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–
development of a new method

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Populationsberäkningar för den skandinaviska vargstammen och stickprovsbaserad inventering – utveckling av en ny metod

Svensk sammanfattning

<u>Uppdraget</u>

Naturvårdsverket gav det skandinaviska vargforskningsprojektet (SKANDULV), Sveriges Lantbruksuniversitet (SLU) i uppdrag (NV-07425-14) att:

1) Beräkna omräkningsfaktorer för omvandling från antal dokumenterade familjegrupper till total populationsstorlek och till antal föryngringar av varg i Sverige och Norge. Populationsberäkningen ska resultera i det totala antalet vargar vid en given tidpunkt i slutet av inventeringsperioden. Vid populationsberäkningen ska hänsyn tas till den totala dödligheten. Beräkningarna ska baseras både på registrerade familjegrupper och revirmarkerande par.
2) Analysera förutsättningarna för stickprovsbaserad inventering av det totala antalet vargindivider i utvalda revir for att erhålla data på gruppstorlek.

Inom ramen for uppdraget skall omräkningsfaktorer beräknas genom demografisk populationsmodellering av den skandinaviska vargpopulationen utifrån befintlig data från sändarförsedda vargar samt data erhållna via resultat från DNA-analyser. Inom uppdraget ingår även att genomföra beräkningar som ger ett mått på osäkerheten kring de erhållna omräkningsfaktorerna.

Data på kullstorlek i revir är en viktig parameter vid beräkningen av omräkningsfaktorer under rådande förhållanden samt att studera och övervaka eventuella inavelseffekter i framtiden. Inom uppdraget (punkt 2) ingår att belysa frågor kring hur många revir av olika kategorier (förstaårsföryngring, revir med föryngring under flera år, respektive revir med olika inavelsgrader) som årligen måste inventeras mer intensivt för att med en viss säkerhet upptäcka en förändring av den verkliga gruppstorleken i populationen.

<u>Introduktion</u>

Den skandinaviska vargpopulationen har ökat i både antal och utbredning sedan början av 1990-talet. Målen med inventeringen har ändrats i takt med att populationen har ökat. I början inventerades alla kategorier av djur d.v.s. revirmarkerande par, alla individer i familjegrupperna, föryngringar (reproduktioner), vandringsvargar, samt övrig stationär förekomst av varg. De tidigare omräkningsfaktorerna som använts för att skatta populationsstorleken behöver uppdateras då dessa bygger på data insamlade under inventeringssäsongerna 2000/2001-2002/2003 och då med antagandet att samtliga individer i populationen återfanns vid inventeringen. Den senaste ändringen innebär att målet i inventeringen numera är att dokumentera antal familjegrupper och revirmarkerande par under vintern. Den totala populationsstorleken och även antalet reproduktioner skall framöver

beräknas utifrån antalet funna familjegrupper i populationen. För antalet reproduktioner innebär de nya kriterierna att en omräkningsfaktor från antal familjegrupper måste tas fram för att skatta antalet reproduktioner då det inte längre är ett mål att inventera dessa i fält. Eftersom fastställande av antal familjegrupper fortsatt är en central uppgift för inventeringsarbetet, är det avsikten att denna enhet ska vara utgångspunkten för omräkningsfaktorerna.

<u>Metod och resultat</u>

Beräkning av omräkningsfaktorer

Omräkningsfaktorerna beräknades genom att använda en individbaserad demografisk populationsmodell som simulerar populationsutvecklingen under en specifik tidsperiod baserat på egenskaper hos individerna. Dessa egenskaper är t.ex. åldersspecifik överlevnad, kullstorlek, ålder för utvandring och reproduktion. Datat som används i modellen är baserat på insamlade data från 154 stycken sändarförsedda vargar under åren 1998-2014. Inventeringsdata från de årliga inventeringarna används för att ange sammansättningen på startpopulationen och för att få ett mått på genomsnittlig överlevnad från födsel till 6 månaders ålder samt för att få ett mått modellens kapacitet att återskapa populationens funna dynamik. Precis som den verkliga populationen utvecklar den simulerade modellpopulationen en social struktur med familjegrupper, revirmarkerande par och ensamma djur. För att kunna beräkna omräkningsfaktorer genom modellering är det en förutsättning att sammansättningen av modellpopulationen speglar sammansättningen i den verkliga populationen tillräckligt väl.

I modellen klassas individerna som valpar (0-12 månader), ungvargar i sitt föräldrarevir (>12 månader gamla), vandringsvargar, samt vuxna revirmarkerande individer. I de simulerade populationerna klassificeras individerna varje månad enligt kön, ålder och status. Överlevnaden från födsel till den 1 december, vilket är tidpunkten när inventeringen av varg sker i modellen, beräknades till 0.70 medan individer äldre än 6 månader (den tidigaste åldern när vargarna kan sändarförses) och ungvargar hade en årlig överlevnad på 0.78. Vandringsvargarna överlevnad beräknades till 0.42 och vuxna individer till 0.82. Ålder för första reproduktion var tidigast 24 månader. Dödligheten i de olika klasserna bygger på data från de radiomärkta djuren. Detta gäller dock bara den typ av dödlighet där det inte finns exakt kunskap, det vill säga huvudsakligen naturlig dödlighet och illegal jakt. För den lagliga jakten finns däremot exakt kunskap, inte bara på hur många djur som skjutits, utan också deras ålder, kön och social status, samt datum för dödsfallet, vilket utnyttjas i simuleringarna. Där läggs denna jakt till exakt som den skett i verkligheten. Har t. ex. ett revirmarkerande djur skjutits under skyddsjakt i september 2007, så plockas en motsvarande varg bort från modellpopulationen vid denna tidpunkt. All dödlighet klassas som så kallad additiv dödlighet, det vill säga att det finns inte någon kompensatorisk effekt mellan olika typer av dödlighet.

