in endangered species recovery plans it should incorporate **short-term projections** that are evaluated over time against a long-term goal (see also Goodman 2002). The **long-term** viability assessment should include goals that are biologically based (but not be so far in the future as to be patently disconnected from management reality; we would venture that it would be hard to defend >100 years, for example). The short-term projections should explicitly incorporate political/legal/social constraints; monitoring and the iterative application of short-term PVAs can be used to evaluate how well long-term goals are being achieved. Thus, public review (and political trade-offs) can be incorporated in choosing short-term management strategies, but ultimate success is judged against the yardstick of the long-term, biologically-based goal. Although we use some arbitrary projection intervals in this report (e.g. 20 years), we encourage stakeholders in Sweden to apply these guidelines to develop short and long-term projection intervals.

A variety of metrics may be used in PVA projections. Early PVAs focused strongly on probability of persistence only in terms of avoiding extinction

(e.g. >1 animal or mating pair). Current practice often includes multiple other “quasi-persistence” thresholds of biological or management relevance. Quasi-persistence thresholds might include abundances below which reproduction or survival is compromised through Allee effects, or where harvest might be shut down or captive breeding programs initiated. *For this report we use quasi-persistence thresholds derived from the Large Carnivore Initiative for Europe Report (Kaczensky et al. 2013): for lynx: 870 in Sweden, 310 in Norway; for wolverine: 600 in Sweden, 250 in Norway.* We used these thresholds because they were published in guiding policy documents which continue to drive European carnivore conservation. However, should these thresholds change, or different thresholds deemed desirable, our user-interface can easily accommodate different thresholds, and, time frames for evaluating persistence (e.g., see Appendix 7).

As a forecasting tool, PVA relies on predicting likely outcomes conveyed as probabilities or likelihoods. Sometimes quasi-extinction curves may be used to represent the probability (or cumulative probability) of reaching the specified quasi-extinction threshold over a range of time periods. In this way, the reader can interpret which projection interval is most useful for predicting the quasi-extinction probability. The time that it takes to reach a 0.50 probability of quasi-extinction gives the median time to quasi-extinction.

Because of the multitude of decisions that must be made for any PVA, a user-friendly, transparent and flexible interface for the user will allow the management team to explore the consequences of different assumptions and outputs across scenarios. As we describe below, here, we developed a flexible Bayesian PVA and GUI software application based on the R programming language (R Core Team 2016) that can easily be adapted to alternative time frames and PVA metrics.

4. Management scenarios

We were tasked by SEPA to conduct a demographic PVA for lynx and wolverine in Sweden under current/historic conditions, as well under different management scenarios, including different harvest strategies, inbreeding depression, density-dependence, and under different source-sink dynamics with neighboring Norway. Here, we briefly describe the different harvest and non-harvest scenarios we considered in Table 1, and then refer the reader to the species-specific sections for details.

In general, our first and most extensive set of scenarios were based on current conditions, or the **status quo**. In this scenario, we used mean vital rate estimates from the scientific literature and reports, and unpublished harvest data provided by SEPA to evaluate the current population trajectory and future viability. This included mean harvest, poaching and natural mortality rates reported in the literature, and also estimates of harvest provided by SEPA through unpublished harvest reports for Sweden and Norway that spanned the time period from 2011–2017. This ‘status quo’ scenario is perhaps the most useful for examining current population growth rates, variability, sensitivity, and future projections. Therefore, we report results of this scenario combined with every other scenario (e.g., density-dependence, inbreeding, etc.) for comparison.

Next, we considered the ‘**full protection**’ scenario in Sweden where we simulated no mortality from legal or protective harvest in Sweden, and re-ran simulations with these lower harvest mortality rates. This represents perhaps a useful ‘upper’ bound on abundance, trends, and viability for comparison against other scenarios. Because the main utility of this scenario is comparative as an upper bound, we do not consider effects of inbreeding or density-dependence in the ‘full protection’ scenario.

Next, we considered four main forms of harvest scenarios including proportional, fixed quota, and both of these harvest strategies with a lower threshold. The specific details of each harvest rates varied by species and are described in detail in Sections 5.0 and 6.0. In general, proportional harvest varied harvest as a fixed proportion of the total abundance, while fixed quota harvest model removed some constant number of individuals each year. When the population did not have enough individuals to meet the fixed quota, harvest was set to zero for that year. Threshold harvest scenarios set legal harvest to zero below a specified threshold, with proportional or fixed quota harvest above the threshold (Table 1).

We also considered scenarios with differing levels of inbreeding depression, density-dependence, source-sink dynamics with adjacent Norway, and finally, differing levels of cryptic poaching (Liberg et al. 2012; Table 2).

Table 1. Management scenarios of different harvest strategies that we evaluated in terms of population viability analyses for Eurasian lynx and wolverines in Sweden.

Scenario Name	Description
Status quo	Projections of population viability using mean vital rates under current conditions, with current harvest rates, source-sink structure between Sweden and Norway, no density-dependence and no-inbreeding depression.
Complete protection	Projections of population viability with no harvest in Sweden (but with the same harvest rate in Norway), assuming additive mortality under current harvest rates, source-sink structure, etc., similar to scenario 1.
Proportional harvest	Harvest is a fixed proportion of total abundance distributed equally across stage- and sex- classes.
Quota harvest	A fixed-quota is harvested each year, which we varied based on the observed harvest for each species (see sections below).
Threshold harvest	Harvest is reduced to zero below a minimum abundance threshold given by Swedish and Norwegian management targets. Above the threshold, harvest is either proportional or fixed quota.

Table 2. Non-harvest scenarios considered in population viability models for Eurasian lynx and wolverines in Sweden.

Scenario	Description
Inbreeding depression	Considered at 4 levels of intensity, a) none ($\beta = 0.0$), b) low ($\beta = 6.5$), c) medium ($\beta = 8.5$), and d) high ($\beta = 10.5$) for 3 ratios of effective to total population size (0.3, 0.4, 0.5).
Density-dependence	We considered a) no negative density dependence in adult survival as the baseline scenario, compared to 3 levels of negative density dependence: low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).
Source-sink dynamics	Under the a) status quo scenario in Table 1, we parameterized PVA's with baseline, current movement (immigration, emigration) between Norway and Sweden. Under option b) we considered the consequences of higher dispersal from Sweden to Norway. Under option c) we considered the consequences of higher dispersal from Norway to Sweden.
Cryptic poaching	We examined the consequences of increasing the cryptic poaching loss rate in Sweden. We kept poaching rates constant in Norway since legal harvest rates were high (i.e., 0.20).

5. Population viability analysis methods

5.1 General modeling approach

Bayesian population models use a hierarchical approach to conduct population viability analysis (PVA) by linking models describing the observation process (empirical data collection or prior information) to models describing the biological (or state) process (e.g., true but unknown abundance; see Schaub and Abadi 2011). Despite a long-history in the field of PVA's (Ludwig 1996; Goodman 2002), Bayesian PVAs have only become more common recently given recent advances of Bayesian computational software that has made them widely accessible (for example, see Bauer et al. 2015). The observation models are used to jointly estimate demographic parameters in the process model using all available data, where the process model is the set of difference equations that describe annual change in population abundance for example through a matrix projection model (Caswell 2001). Here, we use prior information from the scientific literature and published reports of abundance, stage-specific survival and fecundity rates, dispersal (i.e., movement between the Sweden and Norway), and harvest to parameterize the models for each species. Future researchers could adapt our approach to include data directly within the model using an integrated modeling approach (Schaub and Abadi 2011). In this section, we present our formulation and parameterization, specification, and fitting for the general Bayesian population model used for both carnivores, and then describe life-history and datasets used for each species in their own specific sections in section 6 and 7, respectively.

5.2 Model formulation and parameterization

Given an annual population cycle based on a biological timescale (e.g., median birth date), we constructed a matrix-population model that described the expected number of animals in each stage at time t as a function of vital rates (survival, fecundity, immigration, harvest and poaching, and the vector of stage-specific abundances) at time $t-1$. Given the relatively similar life histories of lynx and wolverine, we used a pre-birth, 5×5 matrix to model the vector of stage-specific abundances for five stage classes; subadults (or yearlings) of both sexes (N_{sub}), 2-yr-old females (N_{2yrf}), 2-yr-old males (N_{2yrm}), adult females (N_{af}), and adult males (N_{am}). Equation 1 describes the expected number of individuals in each stage class in year t as a deterministic function of the projection matrix (A) and a vector of stage-specific abundances at time $t-1$:

$$\begin{bmatrix} N_{sub,t} \\ N_{2yrf,t} \\ N_{2yrm,t} \\ N_{af,t} \\ N_{am,t} \end{bmatrix} = \begin{bmatrix} 0 & R_{2yrf}(1-M) & 0 & R_{af}(1-M) & 0 \\ \pi\varphi_{subf}F(1-M) & 0 & 0 & 0 & 0 \\ (1-\pi)\varphi_{subm}F(1-M) & 0 & 0 & 0 & 0 \\ 0 & \varphi_{af}F(1-M) & 0 & \varphi_{af}F(1-M) & 0 \\ 0 & 0 & \varphi_{am}F(1-M) & 0 & \varphi_{am}F(1-M) \end{bmatrix} \begin{bmatrix} N_{sub,t-1} \\ N_{2yrf,t-1} \\ N_{2yrm,t-1} \\ N_{af,t-1} \\ N_{am,t-1} \end{bmatrix} \quad (1)$$

where the vital rates that determine the rate of change are female subadult survival (φ_{subf}), male subadult survival (φ_{subm}), adult female survival (φ_{af}), and adult male survival (φ_{am}). We assumed that 2-yr-old and adult females (≥ 3 -yr-old) had the same survival rate, and also that survival of 2-yr-old and adult males was equal. We modeled fidelity (F) that as one minus the probability of emigrating out of the population (i.e., $1-\psi$), and assumed that only individuals ≥ 1 -yr-old could emigrate in a given year (i.e., individuals did not disperse during their first year of life). Although some dispersal events may occur for juveniles at around 9 months of age, such as in lynx (Andrén et al. 2002), most dispersal occurs in older individuals. For instance, the mean age of dispersal was 13 months for wolverines (Vangen et al. 2001). We included the proportion of subadults that were female (π) to partition subadults into the 2-yr-old female and male stage classes; thus $1-\pi$ represents the proportion of subadults that were male; we derived this parameter as a function of the proportion of newborns that are female (p), and the female (φ_{juvf}) and male (φ_{juvm}) juvenile survival rates (Equation 2):

$$\pi = (p\varphi_{juvf}) / (p\varphi_{juvf} + [1-p]\varphi_{juvm}) \quad (2)$$

We used the recruitment rate of young (i.e., number of offspring per breeding-aged female that survive the first year of life) from 2-yr-old (R_{2yrf}) and ≥ 3 -yr-old (R_{af}) adult females as a measure of fecundity, which is the product of the average proportion of females that breed, litter size, and juvenile survival (e.g., DeCesare et al. 2012; note that this assumes in utero mortality rate is negligible). We included a term for the probability of dying from human-caused mortality (M), which is the sum of the probability of dying from legal and protective harvest (M_H) and from other human-caused sources of mortality (M_P , e.g., poaching). Thus, the probability of surviving from human-caused mortality for a given year is $1-M$, and for simplicity, we assumed that all individuals experienced the same harvest mortality rate. Although we do not model juveniles in our pre-birth matrix model, we allow juvenile survival to be reduced by the same population-level harvest rate, which is important as entire litters can be culled in the den in some cases (Andrén et al. 2006, Persson et al. 2009).

The expected abundances in year t from the projection matrix in Equation 1 are a deterministic function of the stage-specific vital rates and populations sizes in year $t-1$, but **demographic stochasticity** is modeled in Bayesian population models by defining the appropriate probability distributions that generate the biological process of abundance changing over time (Schaub and Abadi 2011). The abundance of a particular age or stage class is commonly modeled with a binomial or Poisson distribution (Schaub and Abadi 2011), though

other distributions may be used as well (Hobbs and Hooten 2015). The binomial process model may be more intuitive for those familiar with individual-based stochastic population models, since the binomial process variance is more commonly applied in these traditional settings in the same sense as Bernoulli coin flipping trials. The binomial distribution behaves the same way when used as the process model in a Bayesian population model, where the variance is defined as: $p(1-p)/n$, where p is the survival rate for example, such that demographic stochasticity (or variance) increases as abundances (N) get smaller. The Poisson model is just a limiting case of the binomial model, and is generally used to model reproduction to allow the number of offspring to be greater than one (note that this is not possible with a binomial since the success probability is bound between 0 and 1).

5.2.1 Biological process models

We used a Poisson distribution to model the number of subadults in year t as the sum of contributions from the recruitment rate (R_{2yrf}) and number of 2-yr-old females ($N_{2yrf,t-1}$) and the recruitment rate (R_{af}) and number of adult females ($N_{af,t-1}$) in year $t-1$, multiplied by the probability of not dying from human-related mortality ($1-M$):

$$\begin{aligned} N_{sub,t} &\sim \text{Poisson}((R_{2yrf}N_{2yrf,t-1})[1-M] + (R_{af}N_{af,t-1})[1-M]) \\ &= N_{sub,t} \sim \text{Poisson}((R_{2yrf}N_{2yrf,t-1} + R_{af}N_{af,t-1})[1-M]) \end{aligned} \quad (3)$$

We used separate binomial distributions to model the number of 2-yr-old females and males in year t as a function of the mean proportion of subadults that are female (π), the female (φ_{subf}) and male (m) subadult survival rates, the probability of not dispersing (F), the probability of not dying from human-related mortality ($1-M$), and the number of subadults in year $t-1$ ($N_{sub,t-1}$):

$$N_{2yrf,t+1} \sim \text{binomial}(\pi\varphi_{subf}F[1-M], N_{sub,t-1}) \quad (4)$$

$$N_{2yrm,t+1} \sim \text{binomial}([1-\pi]\varphi_{subm}F[1-M], N_{sub,t-1}) \quad (5)$$

Similarly, we used a binomial distribution to model the number of adult females in year t as the sum of the contributions from the number of 2-yr-old ($N_{2yrf,t-1}$) and adult females ($N_{af,t-1}$) in year $t-1$, the adult female survival rate (φ_{af}), the probability of not dispersing (F), and the probability of not dying from human-related mortality ($1-M$):

$$N_{af,t} \sim \text{binomial}(\varphi_{af}F[1-M], N_{2yrf,t-1} + N_{af,t-1}) \quad (6)$$

We also used a binomial distribution to model the number of adult females in year t as the sum of the contributions from the number of 2-yr-old ($N_{2yrm,t-1}$) and adult males ($N_{am,t-1}$) in year $t-1$, the adult male survival rate (φ_{am}), the probability of not dispersing (F), and the probability of not dying from human-related mortality ($1-M$):

$$N_{am,t} \sim \text{binomial}(\varphi_{am}F[1-M], N_{2yrm,t-1} + N_{am,t-1}) \quad (7)$$

We note that the same biological process models were used to model the Norway population as well, and we allowed for dispersal between the two populations.

5.2.2. Dispersal between populations

Here, we briefly describe the method for modeling dispersal between the two populations. For the adult stage classes above (N_{2yrf} , N_{2yrm} , N_{af} , N_{am}), we simply add the number of immigrants from Norway (or Sweden, in the case of Norway) as a function of the number of individuals in the dispersing stage class multiplied by their probability of dispersal (ψ). For example, the binomial process model in Equation 7 above gives us the expected mean number of adult males in year t for the Sweden population, which here for simplicity we denote as $\mu_{am,t}$. Thus, as an example for Sweden, the contribution from dispersing 2-yr-old ($N_{NOR,am,t-1}$) and adult males ($N_{NOR,am,t-1}$) from Norway in year $t-1$ ($N_{NOR,am,t-1}$) given the dispersal rate from Norway to Sweden (ψ_{NS}) to the number of adult males in Sweden in year t ($N_{am,t}$) is given as:

$$\mu_{am,t} \sim \text{binomial}(\varphi_{am}F[1 - M], N_{2yrm,t-1} + N_{am,t-1}) \quad (8)$$

$$N_{am,t} = \mu_{am,t} + ([N_{NOR,2yrm,t-1} + N_{NOR,am,t-1}]\psi_{NS}) \quad (9)$$

Adult females used the exact same formulation, while the contribution of dispersing subadults to 2-yr-old female and males includes the proportion of subadults that are yearling (π) to separate female and male subadult dispersers. Also, the dispersal of individuals from Sweden to Norway is modeled identically in the Norway process model.

5.2.3. Prior for initial abundance

We used an initial abundance from the literature (Kaczensky et al. 2012) for both lynx and sweden to anchor our PVAs at a specific year in time (see Section 6 and 7 for details for both species). We used the mean (y_1) and standard error (SE) of an abundance estimate as prior information for a lognormal prior distribution describing the true, but unknown initial abundance (N_{init}):

$$N_{init} \sim \text{lognormal}(\log(y_1), \sigma_1^2) \quad (10)$$

We converted the SE of the abundance estimate to the variance (σ_1^2) on the log-normal scale using the following transformation:

$$\sigma_1^2 = \log([SE^2/y_1^2] + 1) \quad (11)$$

This formulation is more theoretically correct than truncating a normal distribution for the initial abundance since abundance cannot be negative, and the lognormal distribution covers the range from zero to infinity. We then distributed the initial abundance into each stage class by multiplying N_{init} by the proportion of individuals in stage class j based on the stable stage distribution (SSD) of the mean matrix of vital rates and the human-caused mortality rate in the initial year (i.e., 2011) for each population.

5.2.4 Informative priors for parameters and moment matching

We used the mean survival (ϕ_j) and fidelity (F) probabilities for stage class j and their estimated SEs to construct prior distributions using the alpha (α) and beta (β) parameters of the beta distribution, which is used to model continuous parameters (θ) bound between zero and one:

$$\theta \sim \text{beta}(\alpha, \beta) \quad (12)$$

We matched the moments of a normal distribution (i.e., μ, σ^2) that we parameterized with the mean and SE (converted to variance) of survival and emigration rates to the α and β parameters of beta distributions using the following moment matching expressions:

$$\alpha = (([1 - \mu]/[\sigma^2 - 1]/\mu)\mu^2) \quad (13)$$

$$\beta = \alpha(1/[\mu - 1]) \quad (14)$$

We modeled the mean recruitment rate (R) and the associated SE by matching the moments of a normal distribution (i.e., μ, σ^2) to the α and β parameters of gamma distribution, which has continuous, positive support (i.e., $x \in [0, \infty]$):

$$R \sim \text{gamma}(\alpha, \beta) \quad (15)$$

This allows the recruitment rate to be greater than one, which is the correct distribution for species that can have more than one offspring per female such as wolverine and lynx. We matched the moments of a normal distribution (i.e., μ, σ^2) that we parameterized with the mean and SE (converted to variance) of recruitment rates to the α and β parameters of the gamma distribution using the following moment matching expressions (Hobbs and Hooten 2015):

$$\alpha = \mu^2 / \sigma^2 \quad (16)$$

$$\beta = \mu / \sigma^2 \quad (17)$$

5.2.5 Deterministic parameters and derived quantities

We modeled the mean proportion of subadults that are female (π) and the harvest rate (M_H) as deterministic parameters in the model, and, as such, they did not contribute to the uncertainty in the model (movement probabilities were also deterministic for populations in Norway since they were simulated as a function of harvest rate; see below). We derived the annual geometric mean population growth rates (λ_G) using the following expression:

$$\lambda_G = \prod_i^t \lambda_i^{1/t} \quad (18)$$

We also derived the total abundance in year t by summing the number of individuals in each stage class in year t :

$$N_{tot,t} = N_{sub,t} + N_{2yrf,t} + N_{2yrm,t} + N_{af,t} + N_{am,t} \quad (19)$$

5.2.6 Sensitivity analysis

Typically, we would develop a specific set of Bayesian models to derive asymptotic growth rates (i.e., the dominant eigenvalue, λ_{SSD}) and analytical elasticities (or proportional sensitivities) for each vital rate and conduct LSA (Wisdom and Mills 1997, Wisdom et al. 2000; see section 2.0) for a Bayesian approach to sensitivity analysis (Eacker et al. 2017). However, we used an approximately Bayesian approach that utilized the `popbio` package in R (Stubben and Milligan 2007) to solve the transition matrix A at each MCMC iteration. We stored the MCMC samples from the baseline model runs for each species, and then thinned the MCMC chains to retain 1 000 samples of each vital rate and λ_{SSD} to include in simple linear regressions as the explanatory and response variables, respectively. The intercept (β_0) in these regressions provided an estimate of λ when the vital rate was at zero, and the slope (β_1) predicted the increase in λ per unit increase in each vital rate. Also, the coefficient of determination (R^2) is used to estimate the proportion of variance in λ explained by each vital rate (Wisdom and Mills 1997; Wisdom et al. 2000). We used a `for` loop in R to loop over each simulated parameter value and construct A at each iteration, and then we stored the value of λ_{SSD} at each iteration. This approach saved time and provided the exact same results as deriving λ_{SSD} within the model (although this possible using Cholesky matrix decomposition in JAGS). The method is still considered an approximately Bayesian approach since a Bayesian population model and MCMC sampling is used to generate the samples used for the LSA method.

Ideally, enough data are available to estimate the **environmental variances** of vital rates (see Appendix 1). Given sufficient data, the mean and environmental variances can be used to construct a sampling distribution for each vital rate in the model that can be used to populate A at each iteration in the Markov-chain Monte Carlo (MCMC) simulation (Eacker et al. 2017). Here, with a limited number of parameter estimates, environmental and sampling variances were not separately estimable, and thus, our sensitivity analyses of vital rate importance may be influenced by (unknown) sampling variance in especially the vital rate estimates from the literature. Future IPMs for Swedish lynx and wolverine could be useful to address this important limitation.

5.3 Model Implementation

We estimated marginal distributions for the posterior likelihoods of parameters using JAGS 4.2.0 (Plummer 2015), which we conducted in program R using the `R2jags` package (Su and Yajima 2015). JAGS models are coded in the BUGS language, which provides an accessible interface for ecologists to develop and analyze Bayesian models. We assessed model convergence by

visually examining trace plots of posterior distributions for each parameter, and initiated at least two MCMC chains to assess convergence with the Brooks-Gelman-Rubin statistic (Brooks and Gelman 1998). We increased the burn-in period as necessary for models to converge on stable distributions before retaining samples, and thinned samples to reduce autocorrelation in the chains (Abadi et al. 2010). We achieved convergence in all models by running 20 000 iterations in 2 parallel chains with the first 10 000 as burn-in, and retained every 2nd sample for a total of 10 000 samples.

6. Eurasian Lynx

Eurasian lynx populations, like other large carnivores, have recovered in Europe over the last three decades as a result of protective measures after near extirpation due to persecution and overharvest (Linnell et al. 2010, Chapron et al. 2014). In comparison to wolves, however, lynx were never extirpated from Scandinavia. In 2011, lynx were reported as stable in Sweden (1400–1800 individuals) and in Norway (327 individuals) (Kaczensky et al. 2012). Lynx are distributed over a large portion of Sweden, and in Norway they are distributed across most of the country except parts of the southwest (IUCN 2017; Figure 3). Note that we provide Figure 3 simply for background information, and do not derive initial abundances from these figures, nor address spatial variation in population viability in this report.

Despite their recovery and current status as a species of least concern (IUCN 2017), lynx conservation and management continues to face a number of challenges. In Scandinavia, lynx conflict with human activity (e.g., animal husbandry and hunting) due to predation on livestock, semi-domestic reindeer (*Rangifer tarandus*), and roe deer (*Capreolus capreolus*) motivate the need to limit lynx abundances through regulated harvest and culling (Linnell et al. 2001, Andrén et al. 2006). Lynx are protected in Sweden under the European Union's (EU) Habitats Directive, but limited protective and quota hunting of lynx are allowed under article 16 of the directive (Kaczensky et al. 2012).



Figure 2. Eurasian Lynx (photo by Thomas Mørch, Creative Commons Attribution 3.0 Unported license).

Norway is not governed by EU regulation and instead follows the Council of Europe's Bern Convention of 1979, a policy that allows for more liberal control of lynx and other large carnivores to mitigate wildlife-human conflicts. These differences in regulations have resulted in variation in both legal and illegal harvest of lynx between the two countries (Andrén et al. 2006, Nilsen et al. 2012) that may have important implications for population dynamics and viability of the species (Linnell et al. 2001, Sæther et al. 2010).

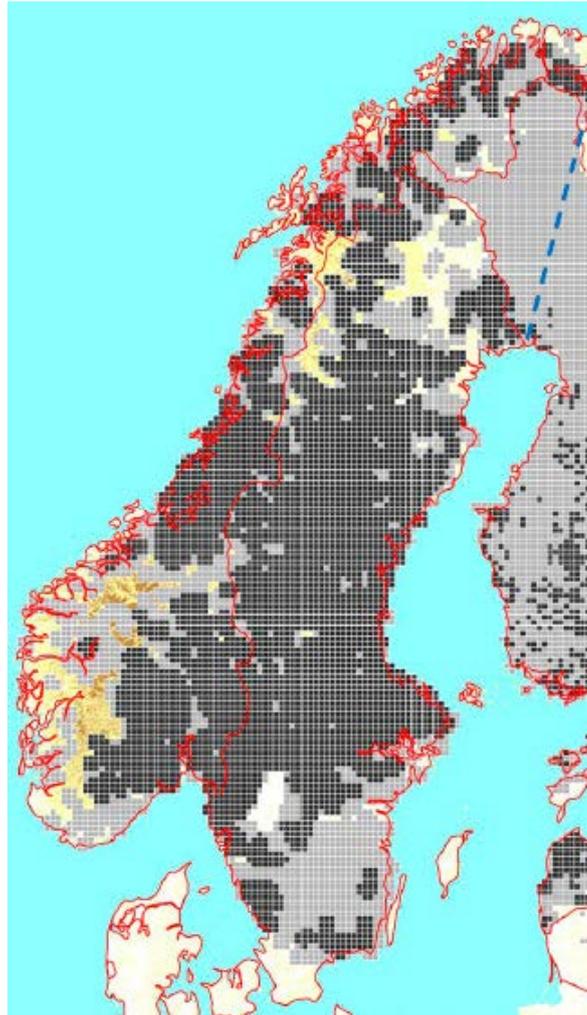


Figure 3. Eurasian lynx (*Lynx lynx*) distribution in Scandinavia during 2006–2011. Figure is borrowed from Kaczensky et al. (2012) and provided here just for background information. Dark cells represent documented reproduction while gray cells represent sporadic occurrence.

6.1 Lynx Population Viability Analysis

We modeled lynx demography using the following life-cycle diagram (Figure 4) following the above formulation described in Section 4.0. Lynx demography was modeled using a pre-birth, 5×5 matrix to model the vector of stage-specific abundances for subadults (yearlings) of both sexes (N_{sub}), 2-yr-old females (N_{2yrf}), 2-yr-old males (N_{2yrm}), adult females (N_{af}), and adult males (N_{am}).

We based our analysis on the best available science from peer-reviewed journals and management reports. We specifically combined the mean and variance of estimates from the literature to establish informative prior distributions for each vital rate (i.e., survival, fecundity; Table 3) to develop population viability scenarios. We used simulated vital rates and management scenario effect sizes when no prior information was available. We used a Bayesian approach of incorporating prior information because 1) much of the data was already analyzed and these estimates were available in peer-reviewed literature, 2) the time frame for reporting did not permit estimating viability from raw data, and 3) we wanted to build a model that would represent viability across the entire range of lynx in Scandinavia. Thus, our objective was to project populations under the most likely baseline scenarios in Sweden and Norway, while accounting for the variance of stochastic parameters (e.g., survival) and simulating over a range of vital rates and other factors such as harvest.

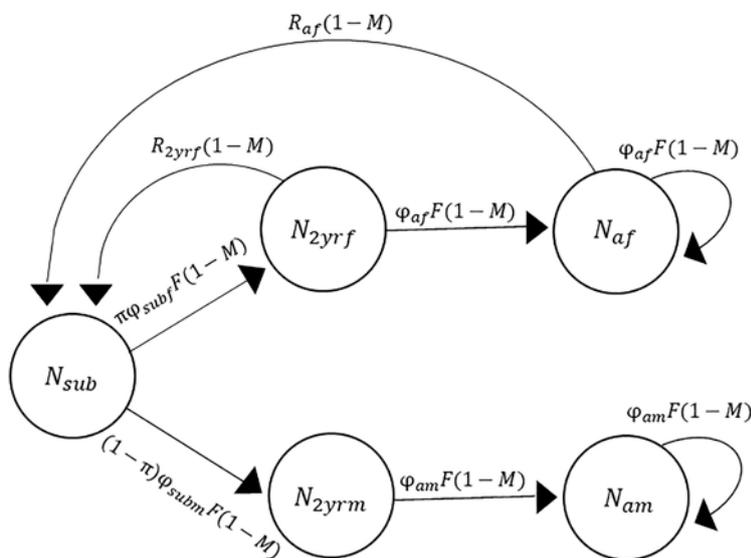


Figure 4. Life-cycle diagram for Eurasian lynx that was used in the Population Viability Analysis showing some 2-year old recruitment (R_{2yrf}) as well as adult recruitment (R_{af}). Note that both 2-year-old and adult females have a non-zero probability of breeding (Table 3). Note that the total mortality rate from legal and protective harvest and poaching are combined into one term (M) for simplicity, but are modeled as separate rates in Bayesian population models.