I simuleringarna användes populationssammansättningen från vintern 2003/2004 som start population (baserat på inventeringsresultatet). Denna bestod av 11 familjegrupper, 11 revirmarkerande par och 11 föryngringar. Modellen används sedan för att simulera populationsutvecklingen genom att använda empiriska data på t.ex. kullstorlek och överlevnad. Från varje simulering beräknas antalet familjegrupper, revirmarkerande par,

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reproduktioner och total populationsstorlek. Eftersom varje individ följs genom varje simulering kan andelen valpar, ungvargar, vandringsvargar, och vuxna stationära vargar beräknas för varje given tidpunkt. Vi förväntar oss inte att modellen exakt skall följa inventeringsresultaten trots att modellen använder data från den skandinaviska vargpopulationen eftersom det i verkligheten finns en slumpmässig variation som inte återspeglas i de data som modellen bygger på.

Samtliga datapunkter från inventeringarna (2003/2004-2013/2014) låg inom konfidensintervallet (95%) för det simulerade resultaten från modellen. Överensstämmelsen var relativt god för familjegrupper och reproduktioner medan det var en större skillnad för revirmarkerande par. Åldersstrukturen i populationen från simuleringarna visade att den största andelen av populationen består av revirhävdande djur, men en nästan lika stor andel utgörs av årsvalpar. Båda grupperna utgör ungefär 40% vardera av populationen. Vandringsvargarna utgör ungefär 20% av populationen, medan ungvargarna (>1 år gamla) som går kvar i föräldrareviret utgör den minsta delen av populationen. Åldersstrukturen i populationen var stabil mellan år och förändras inte efter åren med licensjakter eller år med flera vargar skjutna under skyddsjakt.

Modellen gav en omräkningsfaktor på 8.0 (95% CI = 6.53–10.14) mellan antalet familjegrupper och total populationsstorlek beräknat för den 1 december. Detta ger t.ex. en populationsuppskattning på 344 vargar den 1 december 2013 då det dokumenterades 43 familjegrupper i Sverige och Norge under inventeringssäsongen 2013/2014. Osäkerheten (95% CI) skattas till 281-436 vargar. Motsvarande omräkningsfaktor för 31 mars blev 7.55 (95% CI = 6–10.25). Omräkningsfaktorn mellan antal familjegrupper och antal föryngringar beräknades till 0.95 (95% CI = 0.81–1). Detta ger 41 föryngringar för 2013 med en osäkerhet mellan 35 och 43. Inventeringsresultatet var 40 föryngringar, vilket överensstämmer väl med det beräknade värdet på 41.

Stickprovs-baserad inventering

Vi antog att gruppstorleken under vintern var Poisson fördelad och genomförde simuleringar för att beräkna antalet revir där det krävs extra insatser för att skatta kullstorleken och för att upptäcka en statistiskt säkerställd förändring i kullstorlek mellan år. För att uppskatta gruppstorleken med ett genomsnittligt fel på 10% (d.v.s. avviker från medelvärdet med mer än 10%) krävs extra insatser (snöspårning och DNA-analyser) i minst 15 familjegrupper. För att upptäcka en förändring i gruppstorlek med 1 varg mellan år krävs extra insatser i 15 revir per år om ett genomsnittligt fel på 10% är acceptabelt.

Diskussion

Eftersom den populationsmodell som vi har använt i denna rapport är mycket mera komplicerad än andra traditionella populationsmodeller så bör rapporten genomgå vetenskaplig granskning och publicering innan resultaten används som den huvudsakliga källan för populationsuppskattning i förvaltningen. I detta skede av modellutveckling kan man inte använda populationsuppskattningen som fås från den omräkningsfaktor som presenteras i denna rapport för att jämföra med de populationsuppskattningar som gjorts under tidigare

är vilka är gjorda med andra metoder. Trots att vi anser att modellen fångar upp dynamiken i populationen på ett bra sätt så bygger modellen på ett antal strukturella antaganden som behöver valideras ytterligare. Detta betyder att de omräkningsfaktorer som presenteras i denna rapport kan komma att förändras i framtiden allt eftersom modellen förbättras. Därför avråder vi från att man i nuläget drar slutsatser om att den verkliga storleken på populationen är starkt avvikande från den förväntade utifrån den omräkningsfaktor som presenteras i denna rapport. Nästa steg i processen att göra resultaten tillämpbara i förvaltningen är därmed en vetenskaplig granskning och publicering av rapporten.