Ideally, we could combine enough vital rates estimates (at least 8–10) to estimate their environmental variance (i.e., spatial and temporal) to project populations into the future (Kéry and Schaub 2012; see Appendix 1). However, such data were not available. In the absence of sufficient data to decompose spatial, temporal and sampling variance, we instead averaged the available estimates for each vital rate and applied the Delta method to approximate the variance of the average function of vital rates assuming that estimates were independent of each other (i.e., no covariance structure). We used the vital rate estimate and its associated standard error (SE) when only a single estimate was available for a parameter. Multiple parameters estimates were available for most vital rates for lynx except immigration and emigration rates (Table 1, Appendix 2). We constructed prior distributions from the estimated SE for single vital rate estimates using the methods described above, and we used the variances estimated from the Delta method directly in our moment matching equations (see *informative priors for parameters and moment matching*).

We used 1 June as the start of the recurrent date for the annual population cycle of lynx in our model, which was based on the timing of births (Andrén et al. 2002). We thus had to adjust the initial abundances of lynx since the den count estimates that were used are conducted in the winter around February to March and include ~9-month-old juveniles in the estimate. We first constructed a post-birth matrix that included juveniles as a stage class, and determined the proportion of individuals in each stage class ($n = 6$) by calculating the stable stage distribution. Then, we used the deterministic equations from this matrix model along with the vector of stage class sizes to calculate the number of individuals that would be present in each population in year $t+1$ from the initial counts, but without including the contribution from the recruitment of juveniles into the population in year $t+1$. We then calculated the population growth rate that would have occurred over a 3 month period ($\lambda^{(3/12)}$; March – May) and multiplied this value by abundance estimate from the February – March den count. This resulted in an estimate of the number of individuals just before the birth pulse (June 1), allowing us to model the population with a pre-birth matrix that did not include juveniles. We provide the R code for this count adjustment in Appendix 6. Since lynx harvest occurs nearly all of the year, the exact timing of harvest was not important, only the annual rate that was applied to total population including the recruitment of young.

Thus, we modeled annual estimates of survival for the five stage-classes, along with estimates of the proportion breeding and the litter size of 2-yr-old and adult females (≥ 3 -yr-old) separately for both Sweden and Norway. We derived a single estimate of recruitment rate based on litter size, the proportion breeding, and the juvenile survival rate, and again, used the Delta method to estimate the variance for the gamma prior distributions. We treated all vital rates and initial abundance estimates as stochastic parameters, but modeled

human-caused mortality and other factors influencing vital rates as deterministic. Thus, the uncertainty in the model is due to the mean vital rates and initial abundance estimates and their associated variances, and the deterministic effects are parameterized as functions of these mean vital rates (i.e., density dependence, movement, harvest, etc.).

6.2 Lynx Vital Rate Review

We parameterized our population-level prior distributions based on estimated lynx vital rates from across Scandinavia. We found 4 studies that provided 40 vital rate estimates and SEs for: survival probability ($n = 18$); components of recruitment rate ($n = 16$; e.g., litter size, proportion breeding); human-caused mortality rates ($n = 4$); and abundance ($n = 2$) (Table 3, Appendix 2). Most studies focused on either survival and cause-specific mortality or reproduction, but not both. We applied the Delta method to obtain estimates of average vital rates and their uncertainty because there were not enough estimates available in the literature to estimate the environmental variance using Bayesian methods (see Appendix 1). For lynx in Sweden, this resulted in survival estimates of 0.47 (SE = 0.02) for juveniles, 0.94 (SE = 0.03) for female subadults, 0.74 (SE = 0.07) for male subadults, 0.96 (SE = 0.02) for adult females, and 0.98 (SE = 0.01) for adult males. We attempted to find country-specific estimates, but this was not always possible. We applied vital rate estimates from Sweden to lynx populations in Norway in cases where the estimate was 1.0 with no error in Norway, which is often a result of small samples sizes rather than biological process. Thus, we used the same estimates for male subadult survival, and adult female and male survival probabilities (see Table 3). The higher reproductive rate in Sweden compared to Norway for lynx is mostly a result of differences in litter size, but also results from a higher proportion of breeding females in Sweden compared to Norway (Table 3).

We used starting abundances of 1 452 (SE = 128) and 353 (SE = 6) for lynx populations in Sweden and Norway respectively, in 2011. The estimates are based on the adjusting the numbers provided in Kaczensky et al. (2012), which were estimated using extrapolations from den counts (see Andrén et al. 2002). We note that the abundances reported in Kaczensky et al. (2012) may be disputed, but they provided a starting abundance to base our projections on. We discuss implications of problems with these estimates in the discussion, and recommendations for improving population monitoring and integration with models such as our Bayesian IPM. We found one report regarding the current genetic variability of lynx populations in Scandinavia (Strömbom 2017), but did not encounter any studies that provided specific estimates of dispersal rates (i.e., immigration/emigration) or effects of negative density dependence on vital rates. Thus, we used “what-if” simulated rates for these parameters and describe the specific approach for each simulation in the sections below.

Table 3. Abundance and average vital rates with standard errors (SE) derived using the Delta method for the baseline population viability scenario for Eurasian lynx in Sweden and Norway. The parameters include the initial abundance (estimate from 2011), minimum abundance for persistence, human-caused mortality rate from legal harvest and poaching (as well as others such as motor vehicle collisions), average number of legal harvest mortalities (2011–2016), juvenile survival (ϕ_{juv}), female subadult survival (ϕ_{subf}), male subadult survival (ϕ_{subm}), adult female survival (ϕ_{af}), adult male survival (ϕ_{am}), the litter size, proportion breeding, and recruitment rate for 2-yr-old and adult females, and the dispersal probability from Sweden to Norway and from Norway to Sweden.

Parameter	Sweden		Norway	
	Mean	SE	Mean	SE
Initial abundance	1452†	128	353†	6
Abundance for persistence	870	—	310	—
Human-caused mortality (proportional)				
Legal harvest mortality	0.05	—	0.20	—
Poaching and other human-caused mortality	0.10	—	0.07	—
Average number harvested	80.0	—	78.5	—
Survival probability				
ϕ_{juv}	0.47	0.02	0.48	0.04
ϕ_{subf}	0.94	0.03	0.75	0.22
ϕ_{subm}	0.74	0.07	0.74*	0.07*
ϕ_{af}	0.96	0.02	0.96*	0.02*
ϕ_{am}	0.98	0.01	0.98*	0.01*
Reproduction				
2-yr-old female				
Litter size	2.17	0.29	2.00	0.94
Proportion breeding	0.48	0.09	0.45	0.15
Recruitment rate	0.50	0.12	0.43	0.26
Adult female				
Litter size	2.23	0.10	2.03	0.23
Proportion breeding	0.83	0.03	0.75	0.05
Recruitment rate	0.89	0.10	0.73	0.15
Immigration*				
Sweden to Norway	0.05	0.02	N/A	N/A
Norway to Sweden	N/A	N/A	0.02	0.01

Notes: Values in the table given as blanks (or an —) indicate that no estimate was available in the literature, while N/A indicates that the estimate was not applicable.

† We adjusted these initial starting values from Kaczensky et al. (2012) obtained in February/March to align with the biological cycle of lynx we used for the population model starting June 1.

* We set these parameters in Norway equal to the values of the Swedish population since the estimates were 1.0 (SE = 0) for Norway in the literature or only available in Sweden.

6.3 Density dependence

Empirical estimates of density-dependence were absent for lynx populations in Scandinavia. Recognizing both that density dependence is a real biological phenomenon that can substantially affect PVA projections (Section 3.3), we embraced the uncertainty of density dependence parameters in a sensitivity analysis-type framework.

For reasons discussed in 3.3, we incorporated the coefficient for the effect of negative density dependence (β_1) on both adult female and male survival rates for lynx populations in both countries through a logit link function (Hurley 2016). We constructed the intercept (β_0) for this link function using the logit of the mean adult female and male survival rates (here shown as φ_0), and included the effect size as a function of abundance (N_t) in year t :

$$\beta_0 = \text{logit}(\varphi_0) \quad (20)$$

$$\text{logit}(\varphi_t) = \beta_0 + \beta_1 N_t \quad (21)$$

Given the uncertainty in the effect size of negative density dependence on survival, especially for lynx, we simulated over a range of values. Thus, we centered our what-if scenarios around findings of Brøseth et al. (2010) for wolverine, who found a strong signal of negative density dependence on survival based on abundance. Given the intense decline in adult survival estimated at the study effect size of -0.035 (see Figure 5) that was estimated for a mean abundance of 95 individuals, we reduced the effect size in our simulations to a range of -0.001 to -0.002 , which represented a 11% and a 39% decline in survival respectively, using the mean adult female survival rate of 0.96 and the starting abundance in Sweden of 1 452 individual lynx. The effect size in Brøseth et al. (2010) of -0.035 would result in about a 50% decline in survival using a mean rate of 0.96 and a abundance of 95 (the median observed in the study). However, survival rapidly declines to zero with this effect size at the abundance of lynx of 1 452 individuals (see Figure 5), an unrealistic expression of negative density dependence, leading us to use the effect sizes of -0.001 to -0.002 .

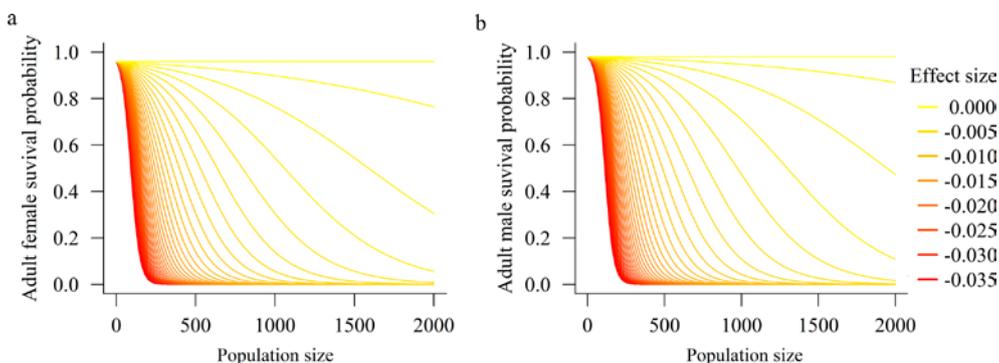


Figure 5. The simulated effect of varying the strength (effect size) of negative density dependence from 0.0 (yellow) to -0.035 (red) to on adult female (a) and adult (b) male survival of Eurasian lynx in Sweden and Norway.

6.4 Inbreeding depression

Available evidence indicates that genetic structure arising from genetic drift is relatively weak for lynx across Sweden and Norway (Strömbom 2017). Nevertheless, we incorporated the potential effects of inbreeding due to drift in our model (see section 3.4 for background). Following convention, our simulations began with the synergistic inbreeding coefficient ($G_t = F_t/(1-F_t)$) set to 0 at the start of simulations. We used a generation time length of 10 years in the calculation of the inbreeding coefficient (section 3.4). We applied inbreeding depression to the recruitment rate, which included juvenile survival. Similar to density dependence, we used an exponential link function to parameterize the effect of inbreeding depression on the recruitment rate (R_t) in year t using the following expression:

$$R_t = R_0 * \exp(-\beta G_t) \quad (22)$$

where R_0 is the mean recruitment rate of breeding-aged females. We parameterized the simulation of inbreeding the same for populations in Sweden and Norway, but used their specific recruitment rates and estimates of G_t .

We considered a range of lethal equivalents per gamete (NONE, LOW:($\beta = 6.5$) to HIGH: ($\beta = 10.5$), following Nilsson (2013). Although simulated inbreeding coefficients for both species models remained low (<0.1 ; see species-specific results), Figure 6 plots cost of inbreeding from zero to 1 (complete fixation of alleles due to drift). This allows a theoretical assessment of what demographic costs could accrue if lynx inbreeding depression were to reach high levels. For example, at an inbreeding coefficient of 0.1, recruitment of 2-yr-old and adult female recruitment rates would decline by 24% and 43% at the low end of lethal equivalents ($\beta = 6.5$), and by 33% and 58% at the high end ($\beta = 10.5$).

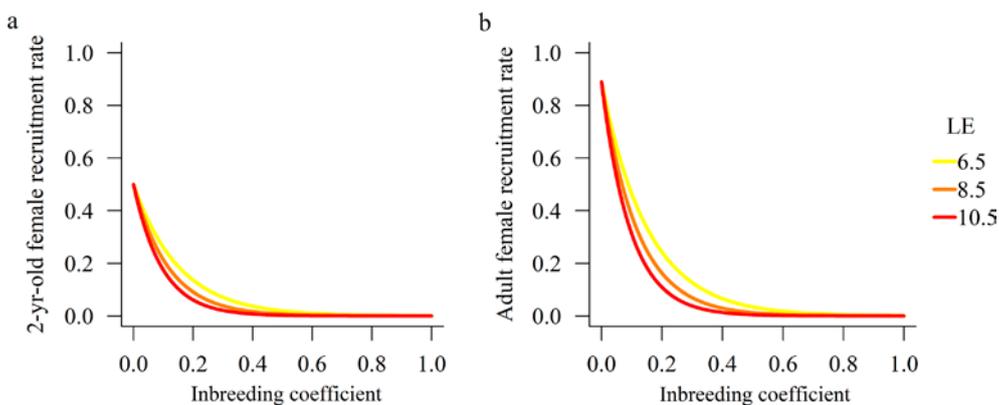


Figure 6. The simulated effect of inbreeding depression on 2-yr-old (a) and adult female (b) recruitment rates predicted over a range of lethal equivalents per gamete (LE) from 6.5 (yellow) to 10.5 (red) for Eurasian lynx in Sweden. Note that the y-intercept represents the mean recruitment rates for 2-yr-old (0.50) and adult females (0.89). Also note that these plots consider inbreeding coefficients (F) going all the way to fixation (1.0), while simulated F values were <0.1 .

6.5 Human-caused Mortality

Lynx mortality rates due to hunter harvest have been relatively low in Sweden compared to Norway. For instance, lynx abundance in Sweden was estimated at about four times as large as populations in Norway in 2011 (Table 4), but the average number of legally harvested lynx was about the same in each country during 2002–2016 at about 80 individuals (see Table 4) leading to harvest rates of 19.9% in Norway and 6.2% in Sweden. Harvest rates in Norway have varied considerably from year-to-year at around 20% over the last decade and may continue to increase in the future (Nilsen et al. 2012). While legal harvest has been an effective tool to manipulate lynx populations for management objectives, other factors such as poaching are difficult to control and add uncertainty to the future viability of lynx populations. For instance, higher legal harvest in Norway may be compensated by lower poaching rates (e.g., Hedmark area, Andrén et al. 2006), whereas in Sweden higher rates of legal harvest may coincide with higher rates of poaching. However, this pattern seems to be inconsistent across other areas of Scandinavia (Andrén et al. 2006), and thus, we were unable to account for these possible correlations between harvest and poaching rates.

Uncertainty also exists in the extent to which harvest may be sex or stage-specific. Some evidence exists that male lynx in Norway have a higher risk of mortality from hunter harvest than females, perhaps due to their larger home range sizes (Linnell et al. 2001). Also, older female lynx and female kittens had similar harvest rates around 18%, while older male lynx had about a 10% higher risk of being harvested (~28%) compared to male kittens (Nilsen et al. 2012). For simplicity, and given the uncertainty in stage or age-specificity in harvest, we applied mortality rates uniformly across age or stage-classes (e.g., Saether et al. 2005). This could certainly be modified in future iterations of the model as more data become available.

Table 4. Retrospective harvest estimates for Eurasian lynx from unpublished data provided by Per Sjogren-Gulve as reported in the ‘Rovbase’ Dead Lynx 2011–2017. Total number of individuals dying from protective and licensed hunting are given (H_{obs}), along with the median number harvested (H_{model}) and 95% Bayesian credible intervals (BCI) from a Bayesian population model. We also give the observed mortality rates from harvest (MH) that were used in Bayesian population models to derive the number of individuals harvested for the retrospective period.

Year	Sweden					Norway				
	M_H	H_{obs}	H_{model}	Lower 95% BCI	Upper 95% BCI	M_H	H_{obs}	H_{model}	Lower 95% BCI	Upper 95% BCI
2011	0.07	121	108	91	129	0.32	139	110	106	114
2012	0.07	107	110	92	132	0.20	81	59	49	75
2013	0.11	124	165	134	201	0.23	79	71	50	104
2014	0.03	26	46	36	57	0.23	73	75	47	122
2015	0.02	23	35	26	45	0.22	79	74	41	129
2016	0.06	78	99	72	133	0.28	36	99	51	178
2017*	0.06	80	107	75	148	0.25	90	89	43	165

* The harvest counts and rates for 2017 were imputed from the mean of the observed counts during 2011–2016 because the estimates were uncertain for this year.

We used the estimates of average poaching rates in Andrén et al. (2006) based on 2 study areas in Sweden and two study areas in Norway to arrive at a baseline poaching rate for simulations of 0.10 for Sweden and 0.07 in Norway. We used the actual harvest data obtained from Rovbase (Per Sjögren-Gulve and Peter Jaxgård, *personal communication*) to derive retrospective harvest numbers in the model based on the estimated abundances during 2011–2017 (see Table 4). Although the actual number of individuals harvested differed between the Rovbase and model estimates during the retrospective period, the harvest rates were the same in both cases, providing the same magnitude of change in abundance due to harvest. However, in future population projections using a fixed quota harvest, we used the number of individuals harvested in the fixed quota to derive the harvest rate in the model. In summary, we varied the proportion of individuals harvested from 0.05 to 0.25 and also simulated fixed quota removals of 80 to 400 individuals in Sweden, while holding the harvest rate constant in Norway at 0.20 (Table 4).

6.6 Lynx Connectivity between Norway and Sweden

Currently, immigration rates between Norway and Sweden are unknown for lynx. There may be a connection to the Karelian population, but it is considered to be inconsequential for population dynamics based on genetic data and the fact there are few lynx in the reindeer husbandry area of northern Finland (Kaczensky et al. 2012). Given the uncertainty in movement rates of lynx between Sweden and Norway, we used 0.05 (SE = 0.02) for the rate of dispersal from Sweden to Norway based on the baseline movement rate observed for wolverine in Scandinavia (Gervasi et al. 2015). For movement of lynx from Norway to Sweden, we also used the baseline rate for wolverine of 0.02 (SE = 0.01). This assumed that Sweden was a source population, especially given the larger abundance, and that Norway was a sink, which is logical given the higher rates of harvest observed there for lynx.

We then simulated scenarios of source-sink dynamics for dispersal from each country to the other. For simulations of dispersal from Sweden and Norway, we increased the baseline movement rate from 0.05 to 0.10 and then 0.15. For simulations of dispersal from Norway to Sweden, we increased the baseline movement rate from 0.02 to 0.07 and then 0.12. The Sweden-to-Norway increasing rates might occur as Norwegian harvest leads to compensatory immigration from Sweden. The Norway-to-Sweden increasing rates might occur if harvest is relaxed in Norway and abundance increases, resulting in greater dispersal to Sweden (Gervasi et al. 2015).

7. Wolverine

Wolverine are still the most narrowly distributed and rarest large carnivore in Europe, especially compared to lynx (Linnell et al. 2010, Chapron et al. 2014). Yet, like lynx, wolverine never became extirpated historically in Scandinavia. In 2011 about 1100 wolverine were estimated to be across Scandinavia, with about 680 (+/- 100 SE) in Sweden and 385 (+/- 46 SE) in Norway (Kaczensky et al. 2012). Again, Figure 8 is simply for background information.

Occupied wolverine range is similarly reported as expanding in Sweden and stable in Norway. Wolverine are distributed over about half of Sweden, whereas in Norway they cover most of the country except in portions of the south (Figure 8). The stable abundance in Norway is thought to be a direct result of higher harvest with the goal of stabilizing wolverine numbers (see also Table 5 below). Population survey methods vary by country and area within the country, but are generally conducted by wildlife management staff using a combination of snow tracking, natal den surveys, and some efforts to conduct non-invasive genetic mark-recapture surveys. Like lynx, wolverine are managed as endangered under the EU Habitats Directive, and limited harvest is allowed by game wardens as 'protective' harvest under article 16 of the Habitats Directive. In contrast, Norway in wolverine are managed as a defacto game species with annual quota-based harvest and more liberal harvest regulations. Wolverines cause most human-wildlife conflict through depredation on semi-domestic reindeer and (to a lesser degree) domestic sheep. In Sweden, annual costs for reindeer compensation is between 2–2.5 million euros (Kaczensky et al. 2012). In Norway, reindeer and sheep compensation range from 1.8–2.2 million euros, and 2.7–3.8 million Euros, respectively (Kaczensky et al. 2012).



Figure 7. Wolverine, image credit to Jenna Määränen, under an Attribution-NonCommercial-NoDerivs 2.0 Generic license.



Figure 8. Wolverine (*Gulo gulo*) distribution in Scandinavia during 2006–2011. Figure is borrowed from Kaczensky et al. (2012) and provided here just for background information. Dark cells represent documented reproduction while gray cells represent sporadic occurrence.

In terms of management goals, the interim goal for Sweden is based on an interim target of 93 annual reproductions, which represents an approximate abundance of 600 individuals. This target has been suggested to be too small, and a higher goal of 850 (133 yearly reproductions) is being considered. In contrast, the Norwegian management goal is to reduce wolverine to a national goal of 39 reproductions/year, or approximately 250 individuals (Kaczensky et al. 2012). Thus, we used 850 and 250 as the threshold for calculating quasi-extinction probability in PVAs in Sweden and Norway, respectively.

7.1 Wolverine Population Viability Analysis

We conducted a PVA for wolverine in Scandinavia to predict population persistence given human-caused mortality factors, and other factors that may influence wolverine demography. The general approach closely followed that described above for lynx. We primarily focused our analysis on Sweden, but also modeled the population in Norway to consider connectivity and to track abundance in Norway. We use the same underlying model for both populations (as noted above), but use a slightly different model formulation for wolverine recruitment probability and timing.

We used 15 February as the start of the recurrent date for the annual population cycle of wolverine in our model, which was based on the timing of births (Persson et al. 2006). This works well for wolverine since the annual den count surveys occur in winter just before females choose a den site and give birth, and as such the counts do not include juveniles (Per Sjögren-Gulve, *pers. comm.*). We modeled annual estimates of survival for the five stage-classes, along with estimates of the proportion breeding and the litter size of adult females (≥ 3 -yr-old) separately for Sweden and Norway. Note in this regard lynx and wolverine life-cycles differed since the model for lynx includes a non-zero reproductive contribution from 2-yr-old females (Figure 9). We assumed that the winter den count estimate of wolverine occurred before the annual legal harvest in Norway, and since protective harvests could occur any time of season, we were able to apply a uniform harvest rate to the all stage classes as well as to recruitment probability of adult females.

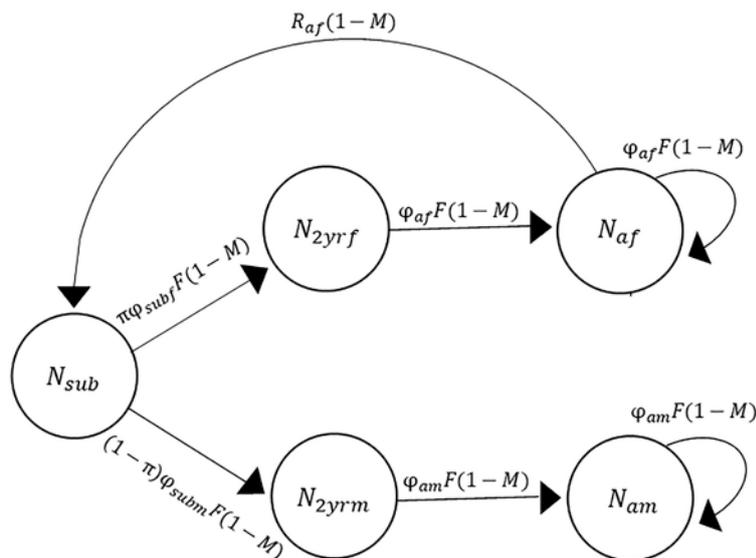


Figure 9. Life-cycle diagram for wolverine that was used in the Population Viability Analysis. Note that only adult females (≥ 3 -yr-old) have a non-zero probability of breeding (Table 3), since wolverine typically do not breed until ≥ 3 -yr-old, so only adult females have a reproductive contribution in the model. Note that the total mortality rate from legal and protective harvest and poaching are combined into one term (M) for simplicity, but are modeled as separate rates in Bayesian population models.

7.2 Wolverine Vital Rate Review

We parameterized our model based on vital rate estimates for wolverine across Scandinavia. A total of 6 studies provided 22 vital rate estimates and SEs for: survival probability ($n = 14$); immigration/emigration rates ($n = 2$); components or estimates of recruitment rate ($n = 6$; e.g., litter size, proportion breeding); human-caused mortality rates ($n = 4$); and abundance ($n = 5$) (Table 5, Appendix 3). We again applied the Delta method to obtain estimates of average vital rates and their uncertainty (see Appendix 1).

For wolverine in Sweden, this resulted in survival estimates of 0.84 (SE = 0.04) for juveniles, 0.94 (SE = 0.03) for female subadults, 0.85 (SE = 0.08) for male subadults, 0.95 (SE = 0.02) for adult females, and 0.99 (SE = 0.01) for adult males. Although we attempted to find country-specific estimates, none existed for survival and reproduction in Norway wolverines, so we applied vital rate estimates from Sweden to lynx populations in Norway (see Table 5). We used a recruitment rate (i.e., number of young surviving their first year of life/breeding female) of 0.46 (SE = 0.08) for adult female wolverine. We used this lower end of wolverine recruitment estimates since some failed reproduction is not accounted for in reproductive surveys and estimates may be biased high (Persson et al. 2006, Nilsson 2013). Harvest rates for wolverines tended to be low in Sweden (<0.05 , see also Table 6), and much higher in Norway (ranging from 0.04–0.20, again, see Table 6, and section 6.5 below).

We used starting abundances of 680 (SE = 100) and 385 (SE = 46) for wolverines in Sweden and Norway respectively, in 2011. The estimates are based on the numbers provided in Kaczensky et al. (2012), which were estimated using DNA capture-recapture methods for wolverine in Norway, while estimates in Sweden were provided from extrapolated den counts. In general, DNA estimates are much more precise than estimates from den counts because they correct for probability of detection or survey effort, which is a known problem with den count indices (Gervasi et al. 2014). But like our caveats for lynx, we note potential disagreements with these population estimates which we return to in the discussion/conclusions. We used the lower threshold of 600 and 250 as the threshold abundance for calculation of quasi-extinction probabilities in the context of evaluating risks of extinction in PVA models.

One study examined dispersal (i.e., immigration/emigration) in wolverine between Norway and Sweden, Gervasi et al. (2015). They reported asymmetric migration between the two countries as expected by the higher harvest rates in Norway consistent with Norway being a potential sink population. Mean migration rates from Norway to Sweden were 0.05 (SE = 0.02), and from Sweden to Norway were 0.02 (SE = 0.01).

Table 5. Abundance and average vital rates with standard errors (SE) derived using the Delta method for the baseline population viability scenario for wolverine in Sweden and Norway. The parameters include the initial abundance (estimate from 2011), minimum p+opulation size for persistence, human-caused mortality rate from legal harvest and poaching (as well as others such as motor vehicle collisions), average number of legal harvest mortalities (2011–2016), juvenile survival (φ_{juv}), female subadult survival (φ_{subf}), male subadult survival (φ_{subm}), adult female survival (φ_{af}), adult male survival (φ_{am}), the litter size, proportion breeding and recruitment rate for adult femlaes, and the dispersal probability from Sweden to Norway and from Norway to Sweden.

Parameter	Sweden		Norway	
	Mean	SE	Mean	SE
Initial abundance	680	100	385	46
Abundance for persistence	600	—	250	—
Human-caused mortality (proportional)				
Legal harvest mortality	0.03	—	0.20	—
Poaching and other human-caused mortality	0.05	—	0.05	—
Average number harvested	17.57	—	101.4	—
Survival				
φ_{juv}	0.84	0.04	0.84†	0.04†
φ_{subf}	0.94	0.03	0.94†	0.03†
φ_{subm}	0.85	0.08	0.85†	0.08†
φ_{af}	0.95	0.02	0.95†	0.02†
φ_{am}	0.99	0.01	0.99†	0.01†
Reproduction				
Adult female				
Litter size	1.88	0.10	1.88†	0.10†
Proportion breeding	0.53	0.05	0.53†	0.05†
Recruitment rate	0.65	0.08	0.65†	0.08†
Immigration				
Sweden to Norway	0.05	0.02	N/A	N/A
Norway to Sweden	N/A	N/A	0.02	0.01

Notes: Vales in the table given as blanks indicate that no estimate was available in the literature, while N/A indicates that the estimate was not applicable.