Den modell som ligger till grund för alla simuleringar och beräkningar, bygger på demografiska data (reproduktion, dödlighet, spridning, etablering etc.) som uppmätts med hjälp av radio-märkta djur. Ett viktigt antagande är därför att de radiomärkta djuren är representativa för den nuvarande populationen. Detta antagande är förmodligen inte helt korrekt. Vissa kategorier av vargar, framförallt de ett- och tvååriga vargar som ännu inte etablerat sig i ett eget revir är relativt dåligt representerade bland de radio-märkta individerna. Ett annat antagande är att de demografiska parametrarna hållit sig relativt konstanta under perioden 1999-2014, eftersom våra data från de radio-märkta djuren kommer från hela denna period, vilket inte nödvändigtvis är helt korrekt. Trots dessa antaganden visar modellen relativt god samstämmighet med empiriska inventeringsdata för antal par, antal familjegrupper och antal reproduktioner (Figur 1). Detta tyder på att även om det finns svagheter i ingående data för modellparametrarna så fångar modellen upp de viktigaste dragen i den verkliga populationens dynamik.

Den beräknade omräkningsfaktorn från familjegrupper till antal reproduktioner var 0.95. Detta värde skiljer sig endast marginellt från förhållandet mellan familjegrupper och reproduktioner i inventeringsdata (0.96). Däremot ligger omräkningsfaktorn från familjegrupper till totalt antal individer lägre (8.0) än motsvarande kvot från inventeringsdata (9.6), vilket är en skillnad på 17%. Detta innebär t.ex. att antalet individer i populationen beräknat med omräkningsfaktorn från populationsmodellen för 2013/2014 skulle blivit 344 (95% CI = 281-436) medan beräkningarna byggda på inventeringsresultaten som redovisas i årsrapporten gav ett värde på 400 vargar (vilket inkluderar döda vargar). Denna diskrepans mellan de två beräkningssätten kan bero antingen på att det tidigare beräkningssättet gav överskattningar, eller att den här presenterade modellen ger en underskattning, eller på en kombination av dessa. Det skulle behövas bättre data på främst överlevnad hos ungdjur samt för processen med övergång från utvandringsvarg till stationär, och från stationär varg till parbildning. Känslighetsanalyserna visar att modellen är som mest känslig för dessa övergångar. De tidigare beräkningarna av populationsstorlek byggde även dessa på korrektionsfaktorer, hämtade från endast tre inventeringssäsonger (2000/2001-2002/2003) när det totala antalet individer inventerades både i Sverige och Norge. Den omräkningsfaktor som använts för de senaste tre åren (2011/2012-2013/2014) och som bygger på en omräkning från antal reproduktioner till antal individer uppgick till 10.0 men med stor variationsbredd i skattningen (för 2013/2014 gav detta ett intervall på 316-520 vargar). Det är omöjligt att fastställa var den största orsaken till diskrepansen mellan de två beräkningssätten ligger, men båda har stora konfidensinverall, som till stor del också överlappar varandra. Med mycket stor sannolikhet ligger det sanna värdet av kvoten mellan familjegrupper och antal individer

någonstans inom detta överlappande intervall. Endast mer data på demografin i den skandinaviska vargstammen, och särskilt för processen från valpstadiet till dess att djuret har bildat par, kan ge oss en bättre uppfattning om var detta värde ligger.

Eftersom det inte är sannolikt att olika demografiska parameterat och deras inbördes relationer, kommer att förbli konstanta för all framtid, kommer det att krävas uppdateringar av modellen, och omräkningsfaktorerna efter hand. Därför är det viktigt även ur denna aspekt att man fortsätter med en kontinuerlig insamling av demografiska data för varg.

<u>Manual</u>

Modellen visar populationens utveckling månadsvis. Detta ger de kurvor som visar utvecklingen hos de olika kategorierna av varg i figurerna 1, 2 och 3 ett vågformigt utseende. Antal vargar är som högst i maj, direkt efter födseln av valpar (som i modellen antas ske 1 maj) för att sedan sjunka under hela året till följd av en kontinuerlig dödlighet, fram till nästa reproduktionstillfälle kommande år. Antalet familjegrupper följer samma mönster, liksom antal reproduktioner. Även dessa två parameterar visar en sjunkande tendens under året mellan reproduktionstillfällena, därför att dödligheten medför att en del av dem efter en tid inte längre uppfyller kriterierna för att räknas som familjegrupp respektive reproducerande familjegrupp. Antal revirmarkerande par däremot sjunker snabbt vid reproduktionstillfället i maj, eftersom många av dem då övergår till att bli reproducerande familjegrupper. Därefter stiger antalet igen långsamt, i takt med att nya par bildas, främst som ett resultat av utvandrande ungvargar, fram till nästa reproduktion. De medianvärden från simuleringarna som visas i diagrammen, och i tabeller och text, hänför till situationen den 1 december varje år. Det innebär att dessa medianvärden är närmast jämförbara med siffrorna i tidigare inventeringsresultat som då angavs som bruttosiffror för populationen under vintern.

De omräkningsfaktorer som modellen ger gäller för hela den skandinaviska vargpopulationen. Dessa är inte tillämpningsbara för mindre geografiska områden, som till exempel enskilda län, eller den norska vargzonen. Sådana delar av hela populationen är så små, att slumpfaktorerna blir mycket starkare, vilket ger väldigt stora osäkerhetsintervall. Dessutom kan det vara så att det finns systematiska skillnader, vad gäller till exempel habitat eller bytestillgång mellan olika delområden. Modellen genererar värden för hela populationen, varifrån det alltså kan finnas lokala avvikelser som sannolikt kommer att ge mindre god överensstämmelse vid försök att tillämpa omräkningsfaktorerna lokalt.