† We set these parameters in Norway equal to the values of the Swedish population since the estimates were 1.0 (SE = 0) for Norway in the literature or only available in Sweden.

7.3 Density dependence

The only evidence we found for density-dependence for wolverine in Scandinavia was reported by Brøseth et al. (2010), who reported a negative effect of increasing population abundance on adult survival. Similar to lynx, we incorporated density dependence in a ‘what-if’ sensitivity analysis framework. We incorporated the effect of negative density dependence (β_1) on both adult female and male survival rates for wolverine in both countries through a logit link function (Hurley 2016). We constructed the intercept (β_0) for this link function using the logit of the mean adult female and male survival rates (here shown as φ_0), and included the effect size as a function of abundance (N_t) in year t :

$$\beta_0 = \text{logit}(\varphi_0) \quad (23)$$

$$\text{logit}(\varphi_t) = \beta_0 + \beta_1 N_t \quad (24)$$

As described above for lynx the (Brøseth et al. 2010) effect sizes would cause survival to decline towards zero at a abundance of 680 individuals (see Figure 10), an unrealistically strong effect of negative density dependence. Thus, we adjusted effect sizes to provide a reasonable simulation at larger abundances.

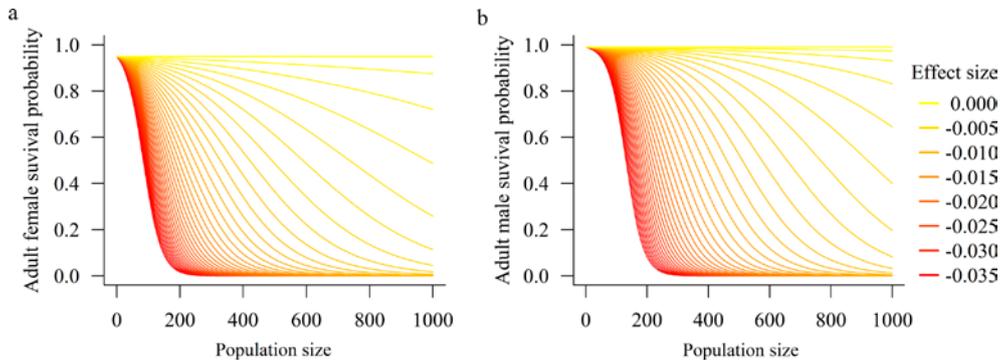


Figure 10. The effect of varying the strength (effect size) of negative density dependence from -0.035 (red) to 0.0 (yellow) on adult female (a) and adult (b) male survival of wolverine in Sweden and Norway.

7.4 Inbreeding depression

We found no empirical evidence for inbreeding depression in wolverine. Thus, we used the identical approach described above for lynx to model hypothetical effects of inbreeding depression on wolverines. As with lynx, the realized inbreeding coefficients in the simulations (below) tended to be very small (<0.1), so the hypothetical costs of inbreeding on recruitment rate at higher inbreeding coefficients shown in Figure 11 are for demonstration purposes only.

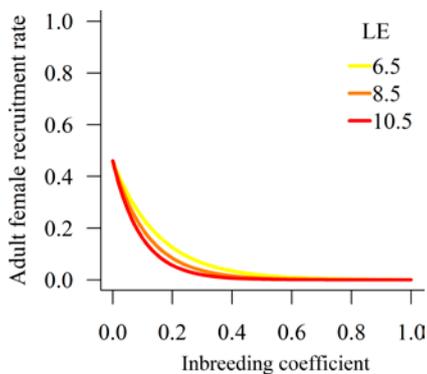


Figure 11. The simulated effect of inbreeding depression adult female recruitment rates predicted over a range of lethal equivalents per gamete (LE) from 6.5 (yellow) to 10.5 (red) for wolverine in Sweden. Note that the y-intercept represents the mean recruitment rate for adult females (0.46). Also note that these plots consider inbreeding coefficients going all the way to fixation (1.0) while in simulations $F < 0.1$.

7.5 Human-caused Mortality

Wolverine mortality rates due to hunter harvest have been relatively low in Sweden compared to Norway where wolverine have been more aggressively harvested. For instance, the wolverine abundance in Sweden was estimated at about 3 times as large as populations in Norway in 2011 (Table 6), but the average number of legally harvested wolverine was much greater in Norway during 2011–2016 at about 100 individuals (see Table 5), owing to higher legal harvest rates in Norway (~25%) compared to Sweden (~5%).

Harvest rates in Norway varied considerably from year-to-year, but have been consistently at around 15–20% over the last decade in Norway and may continue to increase in the future (Table 5; Gervasi et al. 2015). While legal harvest has been effective at manipulating wolverine populations for management purposes, other factors such as poaching are difficult to control and add uncertainty to future viability (Persson et al. 2009). Harvest estimates based on radiotelemetry data show that harvest was low in Sweden (<0.01 , Kaczensky et al. 2012), and higher in Norway (0.15–0.20 – Kaczensky et al. 2012; 0.04–0.24 – Gervasi et al. 2015), and that most harvest was ‘protective’ harvest in Sweden, versus a combination of protective harvest, legal harvest, and some poaching in Norway (Table 5, 6).

Similar to our approach for lynx, we used the actual harvest data obtained from Rovbase (Per Sjogren-Gulve, *personal communication*) to derive retrospective harvest rates in the model based on the estimated abundances in the IPM during 2011–2017 (see Table 6). We used this general formulation of dividing a fixed number of harvested individuals by the total abundance to simulate different levels of fixed quota harvests in models with a non-threshold vs. threshold harvest strategy. In summary, we varied the proportion of individuals harvested from 0.03 to 0.23 and also simulated fixed quota removals of 18 to 138 individuals in Sweden, while holding the harvest rate constant in Norway at 0.20.

Table 6. Retrospective harvest estimates for Eurasian lynx from unpublished data provided by Per Sjogren-Gulve as reported in the ‘Rovbase’ Dead Wolverine 2011–2017. The total number of individuals dying from protective and licensed hunting are given (H_{obs}), along with the median number of individuals harvested (H_{model}) and 95% Bayesian credible intervals (BCI) from a Bayesian population model. We also give the observed harvest mortality rates (MH) that were used as prior rates in Bayesian population models to derive the number of individuals harvested for the retrospective period.

Year	Sweden					Norway				
	M_H	H_{obs}	H_{model}	Lower 95% BCI	Upper 95% BCI	M_H	H_{obs}	H_{model}	Lower 95% BCI	Upper 95% BCI
2011	0.01	6	6	4	7	0.24	100	95	106	114
2012	0.01	9	6	5	9	0.28	136	99	49	75
2013	0.04	33	30	22	41	0.31	95	92	50	104
2014	0.03	22	18	13	26	0.24	88	61	47	122
2015	0.05	35	38	26	54	0.26	118	63	41	129
2016	0.05	13	36	24	54	0.25	89	56	51	178
2017	0.04	5	30	19	47	0.26	54	55	43	165

7.6 Wolverine Connectivity between Norway and Sweden

Like lynx, there appears to be some connection between the Scandinavian wolverine populations and the Karelian populations of Finland and Russia, but no data were available to confirm this (Kaczensky et al. 2012). We used 0.05 (SE = 0.02) for the rate of dispersal from Sweden to Norway based on the baseline movement rate observed for wolverine in Scandinavia (Gervasi et al. 2015). For movement of wolverine from Norway to Sweden, we also used the baseline rate of 0.02 (SE = 0.01). This assumed that Sweden was a source population, which was documented in Gervasi et al. (2015). We considered the same scenarios of varying dispersal rates between the 2 countries.

8. Lynx results

8.1 Status quo and protection scenarios

In general, lynx population growth rate in Sweden was slightly increasing in the years 2011–2017, with a geometric mean population growth rate (λ_G) of 1.03 (95% BCI = 0.98–1.08). Projections of future population growth rate over the next 20 years (2018–2037) were predicted to be slightly higher, with λ_G of 1.05 (95% BCI = 0.99–1.09). In comparison, lynx population growth rate 2011–2017 was slightly lower in Norway, approximately 1.01 (95% BCI = 0.89–1.11), and projected to have higher future growth with λ_G of 1.06 (95% BCI = 1.02–1.11) in the next 20 years (Table 7). Abundances for Sweden ranged from a low of 1462 (95% BCI = 1229–1739) to high of 1748 (1222–2397) during 2011–2017, and was higher than the den count estimates by 500–1000 individuals over the retrospective period (Figure 12a). Abundances for Norway ranged from a low of 301 (95% BCI = 253–378) to high of 363 (95% BCI = 173–659) during 2011–2017, and more closely tracked den count estimates over the retrospective period (Figure 12b).

Under the scenario of complete protection in Sweden, lynx population growth rate would be projected to be 1.10 (95% BCI 1.04–1.14). Further, complete protection in Sweden had a positive effect on lynx growth rate in Norway, which would achieve a similar rate of population growth as Sweden (Table 7). However, projected abundances of lynx in Sweden under complete protection quickly become very high (Figure 13a), approaching 10000 lynx, raising a legitimate concern about the need to integrate the effects of density-dependence in model predictions. Likewise, probability of staying above the quasi-extinction threshold of 870 lynx (“quasi-persistence probability”) was very high under the status quo scenario, remaining near 1.0 over all years (Figure 14a). Likewise, in Norway, the probability of being greater than the management threshold of 310 lynx was also about 1.0 under this scenario by 2025 (Figure 14b).

Table 7. Geometric mean growth rates and 95% Bayesian credible intervals for Eurasian lynx populations given for the status quo and protection in Sweden scenarios. Both retrospective (2011–2017) and projected (2018–2037) estimates are shown for the status quo scenario.

Scenario	Years	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Status quo	2011–2017	1.03 (0.03)	0.98	1.08	1.01 (0.06)	0.89	1.11
	2018–2037	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.02	1.11
Protection in Sweden	2018–2037	1.10 (0.03)	1.04	1.14	1.10 (0.02)	1.05	1.14

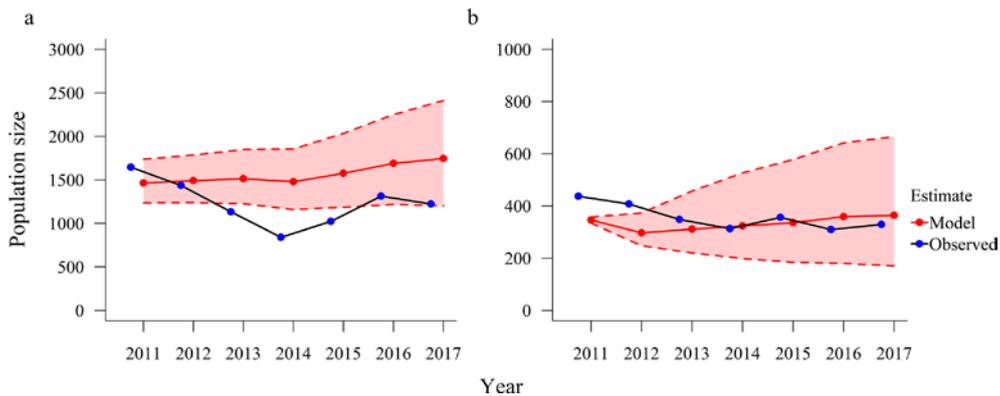


Figure 12. Eurasian lynx retrospective abundance estimates in Sweden (a) and Norway (b) from a Bayesian population model and observed den count extrapolations during 2011–2017. Note that the lynx den counts occur 3 months earlier than the model estimates because dens surveys take place in the winter, while the birth pulse begins in June. The initial abundances for winter 2010–2011 based on den surveys were adjusted 3 months forward using matrix calculations and algebra so that the Bayesian population model would align with the biological cycle of lynx in a pre-birth, stage structured matrix population model. Note that the y-axis scales are different on the two graphs.

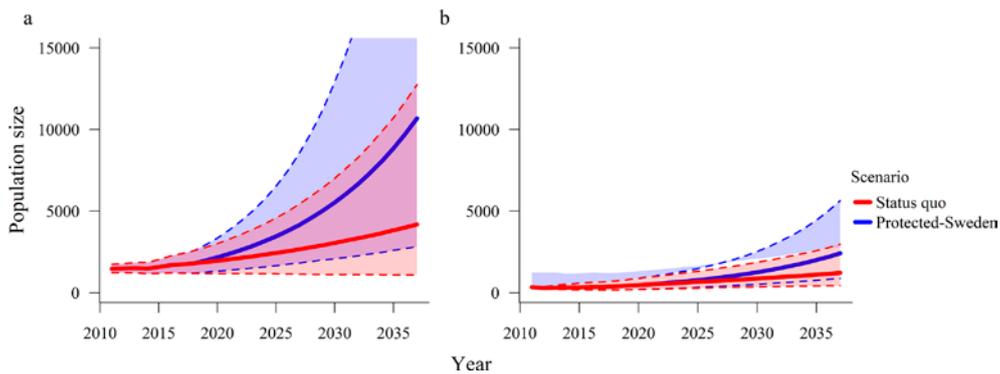


Figure 13. Eurasian lynx abundance in Sweden (a) and Norway (b) projected for the status quo and full protection in Sweden management options from 2011–2037.

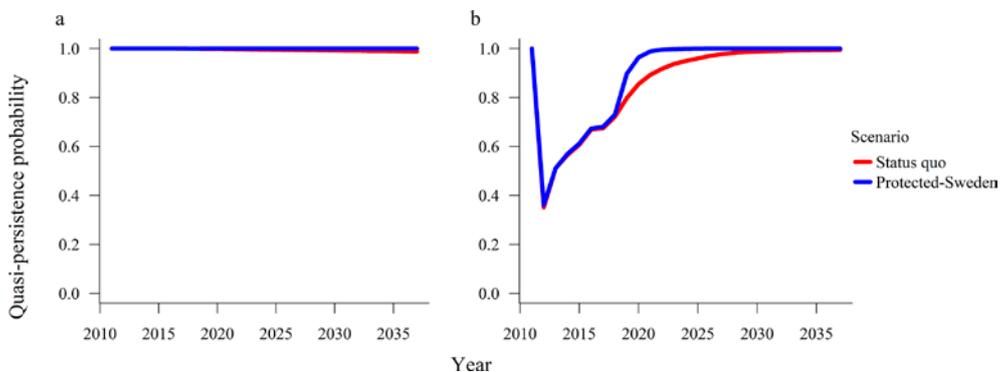


Figure 14. Eurasian lynx quasi-persistence probability modeled from 2011–2037 in Sweden (a) and Norway (b) for status quo and full protection in Sweden. Quasi-persistence probabilities were based on the probability that the abundances were above the management thresholds of 870 and 310 individuals in Sweden and Norway respectively (thresholds from Kaczensky et al. 2013).

8.2 Harvest scenarios

Overall, abundance declined more quickly when the fixed quota harvest was increased compared to increasing proportion harvest (Figure 15, 16), because fewer individuals are harvested with a proportional removal as abundance declines (Figure 15). Also, a threshold harvest with no harvest below the threshold stabilized or increased population growth rates (Figure 16). As for number of lynx harvested over time (Figure 15, 16), a minimum threshold resulted in a stable or slightly increasing number of individuals harvested, except when the proportional harvest was set at > 0.15 or the fixed quota above 240 individuals.

In Sweden, it appears that only the lowest quotas (80–160) and lowest proportional harvest scenarios (0.05–0.10 harvest rate) maintained a high and increasing probability of exceeding the management threshold of 870 lynx (Table 8, Figure 17) in the absence of a minimum no-harvest threshold. For any proportional harvest > 0.05 , population growth rate declined (Table 8), and the probability of quasi-persistence strongly declined (Figure 17). Similarly, above a fixed quota of 160, population growth rate was < 1.0 and quasi-persistence probability quickly declined (Table 8, Figure 17).

However, if the quasi-persistence threshold is set as a minimum floor for harvest, the probability of declines was substantially improved. For all scenarios with a minimum threshold of 870 lynx, population growth rate remained above or close to 1.0, and the probability of staying above the threshold was at least 0.2 and tended to stabilize over time (Figure 17, Table 8).

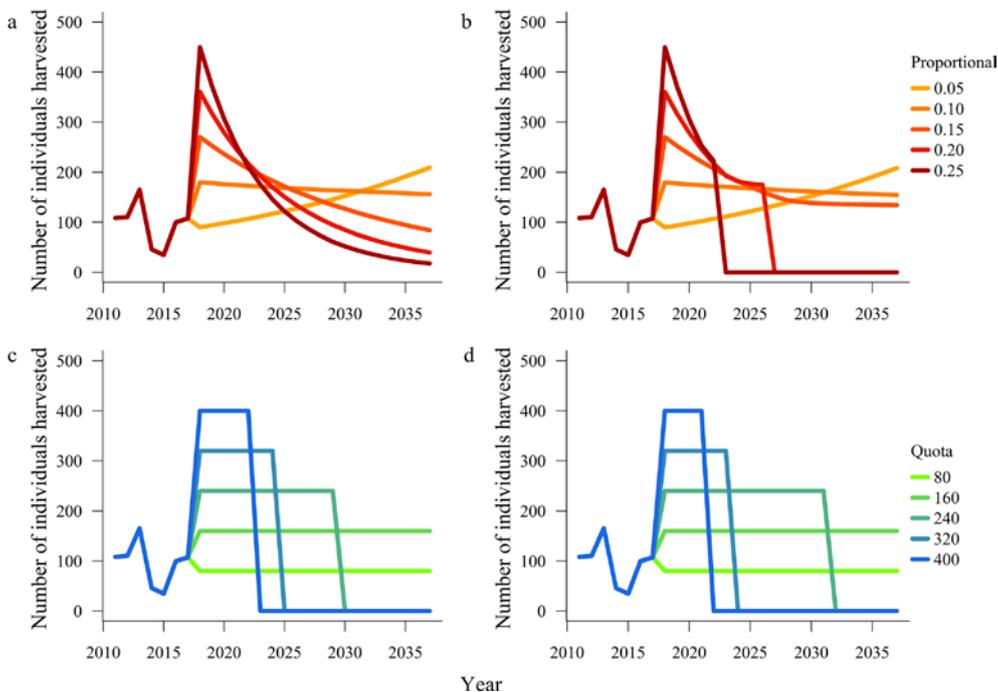


Figure 15. Number of Eurasian lynx harvested during 2011–2017 by proportional harvest without threshold (a), proportional harvest with threshold (b), fixed quota harvest without threshold (c), and fixed quota harvest with threshold (d), in Sweden.

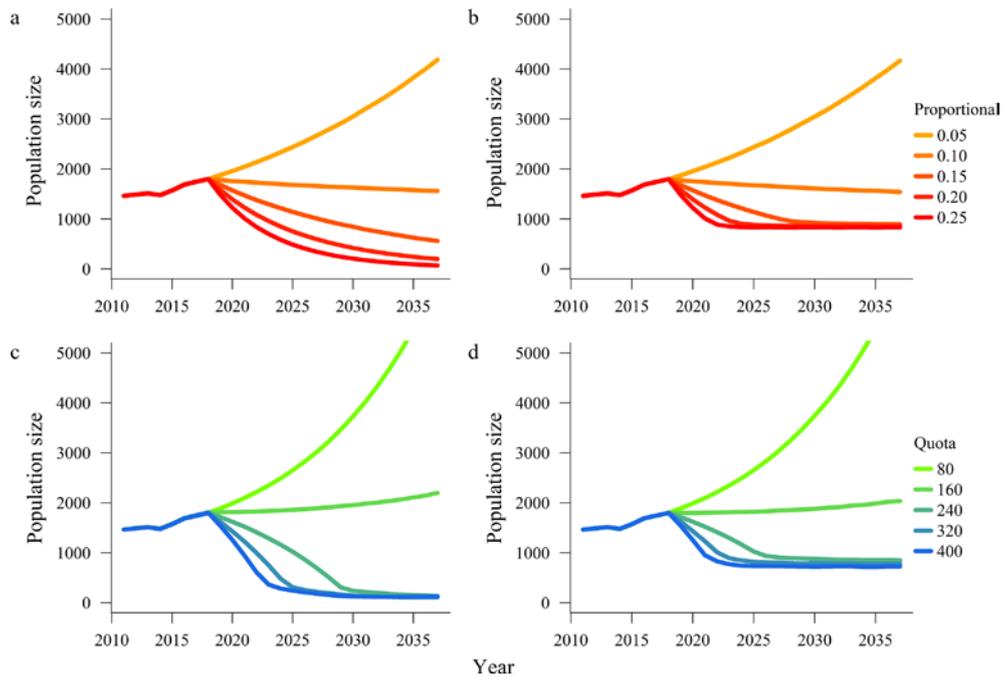


Figure 16. Median abundances for Eurasian lynx during 2011–2017 with proportional harvest without threshold (a), proportional harvest with threshold (b), fixed quota harvest without threshold (c), and fixed quota harvest with threshold (d) in Sweden.

Table 8. Predicted geometric mean growth rates and 95% Bayesian credible intervals for Eurasian lynx populations during 2018–2037 given different simulations of proportional harvest (0.05–0.25), fixed quota harvest (80–400), and proportional and fixed quota harvests with a threshold based on the current management targets of 870 and 310 Eurasian lynx in Sweden and Norway respectively.

Scenario	Value	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Proportional Harvest	0.05*	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.02	1.11
	0.10	0.99 (0.02)	0.95	1.04	1.03 (0.02)	0.98	1.07
	0.15	0.95 (0.02)	0.90	0.98	1.00 (0.03)	0.95	1.04
	0.20	0.90 (0.02)	0.85	0.93	0.97 (0.03)	0.92	1.02
	0.25	0.85 (0.02)	0.81	0.89	0.95 (0.03)	0.90	1.01
Fixed Quota	80	1.07 (0.05)	0.95	1.13	1.08 (0.03)	1.00	1.13
	160	1.01 (0.09)	0.81	1.11	1.04 (0.05)	0.92	1.11
	240	0.88 (0.08)	0.78	1.08	0.97 (0.05)	0.90	1.09
	320	0.87 (0.05)	0.79	1.00	0.95 (0.04)	0.89	1.04
	400	0.88 (0.04)	0.79	0.94	0.95 (0.03)	0.89	1.01
Proportional harvest with Threshold	0.05*	1.05 (0.02)	0.99	1.09	1.06 (0.02)	1.02	1.11
	0.10	0.99 (0.02)	0.97	1.04	1.03 (0.02)	1.00	1.07
	0.15	0.97 (0.01)	0.96	0.99	1.01 (0.01)	0.99	1.05
	0.20	0.97 (0.01)	0.95	0.98	1.01 (0.01)	0.99	1.04
	0.25	0.96 (0.01)	0.95	0.98	1.01 (0.01)	0.99	1.04
Fixed quota with threshold	80	1.07 (0.04)	0.98	1.13	1.08 (0.03)	1.01	1.13
	160	1.01 (0.05)	0.96	1.11	1.04 (0.03)	0.99	1.11
	240	0.97 (0.03)	0.95	1.08	1.01 (0.03)	0.99	1.09
	320	0.96 (0.02)	0.94	1.02	1.01 (0.02)	0.99	1.05
	400	0.96 (0.01)	0.94	0.98	1.00 (0.01)	0.98	1.04

* Note that this is the status quo scenario.

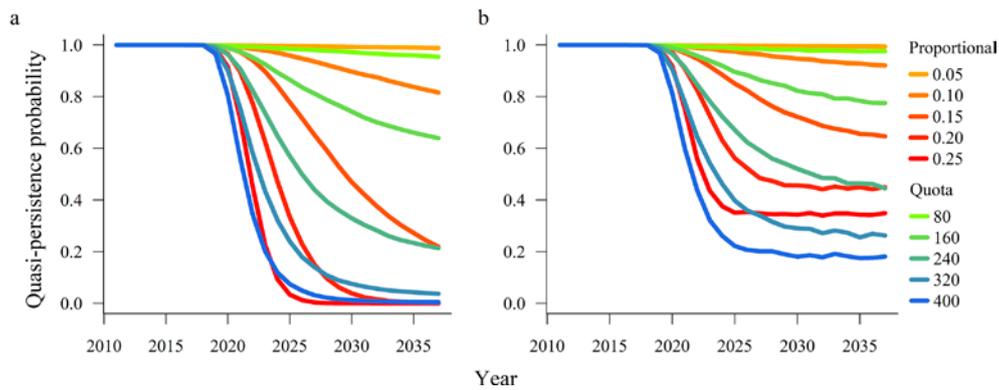


Figure 17. Eurasian lynx quasi-persistence probability for no threshold (a) and threshold (b) harvest strategies modeled from 2011–2037 in Sweden under either proportional harvest (0.05–0.25) or fixed quota harvest (80–400).

8.3 Inbreeding depression

With a 20-year projection interval and relatively large abundances (>1 500), the inbreeding coefficient remained low throughout the simulations (Figure 18). Therefore, effects of inbreeding depression on population viability of lynx were minimal, even under the most severe scenario of a skewed N_{eff}/N_t ratio of 0.3, and the highest inbreeding costs of $B = 10.5$ (Table 9, Figure 18, 19). Even under these conditions, the modeled effect on recruitment was negligible (Figure 18) and population growth rate was only reduced by 1% (Table 9).

Table 9. Predicted geometric mean growth rates and 95% Bayesian credible intervals for Eurasian lynx populations in Sweden and Norway during 2018–2037 over varying intensities of inbreeding depression. The simulated lethal equivalents per gamete (B) were none ($B = 0.0$), low ($B = 6.5$), medium ($B = 10.5$), and high ($B = 11.5$) and populations were projected using effective to total abundance ratios of 0.30, 0.40 and 0.50.

		Sweden			Norway		
N_{eff}/N_t	B	λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
0.30	none	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.02	1.11
	low	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	med	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	high	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
0.40	none	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	low	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	med	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	high	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
0.50	none	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	low	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	med	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10
	high	1.04 (0.03)	0.99	1.09	1.06 (0.02)	1.01	1.10

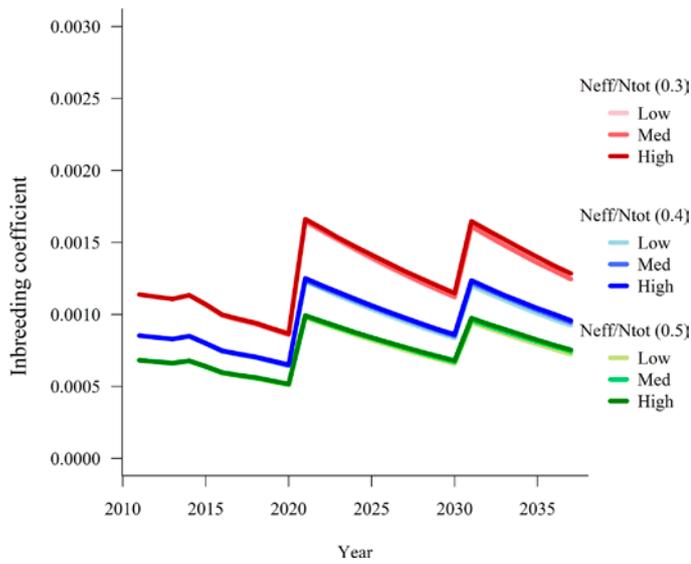


Figure 18. Estimated accumulation of inbreeding coefficient (Gt) for Eurasian lynx from 2011–2037 in Sweden for a range of effective to total abundance ratios (N_{eff}/N_{tot} ; 0.3–0.5) and for varying intensities of inbreeding depression (i.e., lethal equivalents/gamete: 'Low' = 6.5, 'Med' = 8.5, 'High' = 10.5).

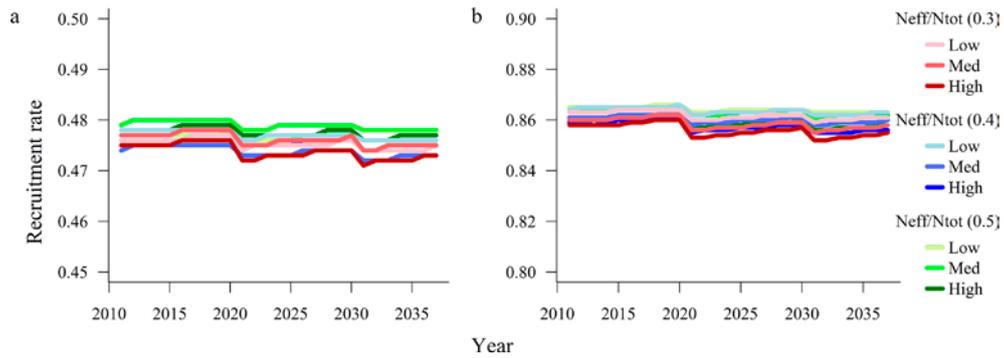


Figure 19. Eurasian lynx recruitment probability for 2-yr-old (a) and adult females (b) in Sweden from 2011–2037 given for a range of effective to total abundance ratios (N_{eff}/N_{tot} ; 0.3–0.5) and for varying intensities of inbreeding depression (i.e., lethal equivalents/gamete: Low = 6.5, Med = 8.5, High = 10.5).