English summary

This report is produced upon request by the Swedish Environmental Protection Agency with the objectives to 1) estimate numbers for converting the number of documented family groups to a) total wolf population size and b) the number of reproductions by wolves in Scandinavia, and 2) estimate the requirements for a sample-based monitoring of wolves in a number of selected territories to obtain reliable data on group size of Scandinavian wolves. The Scandinavian wolf population has increased in both size and range since the beginning of the 1990's and changes in monitoring regimes (for example total number of reproductions and total group size during winter are no longer a target of monitoring of wolves in Sweden) require that new methods are developed for estimating total population size and structure. In addition, data on pack- and litter size are important for future estimations of population size and to follow up the effects of inbreeding on wolf reproduction in Scandinavia.

For question 1, we calculated conversion factors using a wolf specific individual-based model that considers events at the individual or pack level. This kind of model allows including more explicit biological realities and individuals or packs can be tracked during the whole simulation. Because the model functions with rules at the individual or pack level, the demographic consequences of these mechanisms are population-level emerging properties of the model and are not predefined by equations as in more traditional population models.

Because the model is also much more complex than traditional ones, we believe it requires additional validation and a proper peer-review process through a publication in a scientific journal before the population estimates it infers are used as the main source for management purposes. At this stage of model development, we warn against using population estimates based on presented conversion factors in comparison of population trend. While we are confident that our model does a good job in simulating the wolf population dynamic, several structural assumptions in the model had to be made and require further validation. This will mean that the conversion factors we propose here may change in the future as we improve and refine the model. We therefore also warn against blunt claims, on the only basis of our conversion factor, that the true wolf population size is radically different from what is expected. The next required step is a peer-reviewed publication to be able to consider the model as management-ready.

The model is based on data (survival, dispersal, mortality etc.) from radio-collared wolves (N = 154) in the Scandinavian wolf population. Model simulations resulted in a ratio from family groups to total wolf population size of 8.0 (95% CI = 6.53–10.14) and a ratio from family groups to total number of reproductions of 0.95 (95% CI = 0.81–1). The model is strongly dependent on the assumptions that radio-marked wolves are representative for the population, that the demographic parameters have not changed substantially over time and that the relative proportion between different social categories is representative for the current population. The model makes mechanistic assumption for the formation of pairs that attempt to best describe the life history of the wolf while minimizing the number of parameters. The relatively good fit between model results and monitoring data supports the supposition that those assumptions have not resulted in serious flaws with the model, however the consequence on the conversion factor of a different mechanistic formalization for pairing

deserves further attention. The relatively good fit between model and field data concerning the family group-reproduction ratio indicates that using family groups as the base for estimating total population size is possible. A regular updating of demographic parameters from radio-marked wolves is important when modifying the conversion factors in the future.

For question 2, we assumed that litter size was Poisson distributed and run simulations to calculate the number of family groups required to estimate litter size in the population and to detect changes in annual litter size. We find that having an average error of 10% in estimating group size (i.e. deviating from the mean by not more than 10%) requires monitoring at least 15 family groups. Aiming at detecting a change of 1 wolf requires monitoring 15 family groups if an error rate of 10% is acceptable.

Introduction

The Scandinavian wolf population has increased in both size and range since the beginning of the 1990s (Wabakken et al. 2001a, Svensson et al. 2014). In 1978, wolf monitoring started as the first national cross-border monitoring of a large carnivore in Scandinavia (Wabakken et al. 2001a). Since then, the Scandinavian wolf population has been monitored continuously and in close cooperation by various Swedish and Norwegian researchers, NGOs, and management authorities. From every winter since 1998, joint Swedish-Norwegian annual reports have presented the status of the wolf population. Herein, Scandinavian wolves have been classified as: family groups (≥3 wolves sharing a territory), territorial (scent-marking) pairs, other stationary wolves, or vagrants (Wabakken et al. 1999, Liberg et al. 2012) during the period October 1 to February 28 until 2013/2014. Also the number of reproductions has been estimated each year during the period May 1 – February 28 based on visual or vocal observations, scats from pups, rendezvous sites during late summer/early autumn, or confirmed using DNA of pups.

In both countries, national political goals of wolf population size have been set by the Swedish and Norwegian parliaments, respectively. The Swedish parliament has decided a reference value of 270 individuals within Sweden, while the Norwegian parliament has decided on minimum three annual reproductions within entirely Norwegian wolf territories and an unlimited number of cross-border reproductions. Although extensive cooperation in various management issues and joint research on large carnivores have existed cross-border for decades, there is no joint politically decided goal for the entire cross-bordering Scandinavian wolf population.