8.4 Negative density dependence

As expected, density-dependence was capable of affecting abundance, growth and persistence probabilities (Table 10, Figure 20–22). As density-dependence increased, population growth rate declined in Sweden but remained near stationary (Table 10). While our approach to model density dependence did not explicitly set a carrying capacity K , and instead modeled a range of coefficients of density dependence on vital rates, Figure 21 shows that K is implied mathematically by these coefficients. For example, Figure 21a suggests that K may be around 1 200 individuals in Sweden for the lowest strength of density dependence, and about 500–600 at medium to high levels of density dependence (Figure 21a). All density-dependence scenarios, especially medium and high scenarios, had strong effects on the probability of persistence (Figure 22a).

Under current conditions, with limited empirical evidence for density-dependence in vital rates in Sweden, it seems reasonable to infer that K is much greater than 870, otherwise previous studies should have certainly found some evidence of strong density dependence. However, should conditions dramatically change in the future, with associated changes in carrying capacity, our scenarios under strong density dependence might become more realistic. Regardless, without further biological evidence of density dependent effects on lynx populations in Scandinavia, we do not recommend considering density dependence as a factor to base management decisions on in Sweden.

In Norway, results of density dependence were similar (Table 10, Figure 20b, 21b, 22b). However, because the threshold abundance for management is much lower in Norway (250), even with stronger density-dependence we see high probabilities of persistence. In this case, it is equivalent to considering that the implicitly modeled K is much greater than this threshold. Thus, understanding the relationship between the threshold abundance for management and K becomes important in considering the effects of density dependence on population viability.

Table 10. Predicted geometric mean growth rates and 95% Bayesian credible intervals for Eurasian lynx populations in Sweden and Norway during 2018–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

Scenario	Value	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Negative	none	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.02	1.11
Density	low	1.00 (0.02)	0.96	1.02	1.02 (0.02)	0.98	1.05
Dependence	med	0.99 (0.01)	0.95	1.01	1.00 (0.02)	0.96	1.04
	high	0.99 (0.01)	0.95	1.00	1.00 (0.03)	0.96	1.03

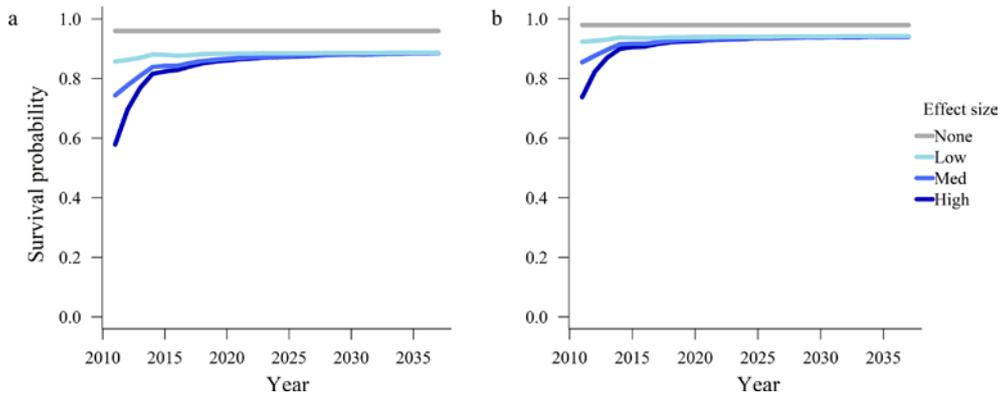


Figure 20. Survival probabilities for adult female (a) and adult male (b) Eurasian lynx during 2011–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

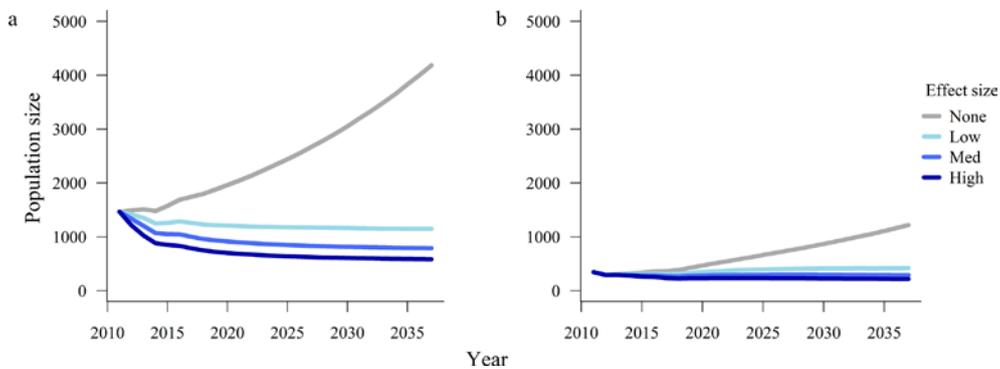


Figure 21. Abundance for Eurasian lynx in Sweden (a) and Norway (b) during 2011–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

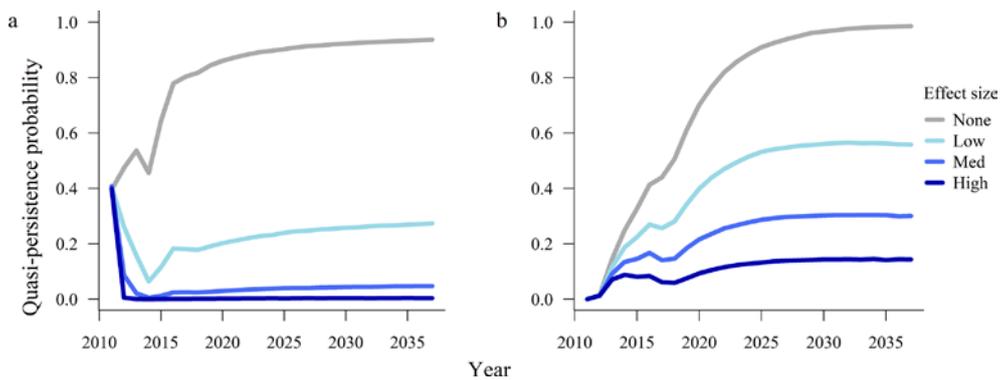


Figure 22. Quasi-persistence probability for Eurasian lynx in Sweden (a) and Norway (b) during 2011–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

8.5 Source-sink dynamics

Source-sink dynamics between Norway and Sweden had strong effects on population viability of lynx in Sweden. We considered 3 basic scenarios for understanding the consequences of immigration and differential harvest between Sweden and Norway. First, under the status quo scenario, we considered baseline dispersal rates of 0.05 from Sweden to Norway and 0.02 from Norway to Sweden based on Gervasi et al. (2015). Under this scenario, population growth rates of Sweden and Norway were similar (Table 11), 1.05 and 1.06, respectively.

Next, we considered the scenario where dispersal from Sweden to Norway increased incrementally from 0.05 to 0.15 while holding all other vital rates constant. Here, we found that population growth rate of lynx declined in both Sweden and Norway (Table 11), especially for Sweden which experienced declines in the numbers of lynx migrating (Figure 23), abundance (Figure 24), and probability of quasi-persistence (Figure 25). In Norway lynx abundance grew initially due to the increased immigration from Sweden, but eventually slowed as the number of Swedish immigrants declined. Norway quickly increased to a quasi-persistence probably near 1.0 under strong immigration from Sweden, and was almost always above its management goal. However, Sweden experienced only about 5–50% probability of quasi-persistence > 870 lynx as dispersal from Sweden to Norway was increased.

Finally, we considered the effects of increasing dispersal from Norway to Sweden from 0.02 to 0.12 (i.e., scenario C). In contrast to scenario B above, increased immigration from Norway to Sweden had a favorable effect on the growth rate of both the Sweden and Norway lynx populations, increasing growth rates by 1% for both populations as compared to the status quo (Table 11). The numbers of lynx migrating (Figure 23), abundance (Figure 24), and probability of quasi-persistence (Figure 25) increased over time. As may be expected, abundance was lower in Norway with higher dispersal from Norway to Sweden, but nonetheless increased over time due to the fact that Sweden remained a source population for Norway. This can be seen in Figure 23 as the number of individuals dispersing from Sweden to Norway was always higher than the number dispersing from Norway to Sweden regardless of the source-sink scenario. This emphasizes the importance of differing abundances of lynx in Norway and Sweden, and the potential for Sweden to counteract high rates of harvest of lynx in Norway (i.e., 20% of the population) as a source population.

Table 11. Predicted geometric mean growth rates (λ_G) and 95% Bayesian credible intervals for Eurasian lynx populations in Sweden and Norway during 2018–2037 for a status quo scenario, and two simulations of source-sink dynamics. In the first simulation, the dispersal rates from Sweden to Norway were incrementally increased from 0.05 (baseline) to 0.15, while in the second simulation the dispersal rates from Norway to Sweden were incrementally increased from 0.02 (baseline) to 0.12. All other vital rates were held at their baseline values for these simulations.

	Sweden			Norway		
Sweden/Norway dispersal rates	λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
0.05/0.02	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.02	1.11
0.10/0.02	1.01 (0.02)	0.96	1.05	1.04 (0.02)	0.99	1.08
0.15/0.02	0.98 (0.02)	0.93	1.02	1.01 (0.02)	0.96	1.05
0.05/0.07	1.06 (0.02)	1.01	1.10	1.07 (0.03)	1.02	1.11
0.05/0.12	1.06 (0.02)	1.02	1.10	1.07 (0.03)	1.03	1.11

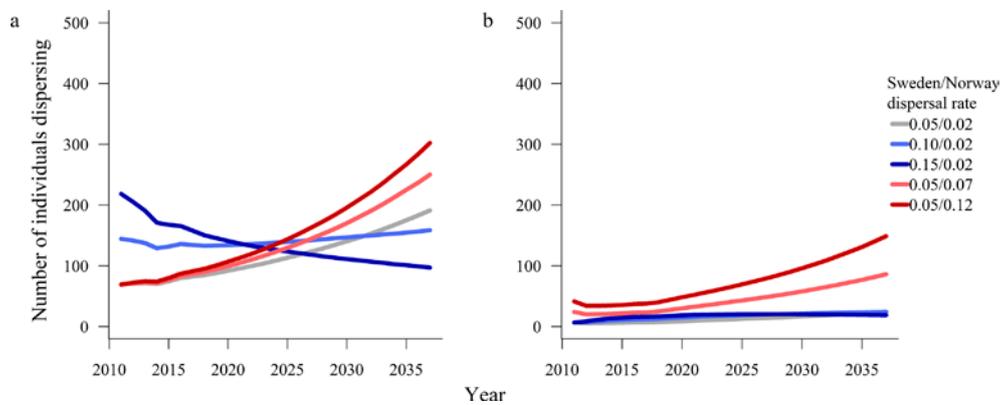


Figure 23. Number of Eurasian lynx dispersing from Sweden to Norway (a) and from Norway to Sweden (b) for source-sink simulations during 2011–2037. Note that the red group simulated higher dispersal rates from Norway to Sweden (0.07 and 0.12), and that the blue group simulated higher dispersal rates from Sweden to Norway (0.10 and 0.15). The dark gray line represents the baseline dispersal rates based on Gervasi et al. (2015) that were 0.05 for dispersal from Sweden to Norway and 0.02 for dispersal from Norway to Sweden.

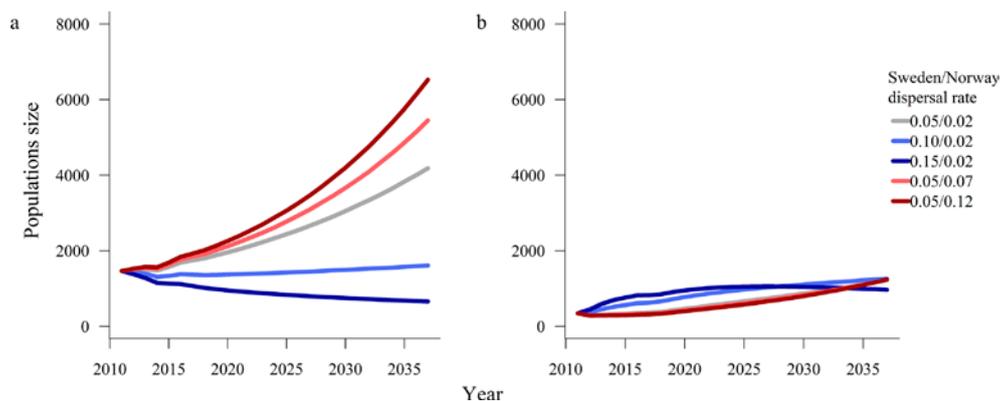


Figure 24. Eurasian lynx abundance for Sweden (a) and Norway (b) from simulations of source-sink simulations during 2011–2037. Note that the red group simulated higher dispersal rates from Norway to Sweden (0.07 and 0.12), and that the blue group simulated higher dispersal rates from Sweden to Norway (0.10 and 0.15). The dark gray line represents the baseline dispersal rates based on Gervasi et al. (2015) that were 0.05 for dispersal from Sweden to Norway and 0.02 for dispersal from Norway to Sweden.

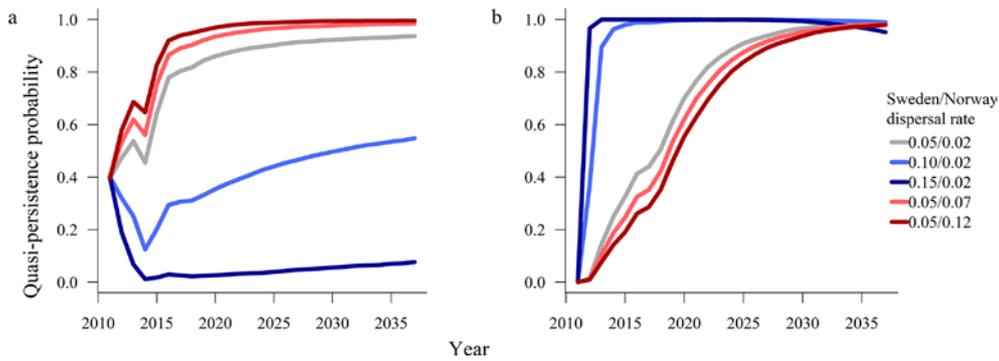


Figure 25. Eurasian lynx quasi-persistence probability for Sweden (a) and Norway (b) under simulations of source-sink simulations during 2011–2037. Note that the red group simulated higher dispersal rates from Norway to Sweden (0.07 and 0.02), and that the blue group simulated higher dispersal rates from Sweden to Norway (0.10 and 0.15). The dark gray line represents the baseline dispersal rates based on Gervasi et al. (2015) that were 0.05 for dispersal from Sweden to Norway and 0.02 for dispersal from Norway to Sweden.

8.6 Cryptic poaching

Here, we investigated consequences of varying cryptic poaching rates for lynx from 0.10–0.25 in Sweden on population viability in Sweden and Norway, on top of baseline harvest rates reported used in the status quo scenario. Baseline harvest rates in Sweden were 0.05 and 0.20 in Norway.

Any cryptic poaching > 0.10 caused population declines in Sweden and Norway, the magnitude of which was stronger for Sweden (Table 12, Figure 26, 27, 28). Only under minimal levels of cryptic poaching, <0.10, did the lynx population continue to grow, and the probability of exceeding the threshold abundance stay high. Again, the difference between Figure 27 and 28 for Norway depends on the much smaller population threshold for Norway, 250. Cryptic poaching caused population declines in Norway as well. This effect on the Norwegian population was through a reduction in immigrants from Sweden to Norway as Swedish populations decline with increased cryptic poaching. Thus, given that both populations decline under higher cryptic poaching rates in Sweden (i.e., ≥ 0.15), the number of individuals lost to poaching also declines.

Table 12. Geometric mean growth rates and 95% Bayesian credible intervals for Eurasian lynx populations in Sweden and Norway during 2018–2037 for a status quo scenario, and different levels of cryptic poaching. The level of poaching in Sweden was incrementally increased from 0.15 to 0.25 (from 0.05 in Figure 21), while all other vital rates were held at their baseline values.

Scenario	Value	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Status quo	0.10	1.05 (0.03)	0.99	1.09	1.06 (0.02)	1.02	1.11
Cryptic poaching	0.15	0.99 (0.02)	0.94	1.03	1.02 (0.02)	0.97	1.06
	0.20	0.94 (0.02)	0.89	0.97	0.97 (0.03)	0.92	1.02
	0.25	0.89 (0.02)	0.83	0.92	0.94 (0.03)	0.88	0.99

* Note that the status quo scenario here is based on the baseline rate of harvest of 0.20 in Norway and 0.10 in Sweden.

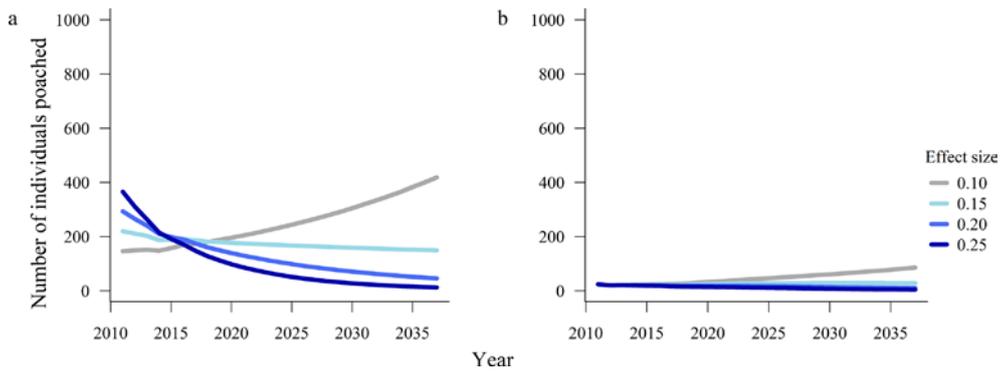


Figure 26. Number of individuals poached from simulations of cryptic poaching on Eurasian lynx populations during 2011–2037 in Sweden (a) and Norway (b) with levels of poaching in Sweden set to the status quo (0.10), 0.15, 0.20, and 0.25, and all other vital rates held at their baseline values.

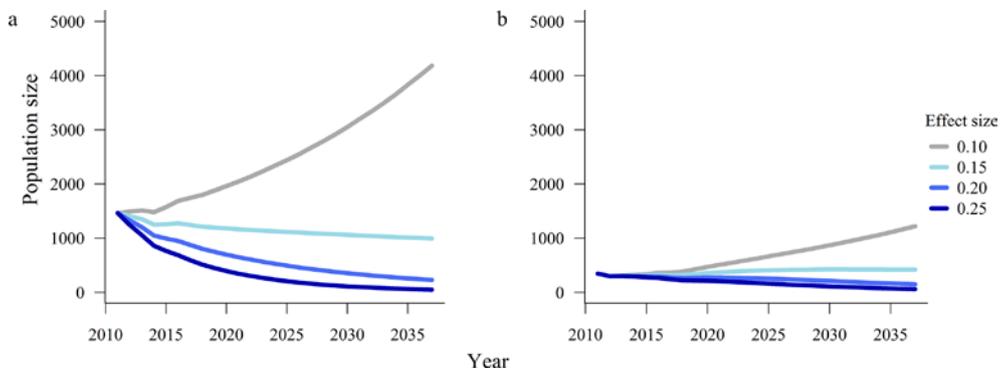


Figure 27. Abundances from simulations of cryptic poaching on Eurasian lynx populations during 2011–2037 in Sweden (a) and Norway (b) with levels of poaching in Sweden set to the status quo (0.10), 0.15, 0.20, and 0.25, and all other vital rates held at their baseline values.

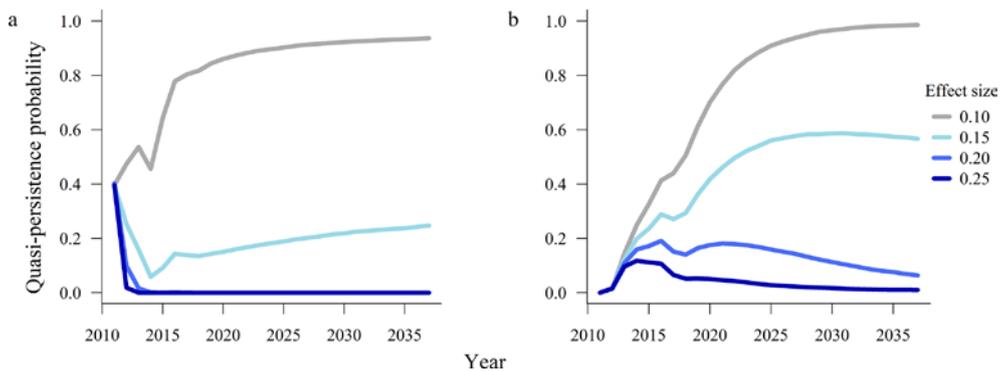


Figure 28. Quasi-persistence probabilities from simulations of cryptic poaching on Eurasian lynx populations during 2011–2037 in Sweden (a) and Norway (b) with levels of poaching in Sweden set to the status quo (0.10), 0.15, 0.20, and 0.25, and all other vital rates held at their baseline values.

8.7 Sensitivity analysis

Bayesian life-stage simulation analysis (LSA) for the Swedish lynx showed that fidelity (1 – probability of emigrating from the population), had the strongest effect on overall population growth rate (Table 13, Figure 29). The slope for the effects of fidelity on population growth rate was 0.90, and the R^2 was the largest, at 0.42, with increasing probability of migration (1 – fidelity) corresponding to decreasing population growth rate in Sweden (Figure 28). After fidelity, the next most important vital rates for population growth were adult female survival and recruitment rates, with slopes of 0.96 and 0.87, and corresponding R^2 values of 0.26 and 0.20, followed by 2-yr-old recruitment rate and female subadult survival (Table 13, Figure 29). As expected, both subadult and adult male survival contributed very little to population growth. We also explored consequences of using the predicted geometric growth rate from our Bayesian models in the LSA, and found that the results were not qualitatively different from regressing the asymptotic population on vital rates (see Appendix 4).

Table 13. Results of Bayesian sensitivity analysis for Swedish lynx, providing the coefficient estimates (β) and standard errors (SE), coefficients of variation (CV) and (R^2) for simple linear regressions of the asymptotic growth rate (λ_{SSD}) against vital rates: female subadult survival (φ_{subf}), male subadult survival (φ_{subm}), adult female survival (φ_{af}), adult male survival (φ_{am}), fidelity (or 1 minus the probability of lynx dispersing from Sweden to Norway; F), and the recruitment rate for 2-yr-old (R_{2yrf}) adult female (R_{af}) Eurasian lynx.

Parameter	λ_{SSD}				
	Mean (SD)	CV	β_0 (SE)	β_1^a	R^2
φ_{subf}	0.94 (0.03)	0.03	0.81 (0.03)	0.24 (0.03)†	0.07
φ_{subm}	0.74 (0.07)	0.09	1.03 (0.01)	0.01 (0.01)	< 0.01
φ_{af}	0.96 (0.02)	0.02	0.37 (0.04)	0.69 (0.04)†	0.26
φ_{am}	0.98 (0.01)	0.01	1.03 (0.09)	0.01 (0.09)	< 0.01
F	0.95 (0.02)	0.02	0.19 (0.03)	0.90 (0.03)†	0.42
R_{2yrf}	0.49 (0.11)	0.22	1.01 (0.01)	0.06 (0.01)†	0.06
R_{af}	0.87 (0.06)	0.07	0.87 (0.01)	0.19 (0.01)†	0.20

†These slope parameters were significant at $P < 0.001$.

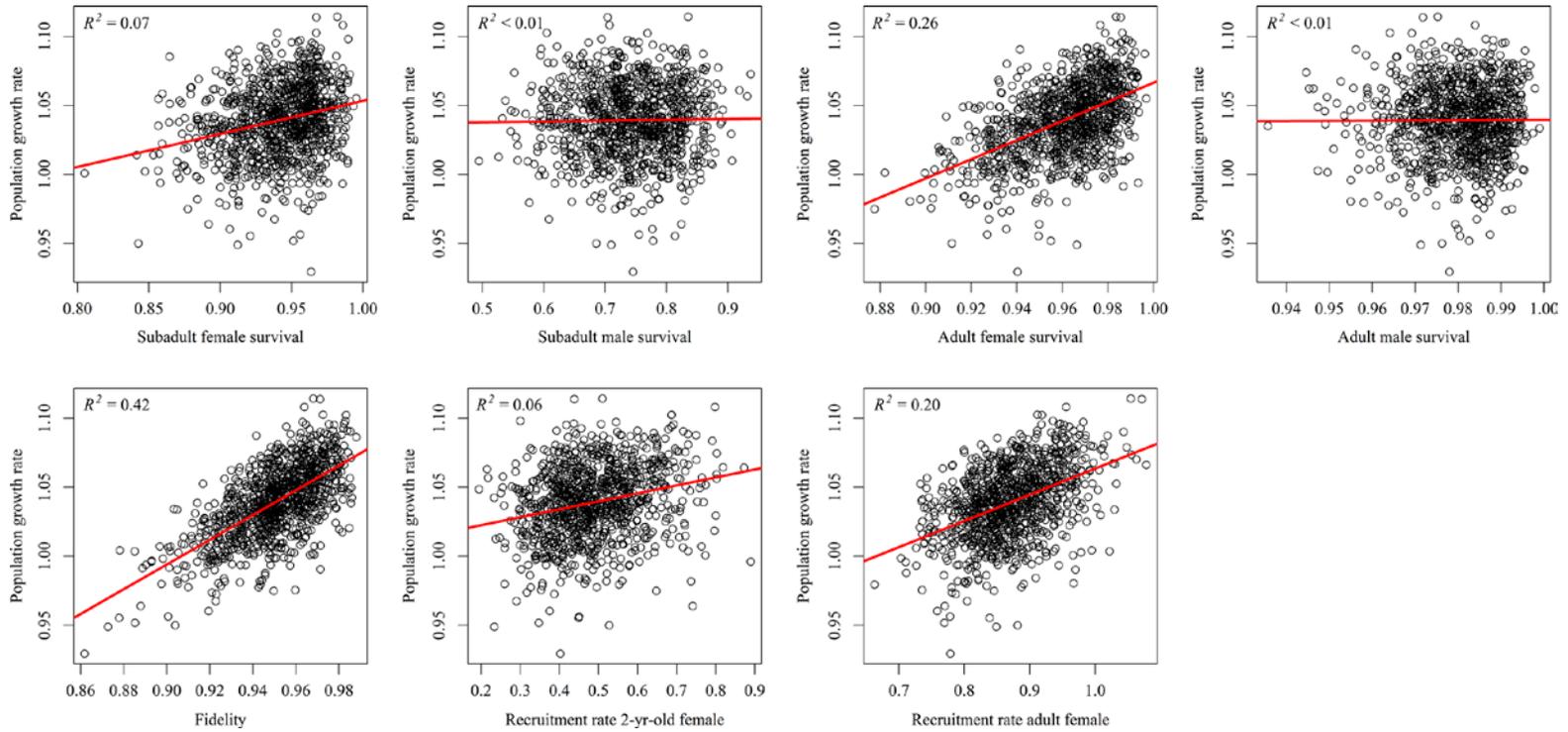


Figure 29. Results of Bayesian sensitivity analysis for lynx in Sweden showing simple linear regressions of the asymptotic growth rate (λ_{SSD}) against female subadult survival, male subadult survival, adult female survival, adult male survival, fidelity (or 1 minus the probability of dispersing from Sweden to Norway), and the recruitment rates for 2-yr-old and adult female Eurasian lynx. We include the coefficient of determination (R^2) for each vital rate, which gives the amount of variation in population growth rate explained by each vital rate.

9. WOLVERINE RESULTS

9.1 Status quo and protection scenarios

In Sweden, wolverine population growth rate was stationary or slightly increasing in the years 2011–2017 and for the next 20 years until 2037 (Table 14). In comparison, wolverine population growth rate was much lower in Norway under current conditions, approximately 0.91 (95% BCI = 0.83–0.98) from 2011–2017, and projected to be 1.01 (95% BCI = 0.96–1.05) in the next 20 years (Table 14, Figure 31b). Abundances for Sweden ranged from a low of 695 (95% BCI = 523–927) to high of 742 (508–1 069) during 2011–2017, and was similar to the den count estimates from 2011–2014 and lower thereafter (Figure 30a). Abundances for Norway ranged from a high of 390 (95% BCI = 173–659) in 2011 to a low of 214 (95% BCI = 126–348) in 2017, and model estimates were generally higher than the den count estimates over the retrospective period (Figure 30b).

Under the scenario of complete protection in Sweden, wolverine population growth rate would increase both in Sweden and Norway (Table 14). Projected abundances of wolverine in Sweden under complete protection quickly become unrealistically high (Figure 30), highlighting the need to integrate the effects of density-dependence. However, compared to the lynx scenarios, population growth rate of wolverines is lower and abundance in Sweden is predicted to only reach about ~1 300 individuals.

The probability of being at or above the minimum population threshold of 600 wolverines in Sweden (quasi-persistence probability) under the status quo scenario was always greater than ~0.60 over the projection interval (Figure 31). Under complete protection in Sweden, the quasi-persistence probability increased to about 0.85 by 2037. Likewise, in Norway, the probability of having greater than 250 wolverines was high and near 0.40–0.70 (Figure 30b).

Table 14. Geometric mean growth rates (λ_G) and 95% Bayesian credible intervals (BCI) for wolverine populations given for the status quo and protection in Sweden scenarios. Both retrospective (2011–2017) and projected (2018–2037) estimates are shown for the status quo scenario.

Scenario	Years	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Status quo	2011–2017	1.01 (0.03)	0.94	1.07	0.91 (0.04)	0.83	0.98
	2018–2037	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
Protection in Sweden	2018–2037	1.03 (0.03)	0.97	1.09	1.03 (0.03)	0.97	1.08

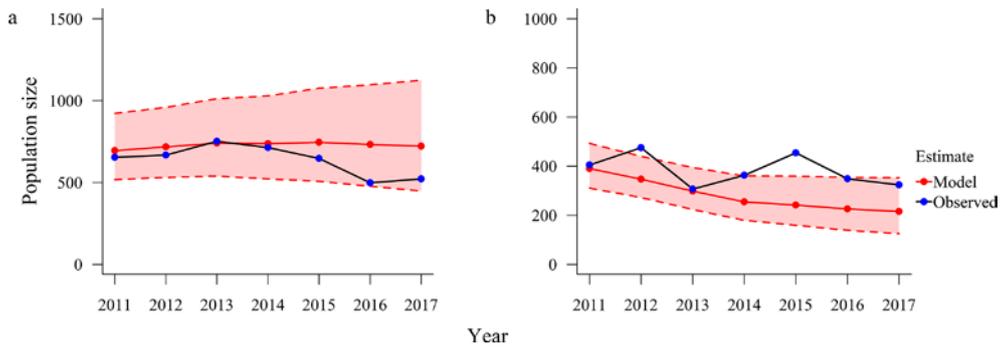


Figure 30. Wolverine retrospective abundance estimates in Sweden (a) and Norway (b) from a Bayesian population model and observed den count extrapolations during 2011–2017. Note that the y-axis scales are different on the two graphs.

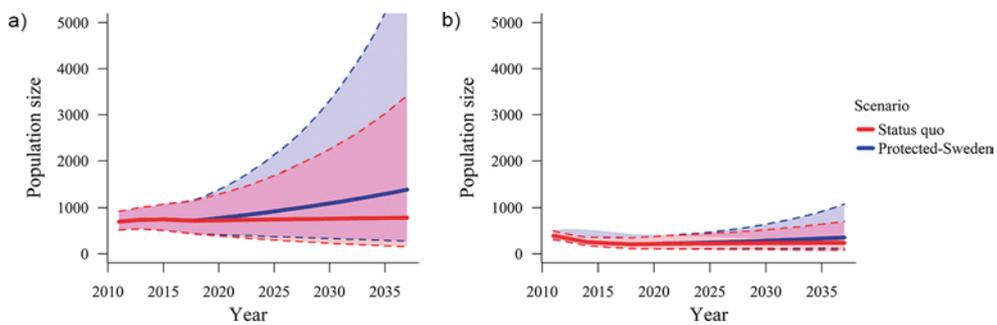


Figure 31. Wolverine abundance in Sweden (a) and Norway (b) projected for the status quo and full protection in Sweden management options from 2011–2037.

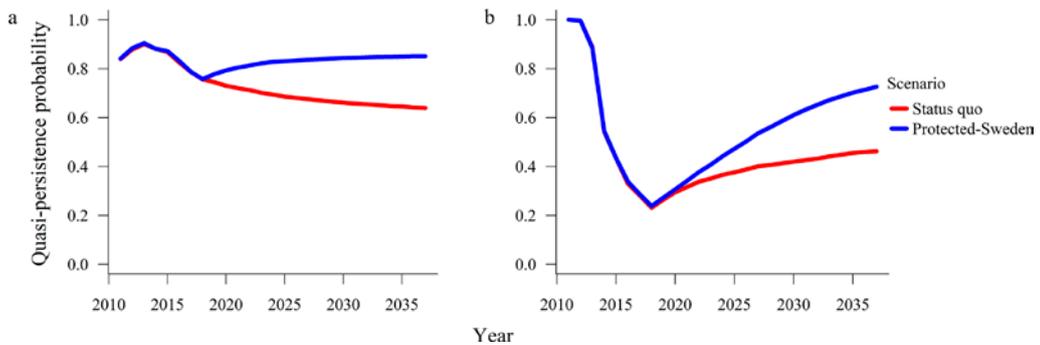


Figure 32. Wolverine quasi-persistence probability modeled from 2011–2037 in Sweden (a) and Norway (b) for status quo and full protection in Sweden. Quasi-persistence probabilities were based on the probability that the abundances were above the management thresholds of 600 and 250 individuals in Sweden and Norway respectively.

9.2 Harvest scenarios

Similar to lynx, wolverine abundance declined more quickly when the fixed quota harvest was increased compared to increasing proportion harvest (Figure 33, 34). Again, a no-harvest lower threshold stabilized population growth (Figure 34). As for number of wolverine harvested over time (Figure 33), a minimum threshold resulted in a stable or slightly increasing number of individuals harvested only for a proportional harvest of 0.03 or a fixed quota of 18 individuals/year.

In Sweden, without a lower no-harvest threshold, only the lowest quota (18) and lowest proportional harvest scenario (0.03 harvest rate) maintained a high and increasing probability of exceeding the management threshold of 600 wolverine (Table 15, Figure 35). For any proportional harvest > 0.03, population growth rate declined (Table 14) and the probability of persistence also declined to 0 (Figure 35). Similarly, above a fixed quota of 18, population growth rate rapidly declined.

Table 15. Predicted geometric mean growth rates and 95% Bayesian credible intervals for wolverine populations during 2018–2037 given different simulations of proportional harvest (0.03–0.23), fixed quota harvest (18–138), and proportional and fixed quota harvests with a threshold based on the current management targets of 600 and 250 wolverines in Sweden and Norway respectively. All other rates including the harvest rate of 0.20 in Norway, were held at their status quo values.

Scenario	Value	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Proportional harvest	0.03*	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
	0.08	0.96 (0.03)	0.90	1.01	0.98 (0.02)	0.93	1.02
	0.13	0.91 (0.03)	0.86	0.96	0.95 (0.02)	0.90	0.99
	0.18	0.87 (0.03)	0.81	0.91	0.93 (0.02)	0.88	0.96
	0.23	0.82 (0.02)	0.78	0.87	0.91 (0.02)	0.86	0.95
Fixed Quota	18	1.01 (0.05)	0.85	1.08	1.01 (0.03)	0.93	1.07
	48	0.91 (0.08)	0.80	1.06	0.96 (0.05)	0.88	1.05
	78	0.87 (0.06)	0.79	1.03	0.92 (0.04)	0.87	1.03
	108	0.87 (0.05)	0.79	0.98	0.92 (0.03)	0.86	1.00
	138	0.87 (0.04)	0.79	0.93	0.91 (0.02)	0.86	0.96
Proportional harvest with threshold	0.03	1.01 (0.02)	0.97	1.06	1.02 (0.02)	1.00	1.06
	0.08	0.99 (0.01)	0.97	1.01	1.01 (0.01)	0.99	1.04
	0.13	0.99 (0.01)	0.97	1.01	1.01 (0.01)	0.99	1.04
	0.18	0.99 (0.01)	0.96	1.00	1.01 (0.01)	0.99	1.04
	0.23	0.98 (0.01)	0.96	1.00	1.01 (0.01)	0.99	1.04
Fixed quota with threshold	18	1.01 (0.03)	0.97	1.08	1.02 (0.02)	1.00	1.07
	48	1.00 (0.02)	0.97	1.06	1.01 (0.01)	0.99	1.05
	78	0.99 (0.02)	0.97	1.03	1.01 (0.01)	0.99	1.04
	108	0.99 (0.01)	0.97	1.01	1.01 (0.01)	0.99	1.04
	138	0.99 (0.01)	0.96	1.00	1.01 (0.01)	0.99	1.04

* Note that this is the status quo scenario.

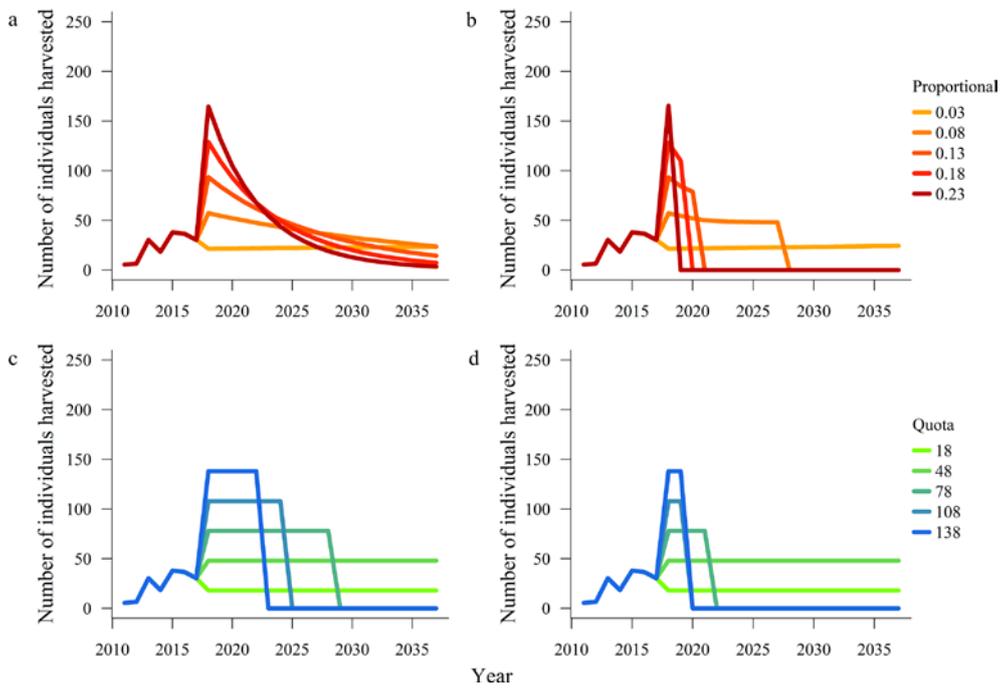


Figure 33. Number of wolverine (*Gulo gulo*) harvested by proportional harvest without threshold (a), proportional harvest with threshold (b), fixed quota harvest without threshold (c), and fixed quota harvest with threshold (d), in Sweden during 2011–2037.

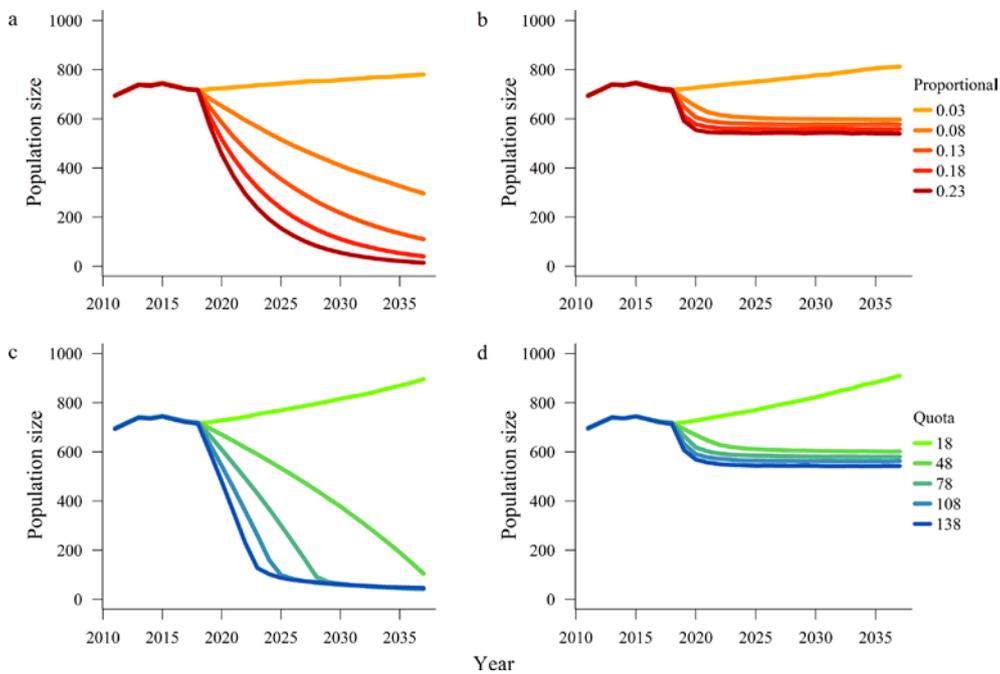


Figure 34. Median abundances for wolverine (*Gulo gulo*) with proportional harvest without threshold (a), proportional harvest with threshold (b), fixed quota harvest without threshold (c), and fixed quota harvest with threshold (d) in Sweden during 2011–2037.

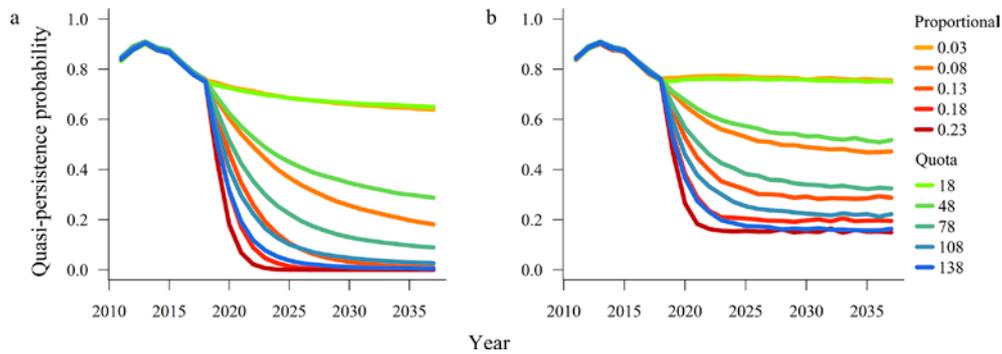


Figure 35. Wolverine (*Gulo gulo*) quasi-persistence probability for no threshold (a) and threshold (b) harvest strategies modeled from 2011–2037 in Sweden under either proportional harvest (0.03–0.23) or fixed quota harvest (18–138).

However, using the threshold abundance as no-harvest floor dramatically increased the probability of avoiding declines. For all scenarios with this minimum threshold, population growth rate was ~ 1.0 (Table 15), the probability of quasi-persistence was >0.5 , and the probability of falling below the minimum threshold was at least 0.2 and tended to increase over time (Figure 35, Table 15), and number of wolverine increased.

9.3 Inbreeding depression

Qualitatively, results for inbreeding depression in wolverines were the same as for lynx. Effects were weak even under the most severe costs of inbreeding and lowest N_e/N ratio primarily due to the large wolverine abundances (Table 16, Figure 36, 37).

Table 16. Predicted geometric mean growth rates and 95% Bayesian credible intervals for wolverine populations in Sweden and Norway during 2018–2037 over varying intensities of inbreeding depression. The simulated lethal equivalents per gamete (B) were none ($B = 0.0$), low ($B = 6.5$), medium ($B = 8.5$), and high ($B = 10.5$) and populations were projected using effective to total abundance ratios of 0.30, 0.40 and 0.50.

		Sweden			Norway		
N_{eff}/N_t	β	λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
0.30	none	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
	low	1.00 (0.03)	0.93	1.06	1.00 (0.03)	0.94	1.05
	med	1.00 (0.03)	0.93	1.06	1.00 (0.03)	0.94	1.05
	high	1.00 (0.03)	0.93	1.06	1.00 (0.03)	0.93	1.05
0.40	none	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
	low	1.00 (0.03)	0.94	1.06	1.00 (0.03)	0.95	1.05
	med	1.00 (0.03)	0.93	1.06	1.00 (0.03)	0.94	1.05
	high	1.00 (0.03)	0.93	1.06	1.00 (0.03)	0.94	1.05
0.50	none	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
	low	1.00 (0.03)	0.94	1.06	1.00 (0.03)	0.95	1.05
	med	1.00 (0.03)	0.94	1.06	1.00 (0.03)	0.95	1.05
	high	1.00 (0.03)	0.93	1.06	1.00 (0.03)	0.94	1.05

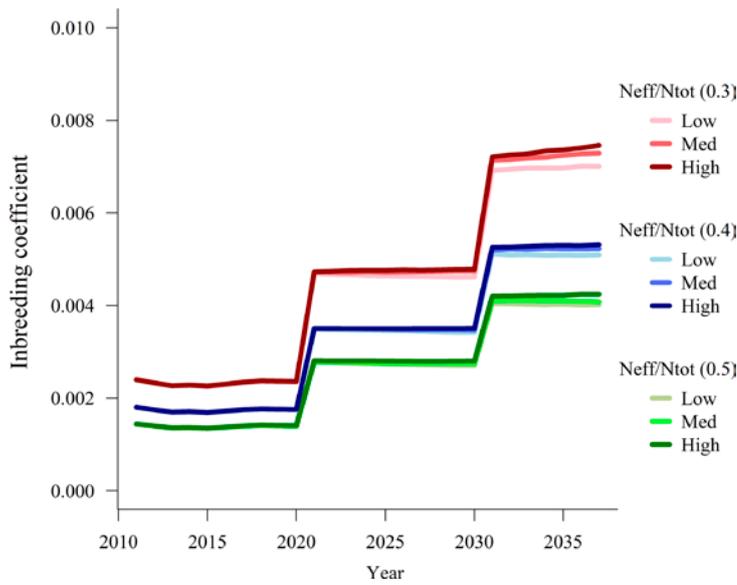


Figure 36. Estimated inbreeding coefficient (Gt) for wolverine from 2011–2037 in Sweden given for a range of effective to total abundance ratios typically found in large carnivores (N_{eff}/N_{tot} ; 0.3–0.5) and for varying intensities of inbreeding depression (i.e., lethal equivalents/gamete: Low = 6.5, Med = 8.5, High = 10.5).

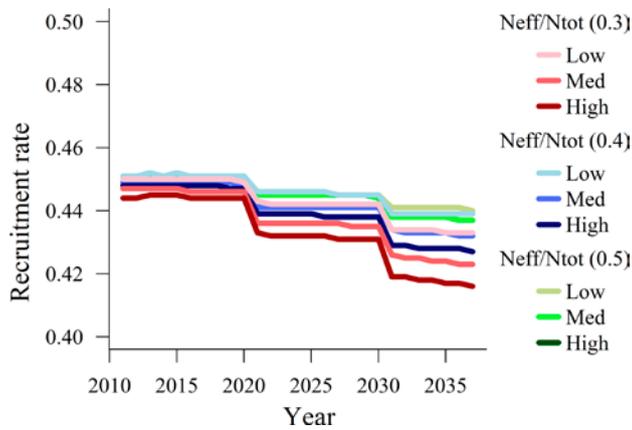


Figure 37. Wolverine recruitment probability for adult females in Sweden given for a range of effective to total abundance ratios typically found in large carnivores (N_{eff}/N_{tot} ; 0.3–0.5) and for varying intensities of inbreeding depression and for varying intensities of effects sizes of inbreeding depression (i.e., lethal equivalents/gamete: Low = 6.5, Med = 8.5, High = 10.5).

9.4 Negative density dependence

Results for density-dependence in wolverine were qualitatively similar to that of lynx (Figure 38–40, Table 17). Medium and high density-dependence scenarios had very strong effects because the population declined close to 200, far below the threshold used of 600. Under current conditions, with limited empirical evidence for density-dependence in vital rates in Sweden, it seems reasonable to infer that K is much greater than 600. However, should conditions dramatically change in the future with increasing density of wolverines, our scenarios under strong density dependence might become more realistic. In Norway, results of density dependence were similar, with declining population growth rate, abundance, and probability of persistence (Table 17, Figure 39b, 40b). However, even with the threshold abundance for management being much lower in Norway (250), probabilities of persistence were lower than in Sweden due to the larger decline in population growth rate (4% vs. 3%; Table 17) and smaller starting abundances; again, this implies that the modeled K is \gg higher than this threshold.

Table 17. Geometric mean growth rates (λ_G) and 95% Bayesian credible intervals for wolverine populations in Sweden and Norway during 2017–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

Scenario	Value	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Negative Density Dependence	None	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
	Low	0.98 (0.02)	0.93	1.02	0.98 (0.02)	0.94	1.02
	Med	0.97 (0.02)	0.92	1.01	0.97 (0.02)	0.93	1.01
	High	0.97 (0.02)	0.92	1.00	0.97 (0.02)	0.92	1.00

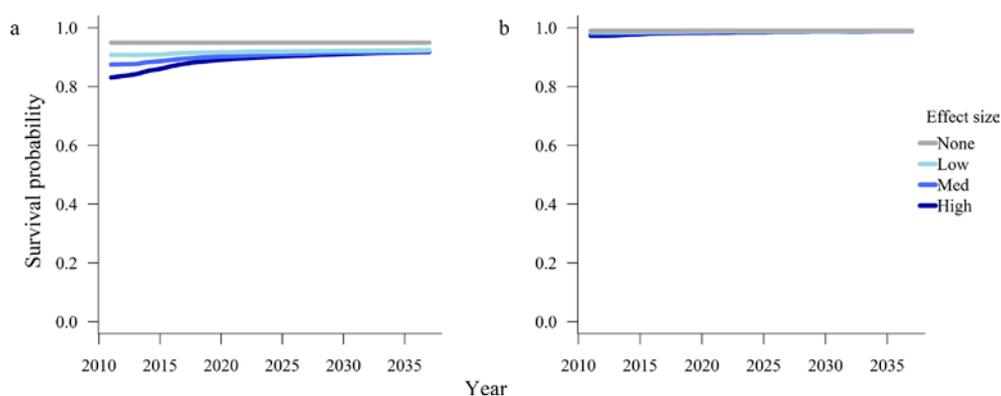


Figure 38. Survival probabilities for adult female (a) and adult male (b) wolverine (*Gulo gulo*) during 2011–2037 over varying intensities of negative density dependence. The simulated effect sizes were low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

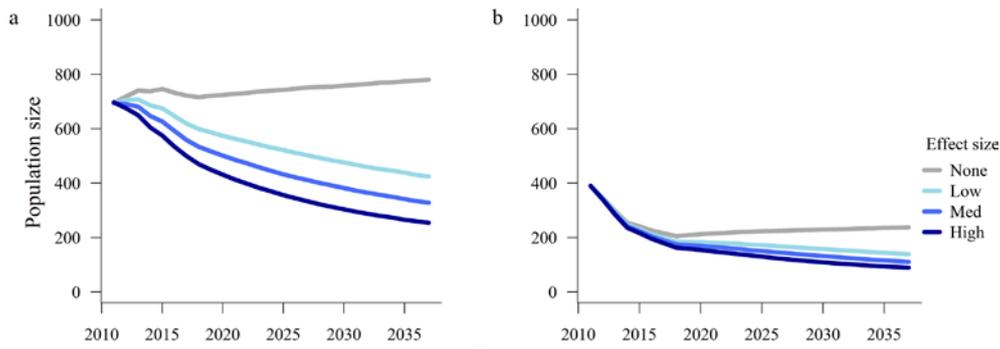


Figure 39. Abundance for wolverine (*Gulo gulo*) in Sweden (a) and Norway (b) during 2011–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

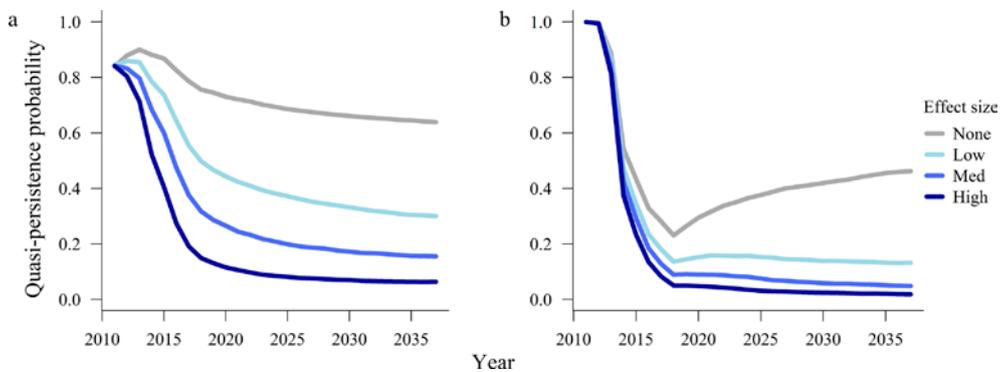


Figure 40. Quasi-persistence probability for wolverine (*Gulo gulo*) in Sweden (a) and Norway (b) during 2011–2037 over varying intensities of negative density dependence. The simulated effect sizes were none ($\beta = 0.0$), low ($\beta = -0.001$), medium ($\beta = -0.0015$), and high ($\beta = -0.002$).

9.5 Source-sink dynamics

Similar to lynx, source-sink dynamics between Norway and Sweden had very strong effects on population viability of wolverine in Sweden. Under the status quo scenario, we considered baseline dispersal rates of 0.05 from Sweden to Norway and 0.02 from Norway to Sweden, and found similar population growth rates in Sweden and Norway (Table 18).

Next, we considered increasing wolverine dispersal from Sweden to Norway incrementally from 0.05 to 0.15 while holding all other vital rates constant. Here, we found that population growth rate of wolverine declined in both Sweden and Norway (Table 18). This resulted in declining abundance (Figure 42) and probability of quasi-persistence (Figure 43) for wolverine after 20 years. Also, in contrast to lynx, wolverine abundance decreased over all years in Norway due to the increased immigration from Sweden, highlighting the inability of Sweden to sustain immigrants to Norway under high rates of dispersal. Sweden experienced <20% probability of quasi-persistence > 600 wolverine when dispersal from Sweden to Norway was increased.

Table 18. Predicted geometric mean growth rates (λ_G) and 95% Bayesian credible intervals for wolverine populations in Sweden and Norway during 2018–2037 for a status quo scenario, and two simulations of source-sink dynamics. In the first simulation, the dispersal rates from Sweden to Norway were incrementally increased from 0.05 (baseline) to 0.15, while in the second simulation the dispersal rates from Norway to Sweden were incrementally increased from 0.02 (baseline) to 0.12. All other vital rates were held at their baseline values for these simulations.

	Sweden			Norway		
Sweden/Norway dispersal rates	λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
0.05/0.02	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
0.10/0.02	0.97 (0.03)	0.91	1.02	0.99 (0.02)	0.94	1.03
0.15/0.02	0.93 (0.03)	0.88	0.99	0.96 (0.02)	0.92	1.01
0.05/0.07	1.02 (0.03)	0.96	1.07	1.01 (0.03)	0.97	1.06
0.05/0.12	1.02 (0.03)	0.97	1.07	1.02 (0.03)	0.97	1.07

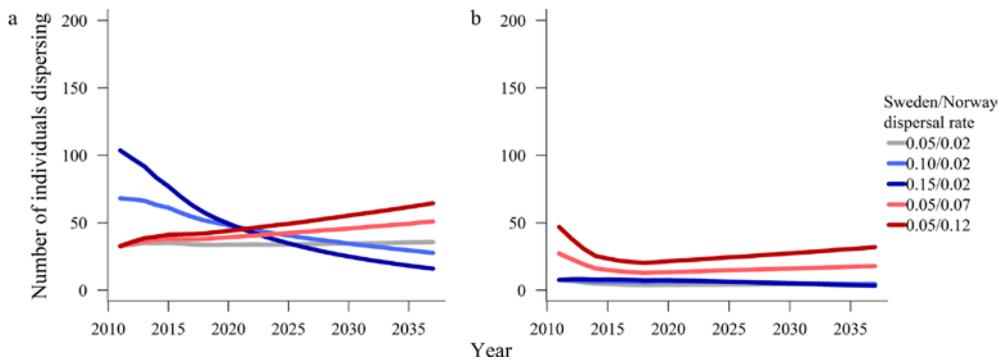


Figure 41. Number of wolverine dispersing from Sweden to Norway (a) and from Norway to Sweden (b) for source-sink simulations during 2011–2037. Note that the red group simulated higher dispersal rates from Norway to Sweden (0.07 and 0.12), and that the blue group simulated higher dispersal rates from Sweden to Norway (0.10 and 0.15). The dark gray line represents the baseline dispersal rates based on Gervasi et al. (2015) that were 0.05 for dispersal from Sweden to Norway and 0.02 for dispersal from Norway to Sweden.

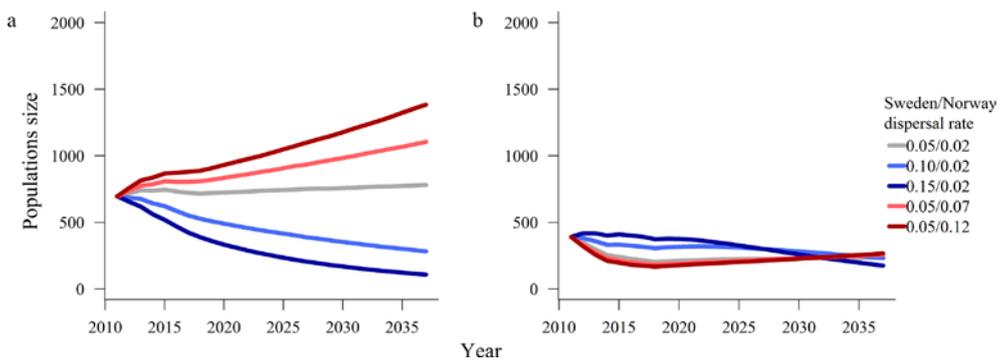


Figure 42. Wolverine abundance for Sweden (a) and Norway (b) from simulations of source-sink simulations during 2011–2037. Note that the red group simulated higher dispersal rates from Norway to Sweden (0.07 and 0.12), and that the blue group simulated higher dispersal rates from Sweden to Norway (0.10 and 0.15). The dark gray line represents the baseline dispersal rates based on Gervasi et al. (2015) that were 0.05 for dispersal from Sweden to Norway and 0.02 for dispersal from Norway to Sweden.