Prior to the winter 2012/2013, estimation of average and minimum-maximum population sizes were based on the assumption that 77-83% of the total number of wolves were territorial, i.e. individuals within family groups or pairs (Wabakken et al. 2011). This estimate of population structure was derived from previous minimum-maximum population estimates during three years (survey seasons 2000/2001-2002/2003) under the assumption that all individuals in the population were observed (Wabakken et al. 2001b, 2002, 2004a). Since winter 2012/2013 total population size (including stationary wolves and vagrants) has been estimated using a conversion factor of 10.0 (with variation between 9.2-10.7 among years) between the number of reproductions and total population size (SKANDULV unpublished

data, see Svensson et al. 2013 for description of the methods). The uncertainty of the population size estimate during the winter of 2013/2014 was calculated by using pseudo-95% confidence interval from the years 2000/2001-2002/2003 (SKANDULV unpublished data, see Svensson et al. 2014 for description of the methods). The previously used population estimates included dead wolves.

The Swedish Environmental Protection Agency and the Norwegian Environment Agency decided in 2012 that monitoring of large carnivores (lynx, wolverine, brown bear, and wolf) should be better coordinated and conducted using the same type of methods in both countries exclusively. This resulted in new criteria (Naturvårdsverket and Rovdata 2014) of wolf monitoring in Sweden and Norway. Starting from the winter of 2014/2015, the primary units of the annual population monitoring in Sweden are family groups and territorial pairs during the period October 1 – March 31. Within the Swedish reindeer husbandry area all individual wolves should be registered per Sami village. In Norway, monitoring of all wolves in the field should be continued (Miljødirektoratet, personal communication). As a consequence, determination of the number of territories with pups of the year (monitored since 1978, Wabakken et al. 2001a) is no longer a target neither for the Swedish monitoring nor for the total Scandinavian monitoring, but will be recorded when the criteria for reproduction are fulfilled without any extra effort for the field personnel. The number of reproductions will instead be estimated from the observed number of family groups during the winter monitoring period. Those changes in monitoring regimes require that the use of conversion factors (from number of family groups to both number of reproductions and total population size) is quantitatively evaluated, including some measurement of uncertainty of the population size and reproduction estimates.

In addition to the new monitoring program described above, Wikenros et al. (2014) suggested using a sample-based monitoring strategy in randomly selected territories in each monitoring season to determine the total group size in those. This will be achieved through intensified snow-tracking efforts combined with an extended number of DNA-samples collected and analyzed in the selected territories. These territories should be selected so they represent the variation of inbreeding in the population, and also represent both first-time breeders as well as those that have bred before. In the latter category pups from previous reproductions can still be present in the territory of birth.

Inbreeding depression and loss of genetic variation are in addition to poaching the most important threats to the Scandinavian wolf population (Liberg et al. 2012). Good empirical data on litter sizes are therefore important to continuously follow up the effect of inbreeding on reproduction. One quantitative measurement of inbreeding depression available for this wolf population is an effect on litter size during the first winter after birth (Liberg et al. 2005). To follow the development of inbreeding depression, and to be able to evaluate various management actions to improve the genetic situation, e.g. natural or artificial introduction of wolves from other populations, a continued monitoring of litter sizes is imperative.

As a consequence the Swedish Environmental Protection Agency has given the Scandinavian Wolf Research Project (SKANDULV) an assignment (NV-07425-14). This assignment contains two main tasks:

1) Calculate a factor for converting number of documented family groups to a) total population size at a given time at the end of the monitoring period, and b) number of reproductions in the same monitoring period. The population estimate must take into account the total wolf mortality. Calculations should be based both on monitored family groups and territorial pairs. In addition, estimates of uncertainty for the estimated mean population size and the number of annual reproductions shall be given.
2) Estimate the requirements for sample-based monitoring of wolves in a number of selected territories to obtain data on group size by a) discussing issues regarding the categories of territories (both first-time reproductions and territories where reproduction has occurred several years, and territories with different levels of inbreeding) that should be intensified in order to obtain good data on group size, and b) to calculate how many territories that annually needs to be monitored more intensively to achieve a certain confidence level for the estimation of group size.

Analysis

Part 1: Conversion factors and population size

The wolf is a monogamous, social animal that lives in family groups, i.e. packs, which is the functional unit of a wolf population. Events at the individual and pack levels (e.g. dispersing from a natal pack and founding a new pack) shape the overall population dynamics. To capture this complex population dynamic, we develop a wolf specific individual-based model that considers events at the individual or pack level and formalize them into probabilistic rules with parameters. The demographic consequences of these events are population level emerging properties of the model and are not predefined by equations as in more traditional analytical population models. Therefore, all our inferences rely on simulations.

Model structure

The time step in the model is 1 month and wolves in the simulated population go through particular events every month according to their sex, age or social status. Wolves can be pups (0-12 months), subadults (>12 months remaining in their natal packs), vagrants (not territorial), and territorial adult animals (which includes newly established loners before they get a partner, pairs before breeding, breeders, and widows/widowers). The population is considered as a closed population (no immigration or emigration).

Model rules and parameters

Litter size

Pups are born in May and the production of litters in packs is modelled by sampling from a Poisson distribution with mean of 5 pups calculated from pup counts at dens (N = 18).