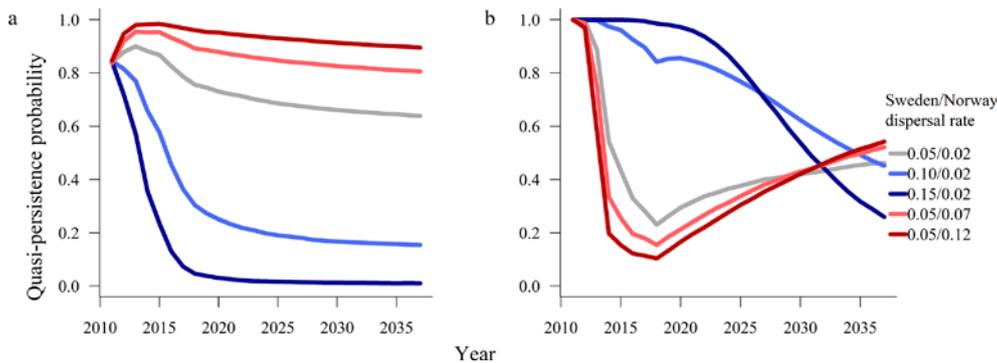


Figure 43. Wolverine quasi-persistence probability for Sweden (a) and Norway (b) under simulations of source-sink simulations during 2011–2037. Note that the red group simulated higher dispersal rates from Norway to Sweden (0.07 and 0.02), and that the blue group simulated higher dispersal rates from Sweden to Norway (0.10 and 0.15). The dark gray line represents the baseline dispersal rates based on Gervasi et al. (2015) that were 0.05 for dispersal from Sweden to Norway and 0.02 for dispersal from Norway to Sweden.

Finally, we considered the effects of increasing wolverine dispersal from Norway to Sweden from 0.02 to 0.12 (i.e., scenario C). In contrast to scenario B above, increased immigration from Norway to Sweden had a positive effect on the growth rate of both the Sweden and Norway wolverine populations, increasing growth rates by 1–2% for both populations as compared to the status quo (Table 18). In both countries, the numbers of wolverine migrating (Figure 41), abundance (Figure 42), and probability of quasi-persistence (Figure 43) increased over time. Interestingly, abundance was similar in Norway as dispersal rate increased from from Norway to Sweden, likely due to the compensation from more individuals dispersing from Sweden. Only under the status quo and higher dispersal from Norway to Sweden (0.07, 0.012) scenarios did Sweden act as a source population; otherwise the number of immigrants moving between populations was similar (Figure 41). This emphasizes the importance of differing abundances of wolverine in Norway and Sweden, especially in comparison to the overall larger abundances of lynx in Scandinavia, and the limited ability for Sweden act as a source population under high rates of harvest of wolverine in Norway (i.e., 20% of the population).

9.6 Cryptic poaching

As with lynx, we investigated consequences of varying cryptic poaching of wolverines from 0.10–0.25 on Swedish and Norwegian wolverine population viability, on top of baseline harvest rates reported and used in the status quo scenario. Baseline harvest rates in Sweden were 0.03 and 0.20 in Norway. Here, any cryptic poaching > 0.05 caused population declines in Sweden and Norway, the magnitude of which was stronger for Sweden (Table 19, Figure 44, 45, 46). Only under minimal levels of cryptic poaching < 0.05 did the wolverine population continue to grow, and the probability of quasi-persistence stay high. Again, the quasi-persistence probability was lower in Norway compared to

Sweden given the smaller abundance and similar level of decline in population growth rates. The negative effect of higher cryptic poaching in Sweden on wolverine in Norway is amplified by reduced dispersal from Sweden to Norway and Swedish populations decline.

Table 19. Geometric mean growth rates (λ_G) and 95% Bayesian credible intervals for wolverine populations in Sweden and Norway during 2018–2037 for a status quo scenario, and different levels of cryptic poaching. The level of poaching in Sweden was incrementally increased from 0.05 to 0.20 while all other vital rates were held at their baseline values.

Scenario	Value	Sweden			Norway		
		λ_G (SD)	Lower 95% BCI	Upper 95% BCI	λ_G (SD)	Lower 95% BCI	Upper 95% BCI
Status quo	0.05	1.00 (0.03)	0.95	1.06	1.01 (0.03)	0.96	1.05
Cryptic poaching	0.10	0.95 (0.03)	0.90	1.01	0.96 (0.02)	0.92	1.01
	0.15	0.91 (0.03)	0.85	0.96	0.93 (0.02)	0.88	0.97
	0.20	0.86 (0.03)	0.81	0.91	0.90 (0.02)	0.85	0.94

*Note that the status quo scenario here of 0.05 cryptic poaching is based on the baseline rate of harvest of 0.20 in Norway and 0.03 in Sweden.

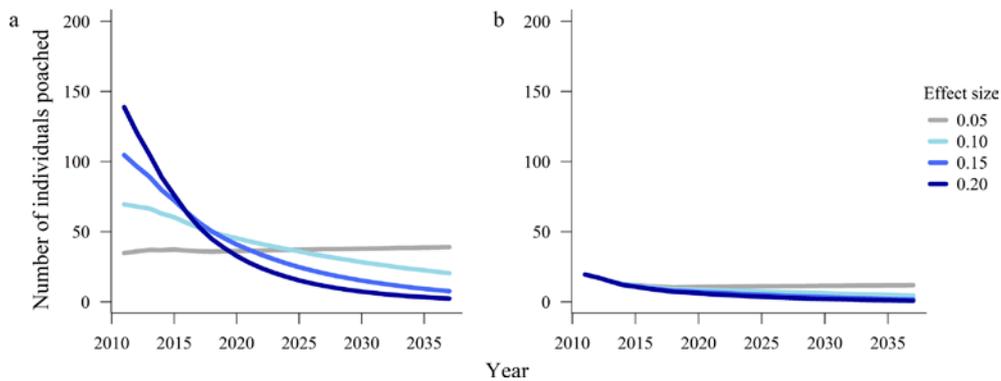


Figure 44. Number of individuals poached from simulations of cryptic poaching on wolverine populations in Sweden (a) and Norway (b) with levels of poaching set to the status quo (0.05), 0.10, 0.15, and 0.20, and all other vital rates held at their baseline values.

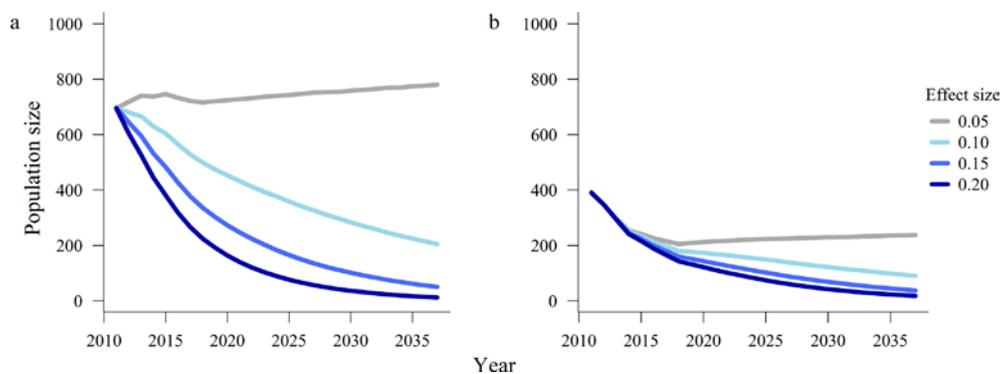


Figure 45. Abundances for simulations of cryptic poaching on wolverine populations in Sweden (a) and Norway (b) with levels of poaching set to the status quo (0.05), 0.10, 0.15, and 0.20, and all other vital rates held at their baseline values.

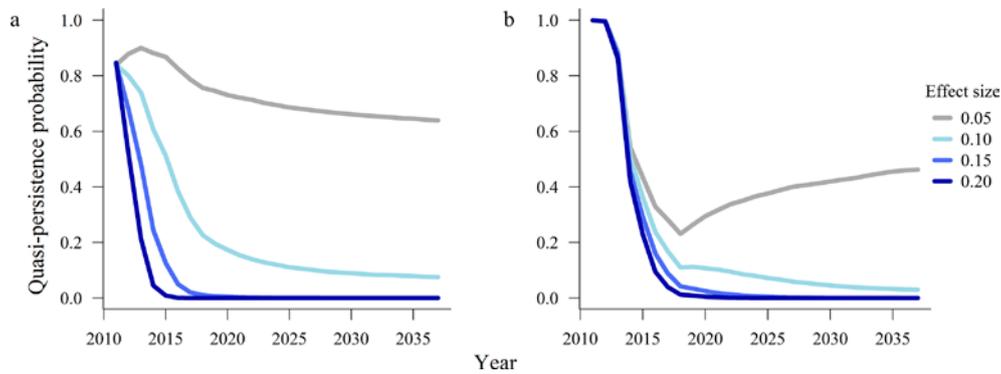


Figure 46. Quasi-persistence for simulated effects of cryptic poaching on wolverine populations in Sweden (a) and Norway (b) with levels of poaching set to the status quo (0.05), 0.10, 0.15, and 0.20, and all other vital rates held at their baseline values.

9.7 Sensitivity analysis

Bayesian life-stage simulation analysis (LSA) for wolverines in Sweden showed that recruitment probability of young from adult females (≥ 3 -yr-old) had the strongest effect on overall population growth rate (Table 20, Figure 47). The slope for the effects of the recruitment probability of young from adult females on population growth rate was 0.28, and the R^2 was the largest, at 0.43 (Figure 45). The next most important vital rate for population growth rate in Sweden was fidelity, with a slope near 1 and R^2 of 0.31, followed by adult female survival ($\beta_1 = 0.84$, $R^2 = 0.27$, Table 13, Figure 47). As expected, especially with a zero rate of recruitment from 2-yr-old females, neither male or female subadult survival, or adult male survival contributed significantly to population growth rate. We also explored using the predicted geometric growth rate from our Bayesian models in the LSA, and found that the results were not qualitatively different from regressing the asymptotic population on vital rates (see Appendix 5).

Table 20. Results of Bayesian sensitivity analysis for Swedish wolverines as for lynx (Table 13).

Parameter	λ_{SSD}				
	Mean (SD)	CV	β_0^a (SE)	β_1^a (SE)	R^2
Φ_{subf}	0.94 (0.03)	0.03	0.90 (0.03)	0.10 (0.03)†	<0.01
Φ_{subm}	0.86 (0.08)	0.09	0.99 (0.01)	0.01 (0.01)	<0.01
Φ_{af}	0.95 (0.02)	0.02	0.20 (0.04)	0.84 (0.04)†	0.27
Φ_{am}	0.99 (0.01)	0.01	1.04 (0.10)	-0.05 (0.10)	<0.01
F	0.85 (0.02)	0.02	0.10 (0.04)	0.94 (0.04)†	0.31
R_{af}	0.46 (0.08)	0.17	0.87 (0.01)	0.28 (0.01)†	0.43

† These slope parameters were significant at $P < 0.001$.

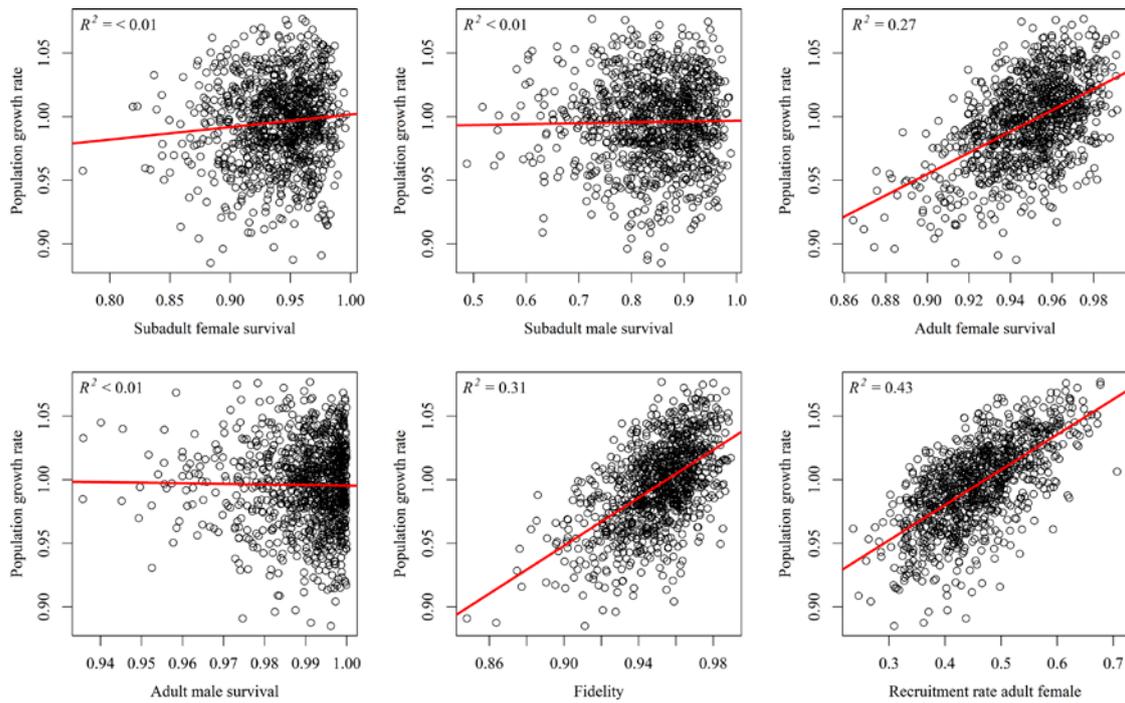


Figure 47. Results of Bayesian sensitivity analysis for Swedish wolverines showing simple linear regressions of the asymptotic growth rate (λ_{SSD}) against female subadult survival, male subadult survival, adult female survival, adult male survival, fidelity (or 1 minus the probability of emigrating), and the recruitment rate for adult female wolverine. We give the coefficient of determination (R^2) for each vital rate, which provides the amount of variation in population growth rate explained by each vital rate.

10. CONCLUSIONS

In conclusion, we found that the main drivers of the viability of lynx and wolverine in Sweden were the choice of harvest strategy, corresponding harvest strategy in neighboring Norway and resultant source-sink dynamics, and the amount of underreported and unknown cryptic poaching. Given current abundances of lynx and wolverine in Sweden, at approximately 1750 and 750 (based on model estimates), there is minimal concern for short-term (20 year) effects of inbreeding depression. And given the dearth of empirical evidence, we do not recommend considering density-dependence in current scenarios. The best harvest strategy in Sweden to maintain the minimum threshold abundance of both species would limit harvest below this management threshold. Our results also highlighted the sensitivity of Swedish lynx and wolverine population growth to the level of unreported, or cryptic, poaching. Given the importance of movement between Sweden and Norway to population viability of Swedish lynx and wolverine populations, and the potential for harvest rates in Norway to affect movement rates between countries through compensatory immigration (Gervasi et al. 2015), we recommend continued efforts to integrate carnivore management between Sweden and Norway.

First, we summarize retrospective population trends of lynx and wolverine during the period from 2011–2017. Again, our approach was to ‘anchor’ abundance at 2011 population estimates reported in the LCIE reports (Kaczensky et al. 2012), and then use mean vital rates from the literature to align the starting estimate to the biological life cycle. We discuss implications and assumptions of this approach below. Focusing first on lynx, during the retrospective time period of 2011–2017, the geometric population growth rate, λ_G , for lynx was 1.03 (95% Bayesian Confidence Interval, BCI of 0.98–1.08) in Sweden, and 1.01 (0.89–1.11) in Norway. These model estimates were very comparable to the population growth rate estimates based on den counts of ~ 0.95 for both Sweden and Norway during 2011–2017, but were about 5–15% lower than estimates used in the Nilsson (2013) PVA report.

Wolverine λ_G was stable or slightly declining between 2011–2017, with $\lambda_G = 1.01$ (95% BCI = 0.94–1.07) in Sweden, but declining in Norway with $\lambda_G = 0.91$ (95% BCI = 0.83–0.98) during the same time period. These modeled estimates for wolverine agreed qualitatively with the figures from Nilsson (2013) of 1.02–1.05; the population growth rate estimated from the den counts during 2011–2017 of ~ 0.96 for wolverine in both Sweden and Norway fell within our 95% Bayesian credible intervals for both countries. Overall, these retrospective results did not differ greatly from future projections of population growth rate from 2017–2037. For example, for lynx and wolverines in Sweden, future population growth was predicted to be 1.05 (95% BCI 0.99–1.09) and 1.00 (95% BCI 0.95–1.06), respectively, similar to their recent retrospective growth rates. In Norway, future growth rates for lynx and wolverine were

projected to be slightly higher at 1.06 (95% BCI 1.02–1.11) and 1.01 (95% BCI from 0.96–1.05), respectively. In summary, from the Swedish perspective, lynx and wolverine in Sweden were maintained at approximate stability or slightly increasing trends during the period of 2011–2017, and are expected to be stable or slightly increase under status quo conditions in the future.

Without a threshold below which harvest is set to zero, only a fixed harvest quota of 80–160 lynx or 18 wolverines or a proportional harvest of 5% for lynx or 3% for wolverines can be sustained with positive population growth and high quasi-persistence probability in Sweden. Only when a harvest threshold of 870/600 (for lynx/wolverine) was initiated, below which harvest was eliminated, did λ_G and abundance stay stationary or increasing. Thus, a recommendation with respect to harvest is to consider a minimum threshold in Sweden below which there no harvest occurs. Obviously, this strategy depends crucially on the target abundance. In this context, our results completely agree with results of previous population viability models for wolverines and lynx in Scandinavia (e.g., Saether et al. 2010). Of course, some hybrid scenario could be evoked whereby the lower threshold abundance for harvest is higher for game hunting and lower for ‘protective harvest’ (i.e., legal harvest to reduce carnivore-livestock conflict). Our API interface could easily be adapted to consider such a scenario.

All of our harvest scenarios also implicitly assumed completely additive effects of harvest. Regardless of the ongoing and unresolved debate about whether harvest of large carnivores is additive or compensatory, managers could consider our additive harvest levels as the worst-case scenario in the presence of even modest levels of vital rate compensation. Future studies should continue to try to understand the degree of compensatory mortality and reproduction in Scandinavian large carnivore populations.

Our evaluation of the importance of cryptic poaching highlights the problems with assuming perfect detection of all mortality through regular monitoring and harvest reporting. As described earlier, there has been an increasing awareness in the large carnivore literature of the difficulty of estimating ‘cryptic poaching’. Our results demonstrate that even modest levels of additive cryptic poaching (an additional 0.10 harvest rate) can drive Swedish lynx and wolverine populations to decline under status quo harvest rates, which were themselves quite low in Sweden. Compared to gray wolves in Scandinavia and Canadian grizzly bears, this level of cryptic poaching (0.10) is modest. Thus, understanding underreported cryptic poaching will be a key for wolverine and lynx management in Sweden. To be conservative, it may be necessary to adjust legal/reported harvest downwards to accommodate some level of unreported cryptic poaching while achieving positive population growth and persistence.

We detected no strong effects of inbreeding depression on recruitment rates or population growth for lynx or wolverine, even under the highest inbreeding cost and ratio of N_e/N . This was likely due mostly to the relatively large abundances, leading to accumulation of only very small inbreeding coefficients (<0.1) over the projection period. Our model could accommodate longer projection intervals, different ways that immigrants might re-set the inbreeding coefficient to zero, and other complexities that emerge with future field and conceptual advancements. At this point and given current abundances, however, we do not find short-term inbreeding risks to persistence for either species. We recognize that these findings contrast with Nilsson's (2013) findings for Scandinavian wolves. Nilsson (2013) used the lethal equivalents of 8.5–10.5 and found strong negative effects of inbreeding depression. However, in contrast to wolves, lynx and wolverines have much higher abundances and have not experienced extinction-refounding dynamics, and so have much less inbreeding due to genetic drift. Based on our analyses, we do not find inbreeding depression to be of primary management concern for wolverine and lynx at present in Sweden.

Similarly, we have no reason to expect density dependence is critical for modeling lynx or wolverine population dynamics at these population sizes. Of course, negative density dependence must always eventually occur for exponentially increasing populations, and omitting it from a model can lead to unrealistically high numbers as we found in our complete protection scenarios with no density dependence for lynx. Therefore, we incorporated density dependence in what we view as the most biologically plausible manner: decrementing adult survival as density increases, as was found in the only field study documenting density-dependence in either Scandinavian lynx or wolverines (Brøseth et al. 2011). Further, we embraced uncertainty by considering several 'what if' scenarios. And indeed, at our strong effect sizes of density dependence (i.e., beta coefficients), abundance and growth rates of both species decreased as expected. However, we are concerned that Brøseth et al. (2011) documented their density dependence effect in a wolverine population of approximately 100, whereas both our lynx and wolverine abundances are well outside that range (eg approximately 700–1 500). Precisely because density dependence is known to affect PVA outcomes (Mills et al. 1994, DeCesare et al 2010), the absence of reliable estimates of form and function make us skeptical of including it in our models.

In contrast, source-sink dynamics and cryptic poaching had compelling effects on viability of Sweden's lynx and wolverines. The harvest rate in Norway under different modeled scenarios of emigration rates to/from Norway/Sweden strongly affected quasi-persistence of lynx and wolverines in Sweden. For example, Sweden maintained only a 50% quasi-persistence probability when Norway harvest rates were above 0.25, even when legal and cryptic harvest in Sweden was set to zero.

Similarly, the status quo scenarios we evaluated assumed all harvest was 100% known and reported. In the face of even modest levels of additional cryptic poaching (> 0.10 additional harvest rate) added to status quo levels of harvest of lynx or wolverines in Sweden, abundance, λ_G and quasi-persistence probability all declined. That is, high harvest in Norway combined with even modest levels of cryptic poaching in Sweden may reduce the ability of Sweden to sustain legal harvest while maintaining at least 870 lynx and 600 wolverines. These findings emphasize the importance of estimating for both species the levels of cryptic poaching and the connectivity between Sweden and Norway. In the context of evaluating population viability, what is important to understand is not necessarily natal dispersal, but emigration between countries. One effective tool may be spatially-explicit capture recapture models (SECR) that directly estimate the proportion of a range or portion of a study area that an individual inhabits, as well as potentially being able to track true emigration/dispersal from one country to another (Bischof et al. 2015). We further discuss the importance of SECR models in transboundary population estimation below. But here, we highlight a data need for future studies in this transboundary context to understand movement broadly (both transboundary movement and dispersal) and the effects of differential harvest across the Sweden/Norway border.

We also conducted a Bayesian life-stage simulation analysis to investigate sensitivity of λ_G to different vital rates for both wolverine and lynx in Sweden. For lynx, the vital rate that had the highest impact on λ_G was fidelity (1–probability of emigrating from Sweden), followed by adult female survival, the recruitment rate for adult female lynx, and the survival of subadult females. For wolverines, population growth rate in Sweden was most influenced by, in rank order: recruitment rate of adult females, fidelity, adult female survival.

Collectively, our sensitivity analyses and transboundary projection models underscore several conclusions relevant to harvest and management of both carnivore species. First, if it were possible to target male lynx and wolverines, or, conversely to avoid harvesting reproductive females (i.e., by avoiding groups), it would reduce the effects of harvest on population growth rates for both species. Second, we emphasize the importance of understanding fidelity, 1–emigration probability, from Sweden to Norway. For both species, fidelity had a strong effect on λ_G , much stronger than most other within-population vital rates. This may seem counterintuitive, but every lynx or wolverine that emigrates from Sweden to Norway is lost to the population in our simulation. Given the lower abundance yet higher harvest rates in Norway, dispersal from Sweden to Norway was not reciprocated from Norway back to Sweden (Gervasi et al. 2015). Future studies of the differential exposure of carnivores in Sweden and Norway to harvest could change these results, but the importance of which is highlighted by our models. The way we modeled fidelity could represent true natal dispersal, but also could reflect transboundary movements of individuals living along the border – both would have the same effect on population growth rate in our approach.

We caution that our sensitivity analyses may be affected by our inability to decompose sampling from process variation as discussed in section 4.0 (Methods) to properly account for sampling variation (Caswell 2001, Eacker et al. 2017). If the estimates of dispersal probability have inflated sample variances relative to other vital rates, our results could be overestimating the importance of fidelity to λ_G . Nonetheless, even with this caveat, our results emphasize the need to better understand dispersal across the Norway-Sweden border. And at the same time, our results emphasize the need to protect prime age female lynx and wolverine from harvest if increasing abundance is the goal.

Finally, we stress the importance of collaborative population size estimation across the international boundary. Given the peninsular nature and long border regions of Norway and Sweden, there is certainly a great deal of transboundary movement of these two species that subject them to differential harvest regimes (e.g., Kojola et al. 2009, Gervasi et al. 2016). If population estimates are conducted independently and without a high-level of coordination even including joint data analyses, there is risk of double counting individual lynx in these extensive transboundary areas. For example, using another Scandinavian large carnivore, brown bears, Bischof et al. (2015) made a strong case that insularism in Norway and Sweden with respect to population monitoring lead to inflated estimates of brown bear abundance. They showed, using spatially explicit mark-recapture (SECR) models, that only by explicitly accounting for space in the context of a long transboundary region of Scandinavia can one accurately estimate in which country individual bears spend the bulk of their time, and hence, where individuals should be counted. For example, up to 49% of brown bears counted in Norway have their activity centers in neighboring countries (Bischof et al. 2015). Recent advances in SECR models can also, for example, integrate DNA obtained from harvested individuals to significantly refine population estimates in the same fashion as dead recovery models (e.g., for mountain lions in Montana, Proffitt et al. 2015). Given the sensitivity of our estimates of population growth rate of Swedish lynx and wolverine to fidelity, or the probability of not emigrating to Norway – and the importance of Norwegian harvest regimes on Swedish lynx and wolverine viability – we recommend strongly considering implementing collaborative SECR-type population estimates. This recommendation echoes comments from previous studies of large carnivores in Scandinavia (Gervasi et al. 2016).

Our results also highlight challenges in understanding large carnivore population dynamics with different methods. Our Figure 12 and 30 highlight the challenge of reconciling ‘minimum’ counts such as the den counts used to monitor abundances of lynx and wolverines with demographically-explicit models based on vital rates of radiocollared animals (Harris et al. 2011). There is a tendency to often view such ‘population counts’ as more accurate than modeled estimates of population growth, but both are at best, estimates and one approach is not necessarily ‘better’ than the other. Moreover, there are numerous case studies in the large carnivore literature of cautionary notes

in relying on time series of index counts. For example, the use of minimum counts from Bengal tiger (*Panthera tigris*) Pug marks in India lead to over-inflated abundances for decades, contributing to continued endangerment of declining tigers (Karanth et al. 2003). In the case of lynx and wolverine, minimum den counts do not provide estimates of uncertainty, and are subject to unknown and changing methodological biases over time (a comment that came up for lynx and wolverine during external review of this report).

For example, Figure 12 shows the modeled abundance of lynx in Sweden and Norway compared to the minimum den counts. While there is wide agreement in most years between the two estimates, in 2013–2015 especially, minimum den counts in Sweden may be underestimating abundance. For wolverines, Figure 30 shows that for the most part, in Sweden, wolverine abundance from den counts were generally similar or lower to that predicted by our Bayesian IPM, but within the 95% credible interval. In Norway, in contrast, there were 3–4 years with particularly high den counts compared to the projected abundance from our IPM. In any case, the comparison of two different methods highlights discrepancies between den counts and true abundance that could arise because of bias in den surveys, den failure post-survey (that meant the den did not contribute to abundance), bias in locations where radiocollared studies were done, etc. While recent studies have also treated estimates from different types of data (e.g., collars and aerial survey data) as independent, and compared their estimates of population growth rate to each other (e.g., Serrouya et al. 2016), in reality, both types of data are imperfect observational data that is related to the true population processes through a hierarchical relationship governed by the sampling or detection issues of the different data types (Schaub and Abadi 2012).

Thus, a significant improvement, and indeed, our recommendation, would be to develop fully-integrated population models that explicitly incorporate information from both types of data into one hierarchical modeling framework. Such approaches that combine data types almost always lead to more precise estimates of the population quantities of interest (size, viability, etc), better understanding of biases in different sampling methods, and help reconcile useful management indices like den counts with true abundances. There have been a growing number of recent IPM models developed for large carnivores that provide a potential template for SEPA in the future (Blanc et al. 2014, Schmidt et al. 2015, Bled et al. 2017). We provide the template for such an IPM in a flexible and user-friendly environment, allowing improved field estimates and new conceptual details to be accommodated, thereby iteratively improving PVA predictions. The reward for strengthening collaborative trans-boundary efforts to improve estimates of population ecology vital rates would include a vastly improved ability to link rigorous field data to realistic modelling efforts that guide conservation prioritization.