Survival

All individuals survive or die following a Bernoulli trial drawn from a monthly survival probability. Survival includes all causes of mortality except the legal management one (license and protective hunt) that are perfectly observable (but see for vagrants below). This way of proceeding means that all other sources of mortality with non-perfect detectability (such as poaching or natural causes of mortality) are included in the model as built-in baseline mortality rates. Environmental stochasticity is modelled by having the mean survival being Beta distributed with shape parameters obtained by moment matching. We estimate pup (0-6 months) survival by dividing the average size of first time breeding packs in winter minus the two breeders (N = 88) by litter size at three weeks of age (see above). We use radio-telemetry data to estimate the survival of animals older than 6 months. For each class (pups > 6 month old and subadults, vagrants, and territorial adult animals), we fit parametric survival models. Mortality rate is then obtained from the rate of the time-to-event exponential models. These rates are constant and indicate the daily mortality rate to which animals are exposed. We then scale daily mortality rate to monthly survival rate.

Dispersal

Pups that are older than 10 months and subadults in packs disperse at a given age parameterized from radio-marked data. The assumption that radio-marked animals provide an informative and representative enough sample of the population is critical here. We assume that the age at dispersal follows a negative binomial distribution (often used in ecology for describing how many times one needs to wait for an event to happen). We fit a binomial distribution to radio-telemetry data of the Scandinavian wolf population (N = 48). In addition to this baseline dispersal mechanism, when a breeding couple in a pack dies, all other members of the pack automatically disperse to join the pool of vagrants and the couple is removed from the population. As long as only one adult breeding individual dies the remaining pack members will still be a family group.

Settlement and pairing

The mechanism for settlement and pairing was the most difficult to model as this is the segment of a wolf's life where we have the least amount of information. We have formalised this mechanism by considering that vagrants older than 14 months can become territorial by either settling in a pack where the breeder of the same sex is missing or by finding a vagrant mate of the opposite sex and creating a new territory. This mechanism assumes a relatively quick formation of pairs as we do not consider the alternative that an animal will settle alone and wait for a vagrant to join and then form a pair. While this may happen in reality, a version of the model with this alternative mechanism was not able to fit well the data and this mechanism deserves further consideration. We assume that the age at which vagrants become territorial adults follows a negative binomial distribution. However the sample size for radio-marked animals is small and we therefore let the model finding what are the best parameters using Pattern Oriented Modelling (see for example Wiegand et al. 2004a,b). The model does not include density dependence or carrying capacity for wolves or territories because

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population density is considered low as compared to many other wolf populations under similar environmental conditions (Mech and Boitani 2003).

<u>Reproduction</u>

Pairs of breeding wolves breed with a probability that is fitted to the data using Pattern Oriented Modelling. When a pair has bred already one year, we assume that they will breed every year as long as they have been together during the mating season. When a breeding couple in a pack dies during any time between birth and up to 6 month after giving birth, all pups of the year are assumed to die as they cannot hunt by themselves.

<u>Hunting</u>

In addition to regular mortality, every month the model additionally removes wolves that have been culled during the protective and license hunts during previous years (this source of mortality is perfectly observable) according to their class (pups and subadults vs. adults). The hunting mortality for vagrants is instead included in their mortality parameter, as treating it as data would open for the possibility that more vagrants than existing are shot in some stochastic runs.

Initial population

The wolf population in 2003/2004 is the initial population size for the simulations (Wabakken et al. 2004). Before 2003/2004 the population growth rate was smaller and may not be representative of the present population dynamics as an Allee effect may have been present. Data from earlier years are therefore not used in the model. The initial population consists of 11 family groups of an average size 6, 11 pairs and 11 vagrants. This initial population structure is reconstructed from what the population was in 2003/2004 and is stochastically generated for each simulation (i.e. number of pups and yearlings in packs). The idea is not to have the exact population structure in 2003/2004 but something that approaches it. It is important to include pairs and vagrants in the initial population structure as failure to do so create a bias in the population structure during the first years of the simulation. When using a model, simulations are always sensitive to initial population structures: for example, an initial population consisting only of breeders would not have the possibility to have new breeders at time $t = 2$ because it did not start with any vagrants. This can lead to oscillation of population structure and several years may be required to have the influence of a biased initial population structure declining. In our case, we structured our initial population as close as possible to the one reported during monitoring in the winter of 2003/2004, and the simulated population structure did not show large changes across years (Figure 2) indicating that the initial population structure was not important for the final model results.

Model fit to data

We use Pattern Oriented Modelling to estimate parameters for which we have a limited knowledge (settling and pairing parameters). This algorithm works by running simulations with many test values of poorly known parameters and then comparing whether the simulations are able to replicate well the observed data (Table 1). We fit the model to annual

number of family groups, reproductions and pairs, but not to annual population estimates (as they were already inferred from a conversion factor). At the end, we select the parameter value that allows the model to explain the data the best. The final parameter values are shown in Table 2.

Table 1: Monitoring data (corrected data, see Anon., 2015) used for Pattern Oriented Modelling with the simulated populations, total number of wolves previously estimated (including dead wolves) and number of harvested wolves (includes protective harvest and license hunts) used in the simulations.

| Monitoring winter	Year[1]	Family groups	Pairs	Reproductions	Individuals (min-max)	Harvested animals
2003/2004	2003	11	11	11	101-120	0
2004/2005	2004	14	15	14	135-152	4
2005/2006	2005	15	14	15	141-160	3
2006/2007	2006	17	14	17	136-169	4
2007/2008	2007	20	19	19	166-210	3
2008/2009	2008	29	14	27	213-252	11
2009/2010	2009	28	24	27	252-291	13
2010/2011	2010	31	29	31	289-325	18
2011/2012	2011	33	32	28	258-332	34
2012/2013	2012	39	26	39	350-410	26
2013/2014	2013	43	25	40	316-520	24

[1]As shown in Figure 1.