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Appendix 1

Estimating the environmental variance of demographic vital rates as the variance of a random effect

Although we were unable to estimate the mean and environmental variance for vital rates (i.e., survival, recruitment, emigration) due to not having data available, but note that it is advantageous for predicting future abundances when vital rates are not constant but vary over space and time (Kéry and Schaub 2012). Regardless, we describe the Bayesian approach here for estimating the environmental variance of vital rates as the variances of a random temporal (i.e., year) effect on the vital rate. For stochastic vital rates (here given as θ), we estimate the grand mean (μ) environmental variance on the logit scale as the variance of a normally distributed random year effect (ε_t):

$$\mathbf{logit}(\theta_t) = \mu + \varepsilon_t$$

$$\varepsilon_t \sim \mathbf{normal}(0, \sigma_\varepsilon^2)$$

Because these parameters are estimated on the logit scale, we must derive mean vital rates (θ) and their environmental variances (σ^2) on the probability scale using the following expressions (Kéry and Schaub 2012):

$$\theta = \mathbf{exp}(\mu) / (1 + \mathbf{exp}(\mu))$$

$$\sigma^2 = \sigma_\varepsilon^2 \times \theta^2 \times (1 - \theta)^2$$

Appendix 2

Summary of literature for Eurasian lynx from which vital rate estimates (survival, fecundity, immigration/emigration, mortality, etc) were derived for the population viability analysis

Location	Years	Citation	Abundance			Harvest <i>H</i>	Survival						Reproduction				Genetic variation		
			<i>N_r</i>	<i>N_m</i>	<i>N_{tot}</i>		<i>S_{juvf}</i>	<i>S_{juvm}</i>	<i>S_{subf}</i>	<i>S_{subm}</i>	<i>S_{af}</i>	<i>S_{am}</i>	Litter size (2yrf)	<i>b</i> (2yrf)	Litter size (af)	<i>b</i> (af)	<i>F_{st}</i>	<i>H_o</i>	
Sweden	2011	Kaczensky et al. 2012			1650 (± 128)														
Norway	2011	Kaczensky et al. 2012			396 (± 6)														
Northern Sweden	1994–2007	Nilsen et al. 2012											1.99 (1.30–3.04)	0.22 (0.06–0.53)	2.09 (1.90–2.30)	0.76 (0.62–0.87)			
Southern Sweden	1997–2006	Nilsen et al. 2012											2.34 (1.94–2.81)	0.74 (0.49–0.89)	2.37 (2.10–2.69)	0.90 (0.76–0.96)			
Northern Norway	1996–2006	Nilsen et al. 2012											2.09 (1.13–3.87)	0.40 (0.09–0.81)	2.10 (1.83–2.41)	0.69 (0.53–0.81)			
Southern Norway	2001–2006	Nilsen et al. 2012											1.90 (1.62–5.18)	0.50 (0.10–0.90)	1.95 (1.35–2.81)	0.81 (0.55–0.94)			
Northern Sweden	1994–2002	Andren et al. 2006				0.02	0.45 (± 0.07)	0.49 (± 0.08)	1 (± 0)	0.82 (± 0.14)	0.97 (± 0.34)	0.95 (± 0.05)							
Southern Sweden	1996–2002	Andren et al. 2006				0.09	0.54 (± 0.10)	0.41 (± 0.12)	0.88 (± 0.11)	0.67 (± 0.22)	0.96 (± 0.05)	1 (± 0)							
South-eastern Norway	1995–2002	Andren et al. 2006				0.09	0.59 (± 0.13)	0.37 (± 0.10)	0.75 (± 0.22)	1 (± 0)	1 (± 0)	1 (± 0)							
Southern Norway	2000–2003	Andren et al. 2006				0.27													
Sweden	2010–2015	Strombrom 2017																X	
Norway		Strombrom 2017																X	

Appendix 3

Summary of literature for wolverine from which vital rate estimates (survival, fecundity, immigration/emigration, mortality, etc.) were derived for the population viability analysis

Location	Years	Citation	Abundance			Harvest	Survival						Reproduction				Genetic variation		Immigration		
			N_r	N_m	N_{tot}	H	S_{juvf}	S_{juvm}	S_{subf}	S_{subm}	S_{af}	S_{am}	R	Litter size	b	Sex ratio	F_{st}	H_o	ω		
Sweden	2011	Kaczensky et al. 2012			680 (± 100)	<0.01															
Norway	2011	Kaczensky et al. 2012			385 (± 46)	0.15–0.20															
Southern Norway	2000–2001	Flagstad et al. 2004			89 (95% CI = 74–104)													X			
Norway/ Sweden	2013	Gervasi et al. 2014									0.89	0.89	0.63								
Southern Sweden	2002–2013	Gervasi et al. 2015									0.87 (0.80–0.91)	0.80 (0.74–0.86)								0.02 (0.01–0.03)	
Southern Norway ¹	2002–2013	Gervasi et al. 2015									0.80 (0.76–0.83)	0.71 (0.66–0.75)								0.05 (0.03–0.08)	
Southern Norway	2003	Gervasi et al. 2015				0.04 (0.01–0.15)															
Southern Norway	2012	Gervasi et al. 2015				0.16 (0.10–0.24)															
Boreal Forests Sweden	2000–2005	Hedmark and Ellegren 2007																X	X		
Northern Sweden ²	1993–2008	Persson et al. 2009									0.79 (0.69–0.90)	0.88 (0.79–0.97)	0.94 (0.84–1.00)	0.85 (0.62–1.00)	0.95 (0.92–0.98)	0.99 (0.96–1.00)					
Northern Scandinavia (Sweden/ Norway)	1993–2002	Persson et al. 2006											0.46 (0.22–0.70)	1.88 (1.68–2.07)	0.53 (0.43–0.63)	0.6F/ 0.4M					
Northern Sweden	NA	Rauset et al. 2015												1.38 (range 0–3)							

Location	Years	Citation	Abundance			Harvest	Survival						Reproduction				Genetic variation		Immigration
			N_f	N_m	N_{tot}	H	S_{juvf}	S_{juvm}	S_{subf}	S_{subm}	S_{af}	S_{am}	R	Litter size	b	Sex ratio	F_{st}	H_0	ω
Norway	1998–2000	Lande et al. 2001 (see Saether et al. 2005 for citation)			269 ± 32														
Sweden	1998–2000	Lande et al. 2001 (see Saether et al. 2005 for citation)			326 ± 45														
Sweden/ Norway	1978–1998	Walker et al. 2001															X	X	

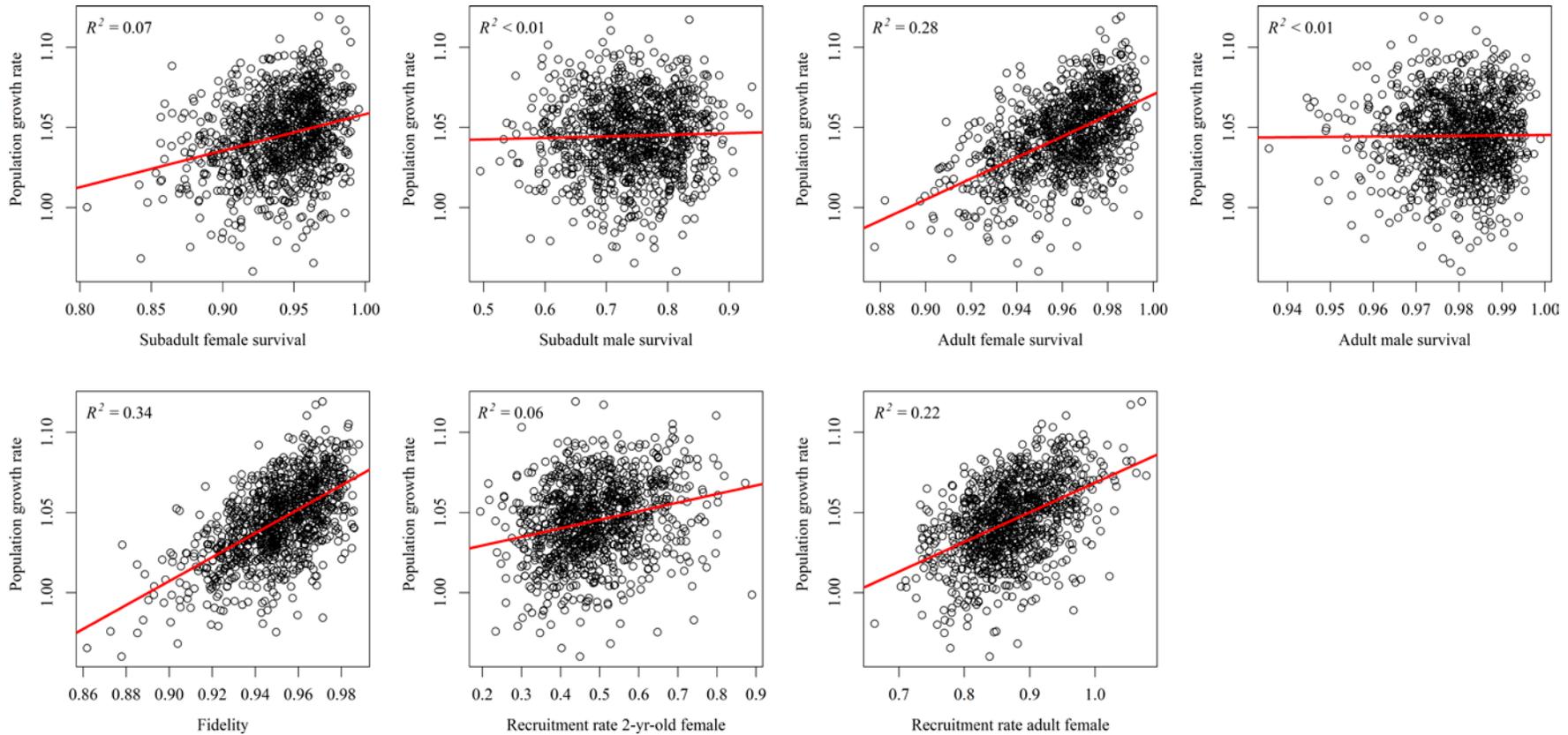
Notes.

1. Note that field estimates of survival from Gervasi et al. (2015) from Southern Norway were not age-structured, as they were obtained from non-invasive DNA estimates, and thus could not be used in age-structured survival rates. But they were quite similar to averages across age classes from other studies.
2. Note that survival rates from Persson et al. (2009) may include some levels of lethal removals and poaching.

Appendix 4

Bayesian sensitivity analysis showing simple linear regressions of the geometric mean population growth rate over prediction years (2018–2037) against female subadult survival, male subadult survival, adult female survival, adult male survival, fidelity (or 1 minus the probability of dispersing from Sweden to Norway), and the recruitment rates for 2-yr-old and adult female Eurasian lynx

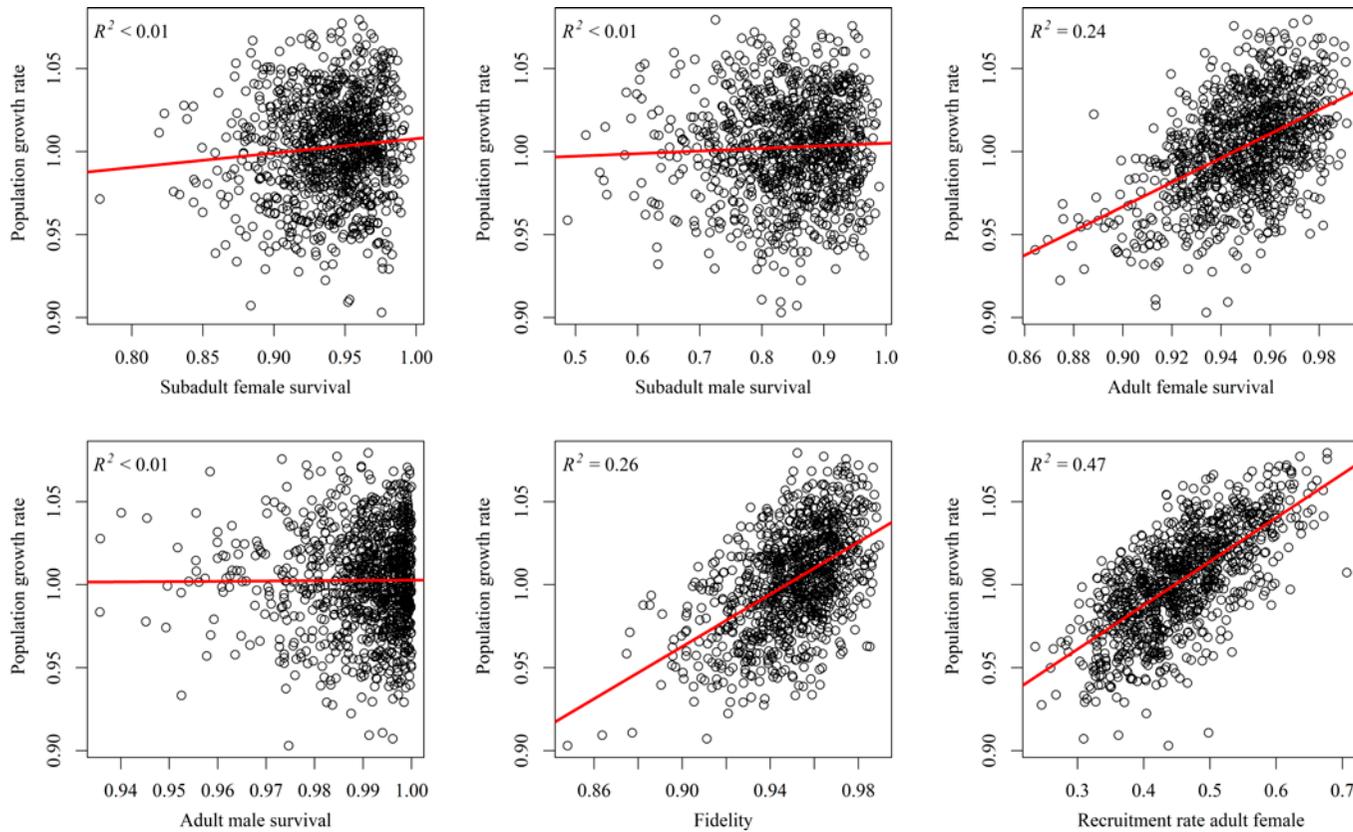
100



Appendix 5

Bayesian sensitivity analysis showing simple linear regressions of the geometric mean population growth rate over prediction years (2018–2037) against female subadult survival, male subadult survival, adult female survival, adult male survival, fidelity (or 1 minus the probability of dispersing from Sweden to Norway), and the recruitment rates for adult female wolverine

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Appendix 6

R code used to adjust the timing of den count survey estimates to a biological cycle for the initial starting abundances of Eurasian lynx in Bayesian population models

```
#install.packages("popbio")
require(popbio)

# Define parameters and create empty vectors to hold abundances
nYears=10
Njuv=numeric(nYears)
Nsub=numeric(nYears)
N2yrm=numeric(nYears)
N2yrf=numeric(nYears)
Nafa=numeric(nYears)
Nama=numeric(nYears)
Ntot=numeric(nYears)
NjuvNOR=numeric(nYears)
NsubNOR=numeric(nYears)
N2yrmNOR=numeric(nYears)
N2yrfNOR=numeric(nYears)
NafaNOR=numeric(nYears)
NamaNOR=numeric(nYears)
NtotNorway=numeric(nYears)
pop.growthNOR=numeric(nYears-1)

#Sweden
HarvSWE=0.074 # initial harvest rate
P=0.10 # poaching rate
phijuv=0.47
propbreed2=0.48
litsize2=2.17
propbreedAF=0.83
litsizeAF=2.23
phisubf=0.94
phisubm=0.74
phiaf=0.96
phiam=0.98
sexRatioF=0.53 # proportion of females at 1 yr of age
sexRatioM=0.47 # proportion of males at 1 yr of age
Ninit=1650
pop.growth=numeric(nYears-1)
psiSN=0.05 # dispersal from Sweden to Norway
```

```

# Norway
HarvNOR=0.318 # initial harvest rate
psiNS=0.02 # dispersal from Norway to Sweden
PNOR=0.07 # poaching rate
phijuvNOR=0.48
propbreed2NOR=0.45
litsize2NOR=2
propbreedAFNOR=0.75
litsizeAFNOR=2.03
phisubfNOR=0.75
phisubmNOR=0.74
phiafNOR=0.96
phiamNOR=0.98
sexRatioF=0.53 # proportion of females at 1 yr of age
sexRatioM=0.47 # proportion of males at 1 yr of age
NinitNOR=396

#create post-birth matrix model for Swedish population starting structure
A = matrix(rep(0,36),ncol=6, nrow=6)
A[1,] = c(0,0,propbreed2*litsize2,0,propbreedAF*litsizeAF,0) # Njuv
A[2,] = c(phijuv*(1-HarvSWE)*(1-P),0,0,0,0,0) # Nsub
A[3,] = c(0,phisubf*sexRatioF*(1-HarvSWE)*(1-psiSN)*(1-P),0,0,0,0) # 2yrf
A[4,] = c(0,phisubm*sexRatioM*(1-HarvSWE)*(1-psiSN)*(1-P),0,0,0,0) # 2yrm
A[5,] = c(0,0,phiaf*(1-psiSN)*(1-HarvSWE)*(1-P),0,phiaf*(1-psiSN)*
(1-HarvSWE)*(1-P),0) # Nafa
A[6,] = c(0,0,0,phiam*(1-psiSN)*(1-HarvSWE)*(1-P),0,phiam*(1-psiSN)*
(1-HarvSWE)*(1-P)) # Nama
EA = eigen.analysis(A)

# intial stable stage structure
Njuv[1] = Ninit*round(EA$stable.stage,2)[1]
Nsub[1] = Ninit*round(EA$stable.stage,2)[2]
N2yrf[1] = Ninit*round(EA$stable.stage,2)[3]
N2yrm[1] = Ninit*round(EA$stable.stage,2)[4]
Nafa[1] = Ninit*round(EA$stable.stage,2)[5]
Nama[1] <- Ninit*(1-(round(EA$stable.stage,2)[1]+round(EA$stable.stage,2)
[2]+round(EA$stable.stage,2)[3]+round(EA$stable.stage,2)[4]+round(EA$stable.
stage,2)[5]))

#create empty matrix for Norway population starting structure
A = matrix(rep(0,36),ncol=6, nrow=6)
A[1,] = c(0,0,propbreed2NOR*litsize2NOR,0,propbreedAFNOR*litsizeAF
NOR,0) # Njuv
A[2,] = c(phijuvNOR*(1-HarvNOR)*(1-PNOR),0,0,0,0,0) # Nsub
A[3,] = c(0,phisubfNOR*sexRatioF*(1-HarvNOR)*(1-psiNS)*(1-PNOR),0,0,0,0)
# 2yrf

```

```

A[4,] = c(0,phisubmNOR*sexRatioM*(1-HarvNOR)*(1-psiNS)*(1-P
NOR),0,0,0,0) # 2yrm
A[5,] = c(0,0,phiafNOR*(1-psiNS)*(1-HarvNOR)*(1-PNOR),0,
phiafNOR*(1-psiNS)*(1-HarvNOR)*(1-PNOR),0) # Nafa
A[6,] = c(0,0,0,phiamNOR*(1-psiNS)*(1-HarvNOR)*(1-PNOR),0,
phiamNOR*(1-psiNS)*(1-HarvNOR)*(1-PNOR)) # Nama
EA2 = eigen.analysis(A)

# intial stable stage structure
NjuvNOR[1] = NinitNOR*round(EA2$stable.stage,2)[1]
NsubNOR[1] = NinitNOR*round(EA2$stable.stage,2)[2]
N2yrfNOR[1] = NinitNOR*round(EA2$stable.stage,2)[3]
N2yrmNOR[1] = NinitNOR*round(EA$stable.stage,2)[4]
NafaNOR[1] = NinitNOR*round(EA$stable.stage,2)[5]
NamaNOR[1] <- NinitNOR*(1-(round(EA2$stable.stage,2)
[1]+round(EA2$stable.stage,2)[2]+round(EA2$stable.stage,2)
[3]+round(EA2$stable.stage,2)[4]+round(EA2$stable.stage,2)[5]))

for(t in 2:nYears){
  # (i.e. difference equations from matrix math)
  Njuv[t] = (N2yrf[t-1]*propbreed2*litsize2)+(Nafa[t-
1]*propbreedAF*litsizeAF)
  Nsub[t]= Njuv[t-1]*phijuv*(1-HarvSWE)*(1-P)
  N2yrf[t] = ((phisubf*sexRatioF*(1-psiSN)*(1-HarvSWE)*(1-P))*Nsub[t-1])
  + (NsubNOR[t-1]*psiNS*sexRatioF)
  N2yrm[t] = ((phisubm*sexRatioM*(1-psiSN)*(1-HarvSWE)*(1-
P))*Nsub[t-1]) + (NsubNOR[t-1]*psiNS*sexRatioM)
  Nafa[t] = (phiaf*(1-psiSN)*(1-HarvSWE)*(1-P))*(Nafa[t-1]+N2yrf[t-1]) +
  ((N2yrfNOR[t-1]+NafaNOR[t-1])*psiNS)
  Nama[t] = (phiam*(1-psiSN)*(1-HarvSWE)*(1-P))*(Nama[t-
1]+N2yrm[t-1]) + ((N2yrmNOR[t-1]+NamaNOR[t-1])*psiNS)

  NjuvNOR[t] = (N2yrfNOR[t-1]*propbreed2NOR*litsize2)+(NafaNOR[t-
1]*propbreedAFNOR*litsizeAFNOR)
  NsubNOR[t]= NjuvNOR[t-1]*phijuvNOR*(1-HarvNOR)*(1-PNOR)
  N2yrfNOR[t] = ((phisubfNOR*sexRatioF*(1-psiNS)*(1-HarvNOR)*(1-
PNOR))*NsubNOR[t-1]) + (Nsub[t-1]*psiSN*sexRatioF)
  N2yrmNOR[t] = ((phisubmNOR*sexRatioM*(1-psiNS)*(1-HarvNOR)*
(1-PNOR))*NsubNOR[t-1]) + (Nsub[t-1]*psiSN*sexRatioM)
  NafaNOR[t] = (phiafNOR*(1-psiNS)*(1-HarvNOR)*(1-
PNOR))*(NafaNOR[t-1]+N2yrfNOR[t-1]) + ((N2yrf[t-1]+Nafa[t-1])*psiSN)
  NamaNOR[t] = (phiamNOR*(1-psiNS)*(1-HarvNOR)*(1-PNOR))*
  (NamaNOR[t-1]+N2yrmNOR[t-1]) + ((N2yrm[t-1]+Nama[t-1])*psiSN)
}

```

```
for(t in 1:nYears){
  # get total without juveniles in the count
  Ntot[t] <- (Nsub[t] + N2yrf[t] + N2yrm[t] + Nafa[t] + Nama[t])
  NtotNorway[t] <- ( NsubNOR[t] + N2yrfNOR[t] + N2yrmNOR[t] +
  NafaNOR[t] + NamaNOR[t])
}

for(t in 1:(nYears-1)){
  pop.growth[t]<-(Ntot[t+1]+0.0000001)/(Ntot[t]+0.0000001)
  pop.growthNOR[t]<-(NtotNorway[t+1]+0.0000001)/
  (NtotNorway[t]+0.0000001)
}

# adjusted starting pop size Sweden
round((Ntot[1]+Njuv[1])*((Ntot[2])/(Ntot[1]+Njuv[1]))^(3/12))

# adjusted starting pop size Norway
round((NtotNorway[1]+NjuvNOR[1])*((NtotNorway[2])/(NtotNorway[1]+
NjuvNOR[1]))^(3/12))
```

Appendix 7

Example from the Shiny Application for
Population Viability Analysis for Eurasian Lynx
and Wolverines in Sweden

Swedish Environmental Protection Agency Lynx Population Viability Analysis

20 January, 2018



Parameter Estimates: 2011–2038

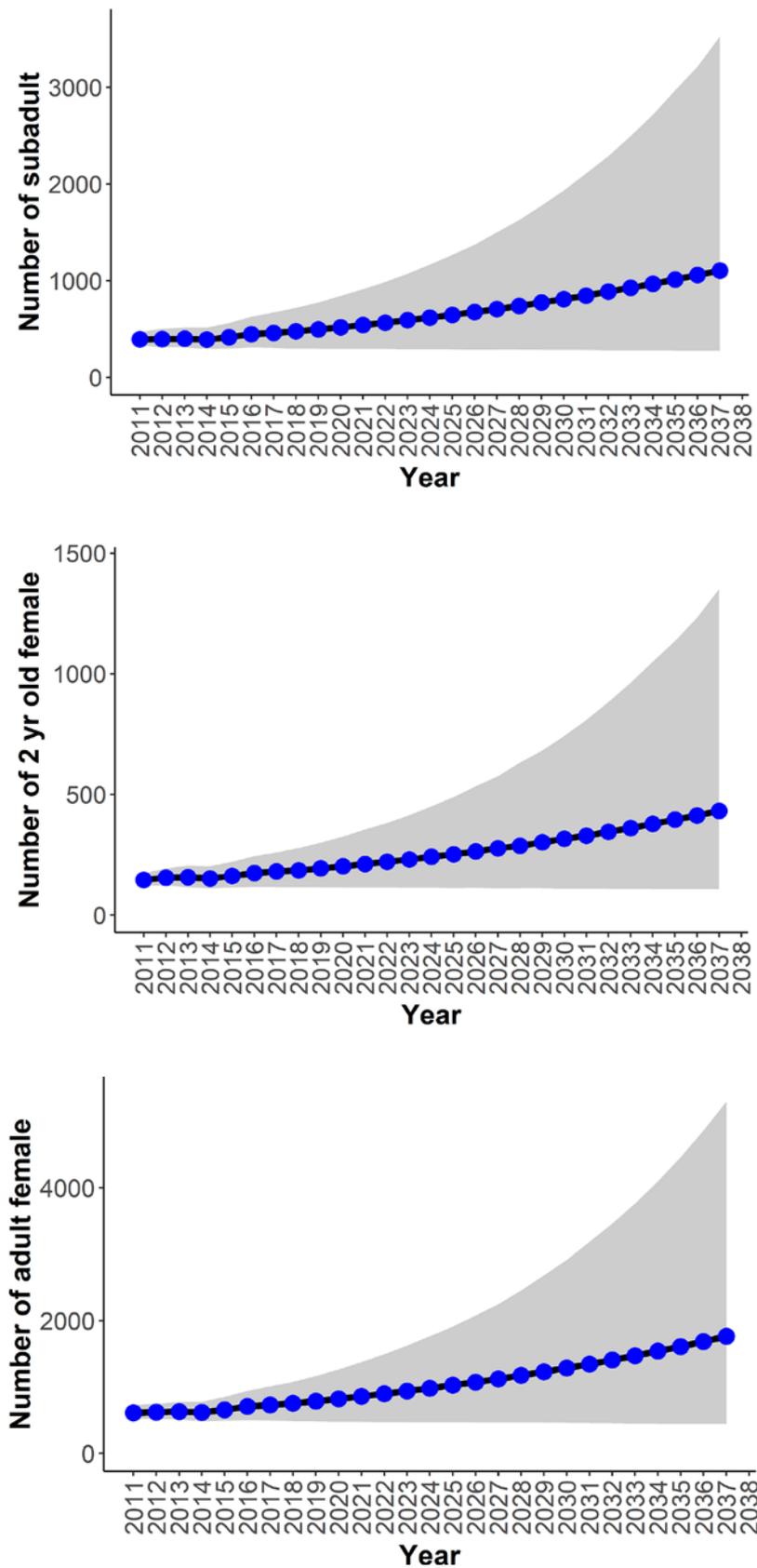
Tabular summary

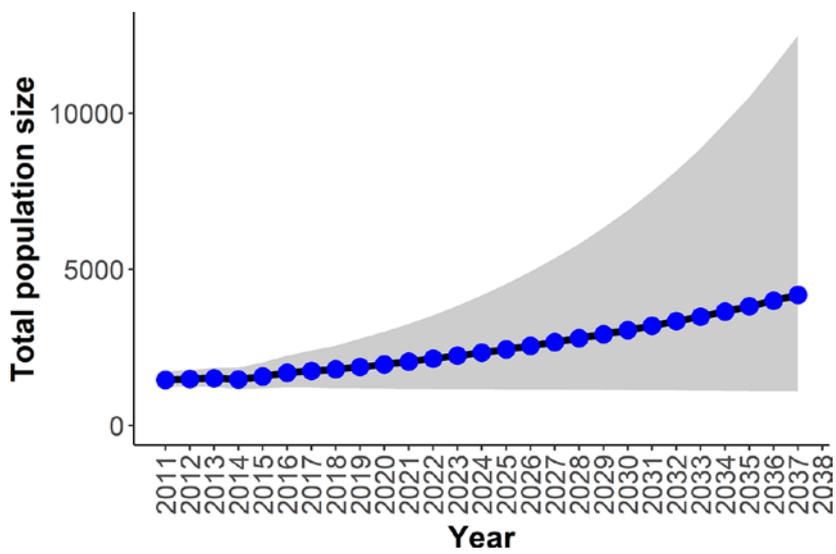
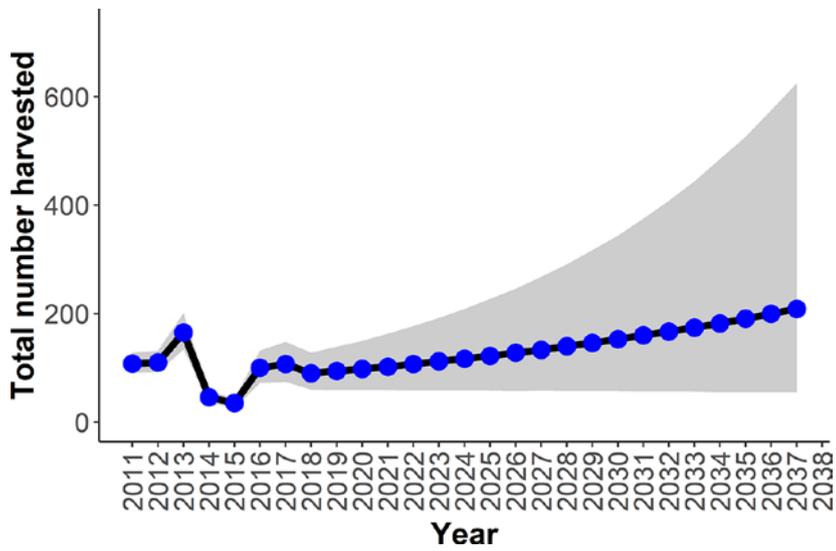
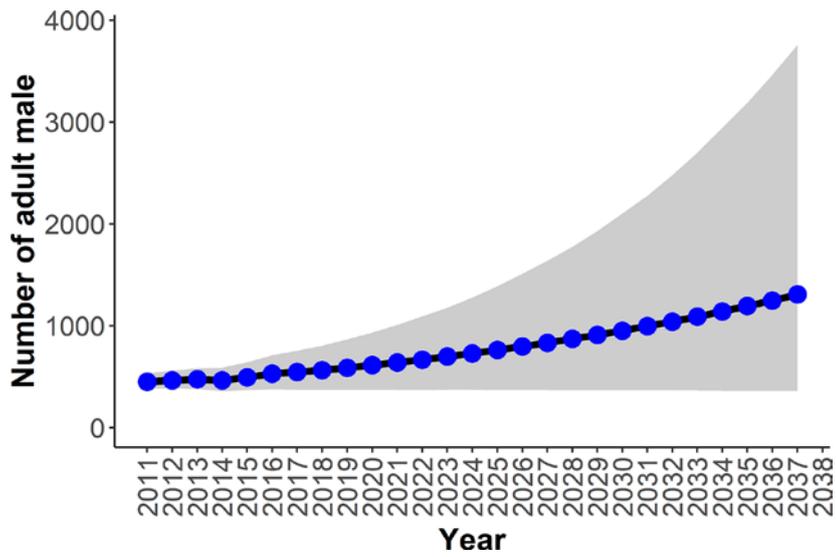
Year	Parameter	Median	SD	Lower.95.CRI	Upper.95.CRI
2011	Population growth rate	1.019	0.033	0.952	1.082
2012	Population growth rate	1.016	0.032	0.951	1.075
2013	Population growth rate	0.978	0.030	0.916	1.034
2014	Population growth rate	1.064	0.032	0.996	1.124
2015	Population growth rate	1.074	0.032	1.006	1.132
2016	Population growth rate	1.033	0.031	0.969	1.090
2017	Population growth rate	1.031	0.031	0.965	1.087
2018	Population growth rate	1.044	0.031	0.978	1.098
2019	Population growth rate	1.044	0.031	0.977	1.100
2020	Population growth rate	1.044	0.030	0.980	1.099
2021	Population growth rate	1.045	0.030	0.981	1.099
2022	Population growth rate	1.046	0.030	0.982	1.099

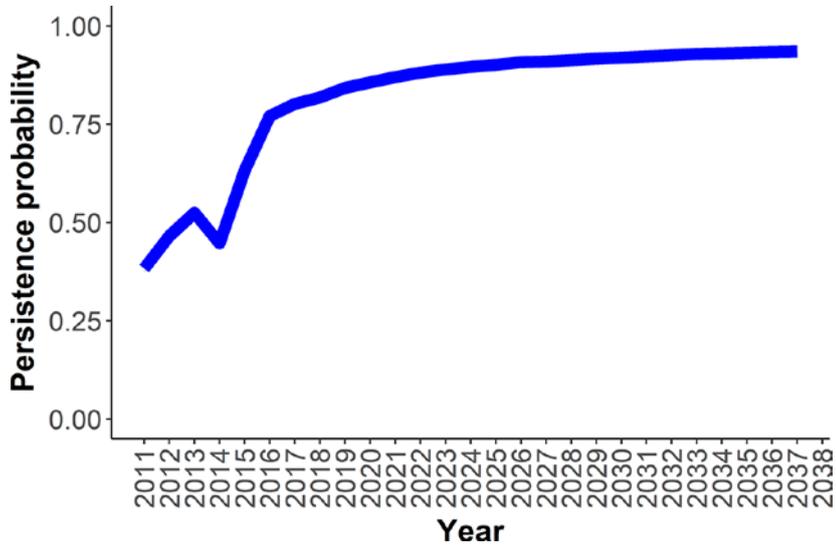
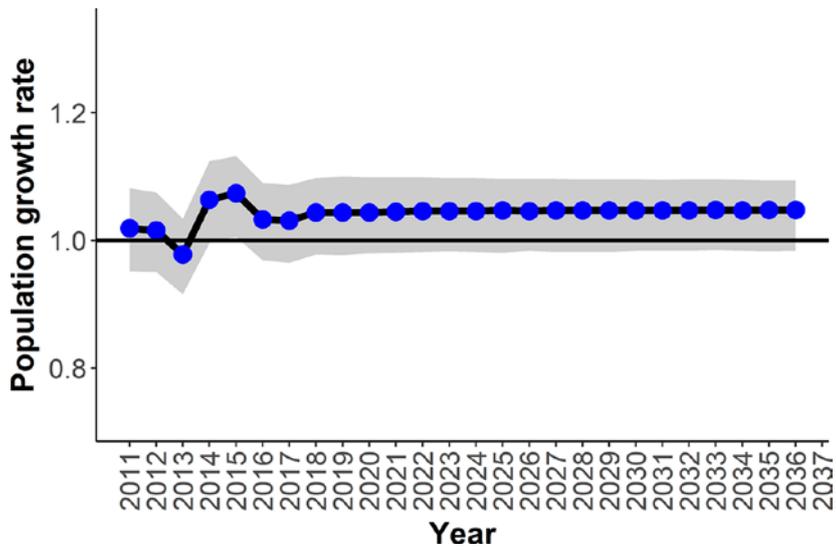
Year	Parameter	Median	SD	Lower.95.CRI	Upper.95.CRI
2023	Population growth rate	1.046	0.030	0.983	1.098
2024	Population growth rate	1.046	0.029	0.982	1.098
2025	Population growth rate	1.047	0.030	0.981	1.097
2026	Population growth rate	1.046	0.029	0.984	1.097
2027	Population growth rate	1.047	0.029	0.982	1.097
2028	Population growth rate	1.047	0.029	0.982	1.096
2029	Population growth rate	1.047	0.029	0.982	1.096
2030	Population growth rate	1.047	0.029	0.984	1.096
2031	Population growth rate	1.047	0.028	0.984	1.095
2032	Population growth rate	1.047	0.029	0.984	1.096
2033	Population growth rate	1.048	0.028	0.985	1.096
2034	Population growth rate	1.047	0.028	0.984	1.095
2035	Population growth rate	1.048	0.028	0.983	1.094
2036	Population growth rate	1.048	0.028	0.984	1.094
NA	Geometric mean population growth rate	1.040	0.025	0.989	1.086
NA	Female sub-adult survival rate	0.944	0.030	0.868	0.984
NA	Male sub-adult survival rate	0.742	0.071	0.589	0.863
NA	Adult female survival rate	0.964	0.020	0.913	0.989
NA	Adult male survival rate	0.982	0.010	0.956	0.995
2011	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2012	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2013	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2014	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2015	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2016	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2017	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2018	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2019	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2020	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2021	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2022	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2023	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2024	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2025	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2026	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2027	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2028	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2029	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2030	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2031	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2032	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2033	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2034	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2035	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2036	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2037	Recruitment rate for 2-yr-old females	0.480	0.115	0.290	0.735
2011	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2012	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2013	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2014	Recruitment rate for adult females	0.868	0.062	0.754	0.995

Year	Parameter	Median	SD	Lower.95.CRI	Upper.95.CRI
2015	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2016	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2017	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2018	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2019	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2020	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2021	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2022	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2023	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2024	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2025	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2026	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2027	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2028	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2029	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2030	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2031	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2032	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2033	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2034	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2035	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2036	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2037	Recruitment rate for adult females	0.868	0.062	0.754	0.995
2011	Persistence probability (N>=600)	0.383	0.486	0.373	0.393
2012	Persistence probability (N>=600)	0.465	0.499	0.456	0.475
2013	Persistence probability (N>=600)	0.525	0.499	0.515	0.535
2014	Persistence probability (N>=600)	0.447	0.497	0.437	0.457
2015	Persistence probability (N>=600)	0.632	0.482	0.622	0.641
2016	Persistence probability (N>=600)	0.771	0.420	0.763	0.779
2017	Persistence probability (N>=600)	0.802	0.399	0.794	0.809
2018	Persistence probability (N>=600)	0.818	0.386	0.811	0.826
2019	Persistence probability (N>=600)	0.843	0.364	0.835	0.850
2020	Persistence probability (N>=600)	0.856	0.351	0.849	0.863
2021	Persistence probability (N>=600)	0.870	0.336	0.864	0.877
2022	Persistence probability (N>=600)	0.881	0.323	0.875	0.888
2023	Persistence probability (N>=600)	0.890	0.313	0.883	0.896
2024	Persistence probability (N>=600)	0.896	0.305	0.890	0.902
2025	Persistence probability (N>=600)	0.902	0.298	0.896	0.907
2026	Persistence probability (N>=600)	0.908	0.289	0.902	0.913
2027	Persistence probability (N>=600)	0.910	0.287	0.904	0.915
2028	Persistence probability (N>=600)	0.914	0.281	0.908	0.919
2029	Persistence probability (N>=600)	0.917	0.276	0.911	0.922
2030	Persistence probability (N>=600)	0.920	0.272	0.914	0.925
2031	Persistence probability (N>=600)	0.923	0.267	0.917	0.928
2032	Persistence probability (N>=600)	0.926	0.262	0.921	0.931
2033	Persistence probability (N>=600)	0.929	0.257	0.924	0.934
2034	Persistence probability (N>=600)	0.930	0.255	0.925	0.935
2035	Persistence probability (N>=600)	0.932	0.252	0.927	0.937
2036	Persistence probability (N>=600)	0.934	0.248	0.929	0.939
2037	Persistence probability (N>=600)	0.935	0.247	0.930	0.940

Graphical summary







Swedish Environmental Protection Agency

Wolverine Population Viability Analysis

20 January, 2018



Parameter Estimates: 2011–2038

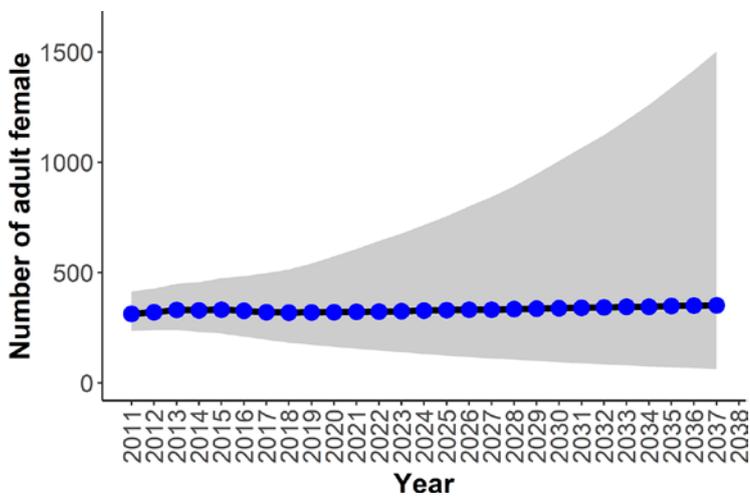
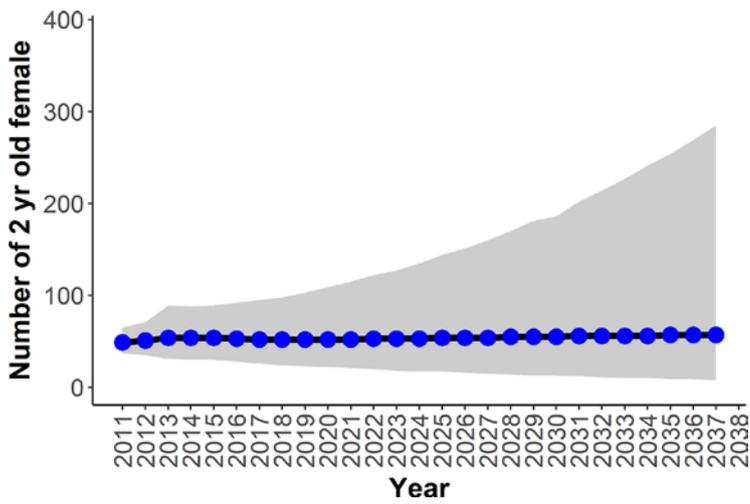
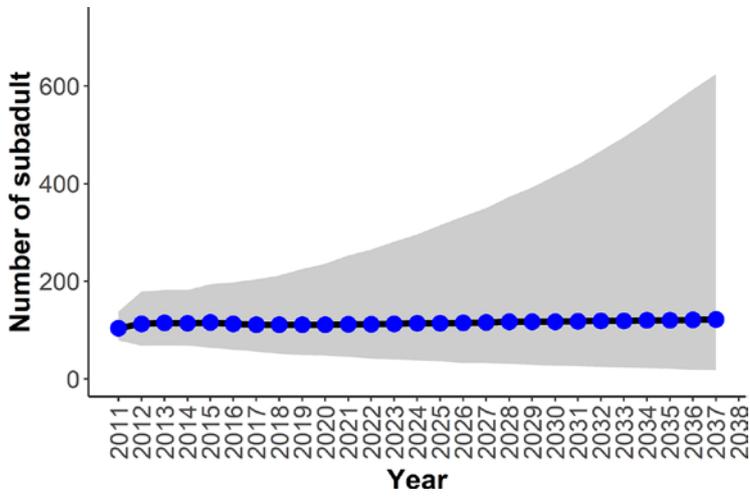
Tabular summary

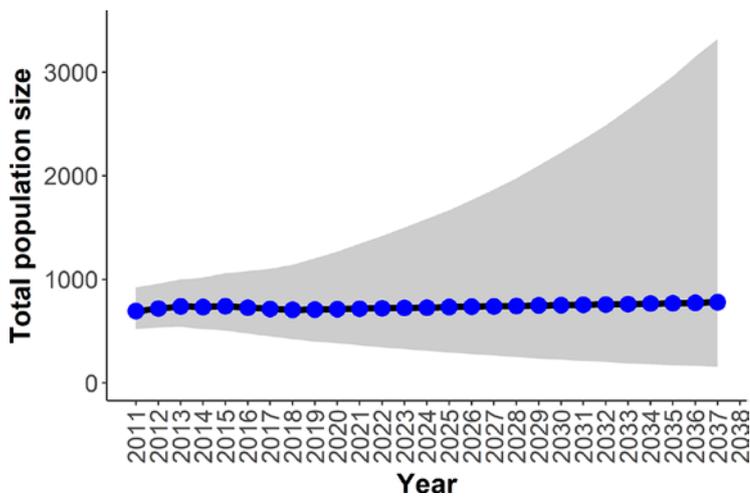
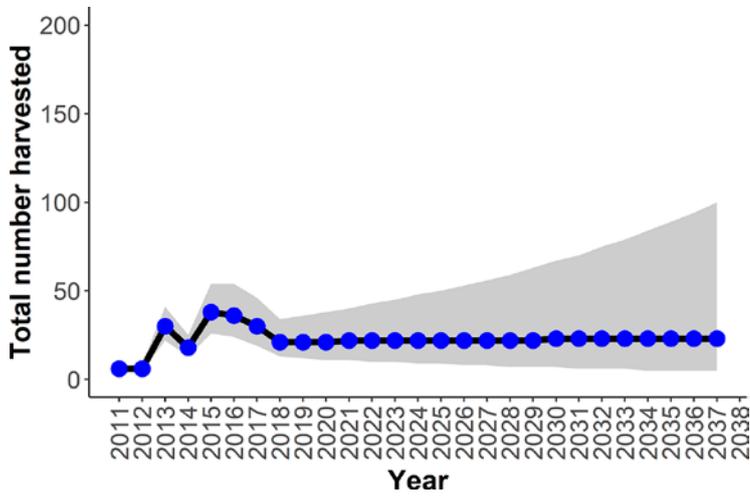
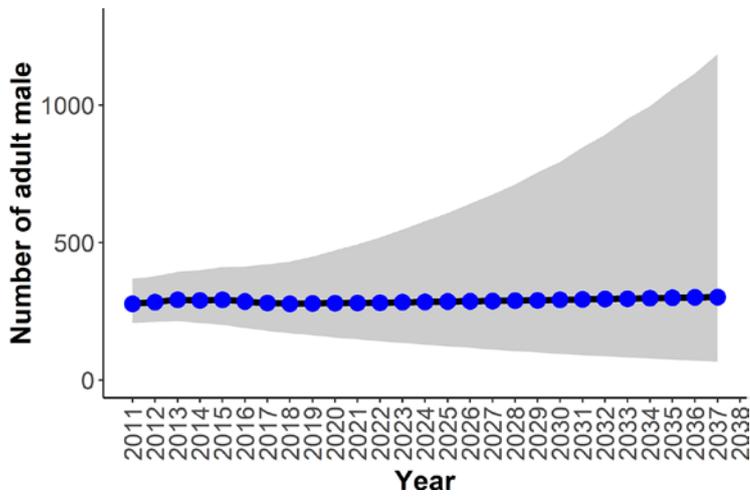
Year	Parameter	Median	SD	Lower.95.CRI	Upper.95.CRI
2011	Population growth rate	1.034	0.042	0.954	1.117
2012	Population growth rate	1.029	0.038	0.955	1.102
2013	Population growth rate	0.993	0.036	0.920	1.061
2014	Population growth rate	1.009	0.037	0.936	1.081
2015	Population growth rate	0.983	0.036	0.910	1.051
2016	Population growth rate	0.983	0.036	0.909	1.051
2017	Population growth rate	0.992	0.037	0.916	1.061
2018	Population growth rate	1.004	0.037	0.929	1.073
2019	Population growth rate	1.004	0.037	0.929	1.073
2020	Population growth rate	1.005	0.037	0.927	1.073
2021	Population growth rate	1.005	0.037	0.927	1.072
2022	Population growth rate	1.006	0.037	0.926	1.072
2023	Population growth rate	1.005	0.037	0.927	1.073
2024	Population growth rate	1.007	0.037	0.927	1.072
2025	Population growth rate	1.007	0.038	0.923	1.072
2026	Population growth rate	1.007	0.037	0.927	1.072
2027	Population growth rate	1.007	0.038	0.924	1.071

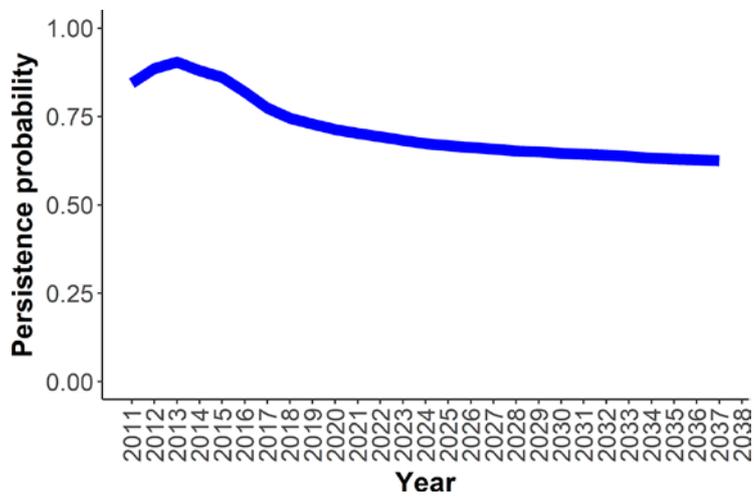
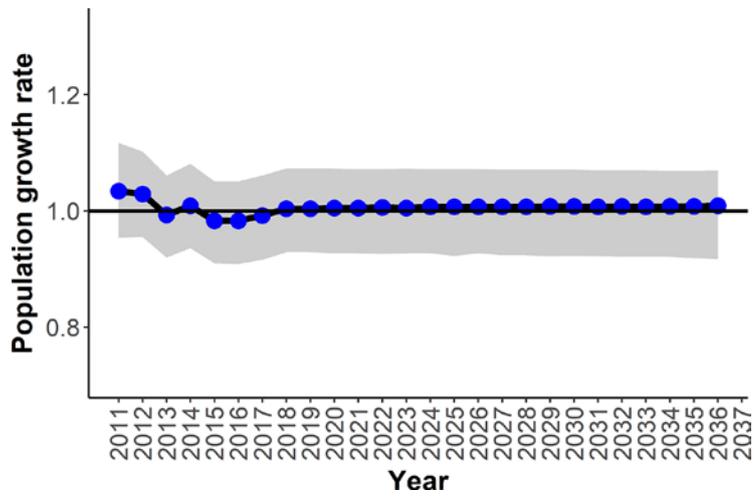
Year	Parameter	Median	SD	Lower.95.CRI	Upper.95.CRI
2028	Population growth rate	1.007	0.038	0.924	1.071
2029	Population growth rate	1.008	0.038	0.922	1.071
2030	Population growth rate	1.008	0.038	0.923	1.071
2031	Population growth rate	1.007	0.038	0.922	1.070
2032	Population growth rate	1.008	0.038	0.921	1.070
2033	Population growth rate	1.007	0.038	0.921	1.070
2034	Population growth rate	1.008	0.038	0.921	1.069
2035	Population growth rate	1.008	0.038	0.919	1.069
2036	Population growth rate	1.009	0.039	0.917	1.070
NA	Geometric mean population growth rate	1.004	0.030	0.945	1.061
NA	Female sub-adult survival rate	0.945	0.030	0.867	0.985
NA	Male sub-adult survival rate	0.862	0.080	0.668	0.968
NA	Adult female survival rate	0.953	0.020	0.905	0.982
NA	Adult male survival rate	0.993	0.010	0.963	1.000
2011	Recruitment rate	0.456	0.080	0.317	0.629
2012	Recruitment rate	0.456	0.080	0.317	0.629
2013	Recruitment rate	0.456	0.080	0.317	0.629
2014	Recruitment rate	0.456	0.080	0.317	0.629
2015	Recruitment rate	0.456	0.080	0.317	0.629
2016	Recruitment rate	0.456	0.080	0.317	0.629
2017	Recruitment rate	0.456	0.080	0.317	0.629
2018	Recruitment rate	0.456	0.080	0.317	0.629
2019	Recruitment rate	0.456	0.080	0.317	0.629
2020	Recruitment rate	0.456	0.080	0.317	0.629
2021	Recruitment rate	0.456	0.080	0.317	0.629
2022	Recruitment rate	0.456	0.080	0.317	0.629
2023	Recruitment rate	0.456	0.080	0.317	0.629
2024	Recruitment rate	0.456	0.080	0.317	0.629
2025	Recruitment rate	0.456	0.080	0.317	0.629
2026	Recruitment rate	0.456	0.080	0.317	0.629
2027	Recruitment rate	0.456	0.080	0.317	0.629
2028	Recruitment rate	0.456	0.080	0.317	0.629
2029	Recruitment rate	0.456	0.080	0.317	0.629
2030	Recruitment rate	0.456	0.080	0.317	0.629
2031	Recruitment rate	0.456	0.080	0.317	0.629
2032	Recruitment rate	0.456	0.080	0.317	0.629
2033	Recruitment rate	0.456	0.080	0.317	0.629
2034	Recruitment rate	0.456	0.080	0.317	0.629
2035	Recruitment rate	0.456	0.080	0.317	0.629
2036	Recruitment rate	0.456	0.080	0.317	0.629
2037	Recruitment rate	0.456	0.080	0.317	0.629
2011	Persistence probability (N>=600)	0.844	0.363	0.837	0.851
2012	Persistence probability (N>=600)	0.886	0.318	0.879	0.892
2013	Persistence probability (N>=600)	0.904	0.295	0.898	0.910
2014	Persistence probability (N>=600)	0.880	0.325	0.873	0.886
2015	Persistence probability (N>=600)	0.860	0.346	0.854	0.867
2016	Persistence probability (N>=600)	0.820	0.384	0.812	0.827

Year	Parameter	Median	SD	Lower.95.CRI	Upper.95.CRI
2017	Persistence probability (N>=600)	0.774	0.418	0.766	0.782
2018	Persistence probability (N>=600)	0.745	0.436	0.737	0.754
2019	Persistence probability (N>=600)	0.729	0.445	0.720	0.737
2020	Persistence probability (N>=600)	0.713	0.452	0.704	0.722
2021	Persistence probability (N>=600)	0.702	0.457	0.693	0.711
2022	Persistence probability (N>=600)	0.693	0.461	0.684	0.702
2023	Persistence probability (N>=600)	0.683	0.465	0.674	0.692
2024	Persistence probability (N>=600)	0.673	0.469	0.664	0.682
2025	Persistence probability (N>=600)	0.667	0.471	0.658	0.677
2026	Persistence probability (N>=600)	0.663	0.473	0.653	0.672
2027	Persistence probability (N>=600)	0.658	0.475	0.648	0.667
2028	Persistence probability (N>=600)	0.652	0.476	0.643	0.662
2029	Persistence probability (N>=600)	0.650	0.477	0.641	0.659
2030	Persistence probability (N>=600)	0.646	0.478	0.637	0.656
2031	Persistence probability (N>=600)	0.643	0.479	0.633	0.652
2032	Persistence probability (N>=600)	0.641	0.480	0.631	0.650
2033	Persistence probability (N>=600)	0.637	0.481	0.627	0.646
2034	Persistence probability (N>=600)	0.633	0.482	0.623	0.642
2035	Persistence probability (N>=600)	0.630	0.483	0.620	0.639
2036	Persistence probability (N>=600)	0.628	0.483	0.618	0.637
2037	Persistence probability (N>=600)	0.625	0.484	0.615	0.634

Graphical summary







Bayesian Population Viability Analysis for Lynx and Wolverine in Scandinavia

REPORT 6793

SWEDISH EPA
ISBN 978-91-620-6793-9
ISSN 0282-7298

This report presents the results from a demographic population viability analysis, combined with sensitivity analysis, for the lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) in Scandinavia under alternative management scenarios using Bayesian integrated population models. In Sweden, the population growth of both species was sensitive to the individuals' propensity to disperse to Norway, and also to female survival and recruitment rate. Main drivers of the viability were the choice of harvest strategy, dispersal rates to Norway and the resultant potential for source-sink dynamics, plus the amount of underreported and unknown cryptic poaching.

Rapporten redovisar resultaten från en demografisk sårbarhetsanalys, kombinerad med känslighetsanalys, av lodjur och järv i Skandinavien under olika förvaltningsscenarier, där Bayesian integrerade populationsmodeller användes. I Sverige påverkas populationstillväxten hos arterna mycket av individernas benägenhet att emigrera från Sverige till Norge, och av honornas överlevnad till vuxen ålder och som vuxna. Huvudfaktorerna för stammarnas livskraft bedöms vara valen av förvaltningsstrategi i de båda länderna, de båda arternas spridning till Norge och den "source-sink"-dynamik som de kan orsaka, plus mängden illegal jakt.

Rapporta čilge bohtosiid demográfalaš hearkkesvuoda-analysas, ovttas rašesvuodaanlysisas, albasiin ja getkkiin Skandinávas sierra hálddahušgovahallamiiguin, gos Bayesian integrerejuvvon populašuvdnašaddan geavahuvvui. Ruotas populašuvdnašaddan šlájain sakka váikkuhuvvo indiviiddaid tendeanšas emigreret Ruotas Norgii, ja čiikkuid birgen ráves ahkái ja rávvásiin. Váldofáktorat máddagiid eallinfápmui árvvoštallo leahkit hálddahušstrategiija válljen goappaš riikkain, goappaš šlájaid leavvan Norgii ja "source-sink"-dynamihka man sáhtttá dagahit, ja vel man ollu lobihis bivdu lea.