Table 2: Estimate of model parameters used in the simulations. * indicates parameters estimated by fitting the model to monitoring data. Other parameters are estimated from radio-marked animal data.

Parameter	Estimate
Pup (0-6 months) annual survival	0.70
Pup (>6 months) & subadult annual survival	0.78 ± 0.1
Vagrant annual survival	0.42 ± 0.1
Adult annual survival	0.82 ± 0.1
Dispersal: negative binomial (n)	1.68
Dispersal: negative binomial (p)	0.32
* Settling: negative binomial (n)	30.5
* Settling: negative binomial (p)	0.8
Probability a pair breeds the first time	0.79
Litter size	5
Sex ratio	0.5
Minimum age at first reproduction (months)	24

Results

We use the model to simulate the dynamics of wolf populations with the fitted parameters and the initial condition and count how many family groups, pairs, individuals and reproductions we get in these simulations (Figure 1). Because we can follow each individual during the whole simulations, we can also calculate the proportion of pups, yearlings, vagrants, and adults (Figure 2), as well as group size (Figure 3) and the time of particular events in the life of a wolf (Figure 4). From the simulations we can then calculate a conversion factor (with a quantified uncertainty) from family groups to population size and from family groups to number of reproductions (Figures 5 & 6).
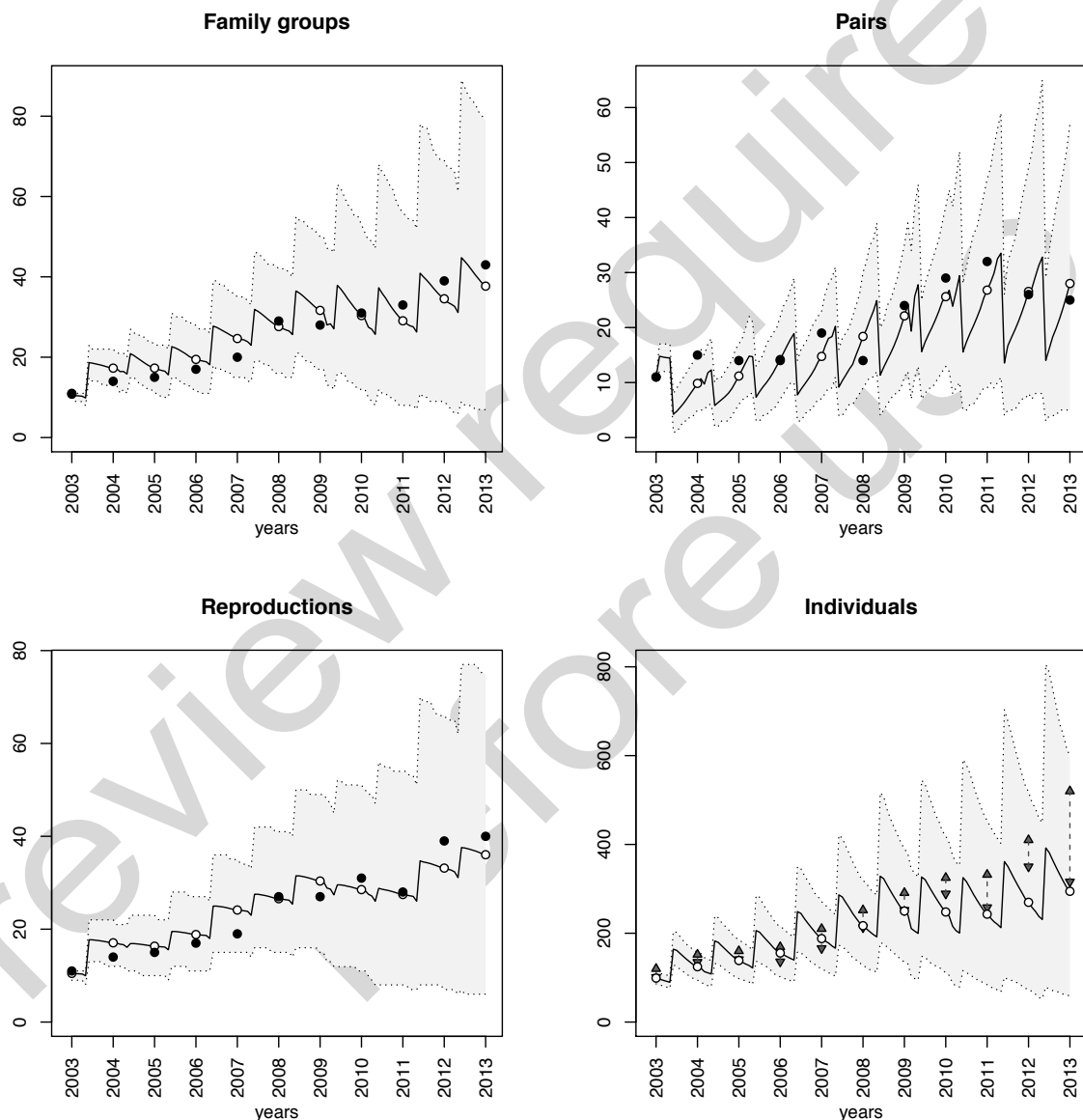
Figure 1: Median number of family groups (top left), territorial pairs (top right), reproductions (bottom left) and number of individuals (bottom right) of simulated populations. Black line is monthly values, empty circles are yearly values (at December 1st), black dots are Scandinavian monitoring data and, grey area between the dashed lines is the 95% CI. For number of individuals, up and down grey triangles indicate minimum and maximum population counts inferred from monitoring. The first year of the simulation is influenced by initial population structure.

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It is important to note that we report the median of 1,000 random population trajectories while the monitoring data from the Scandinavian wolf population is in fact a single stochastic trajectory. As such it should not be expected to have the model perfectly fitting the monitoring data (Figure 1). Despite that a lot of SKANDULV's research-based information from the Scandinavian wolf population is included in the model, it does not consider many other random factors that may affect the wolf population dynamics (yearly variation or trends in poaching rate, incidence of sarcoptic mange etc.).
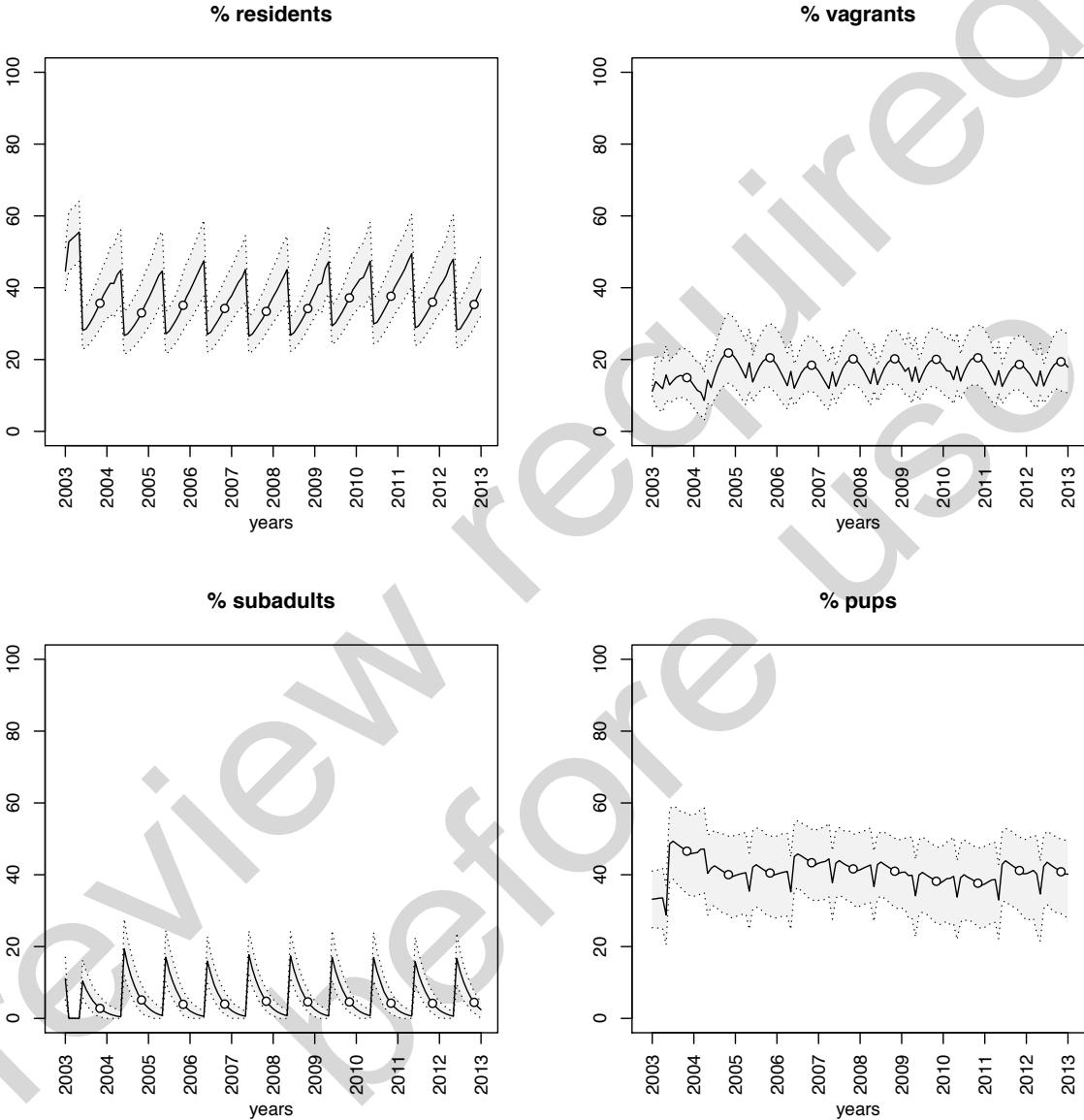
Figure 2: Structure (in classes) of simulated populations (represented as mean proportions in %). Black line is monthly values, empty circles are yearly values (at December 1st), the grey area between the dashed lines is the 95% CI. The first year is influenced by the initial population structure. Note that population structure does not change with the increase in harvest that occurred the most recent years.
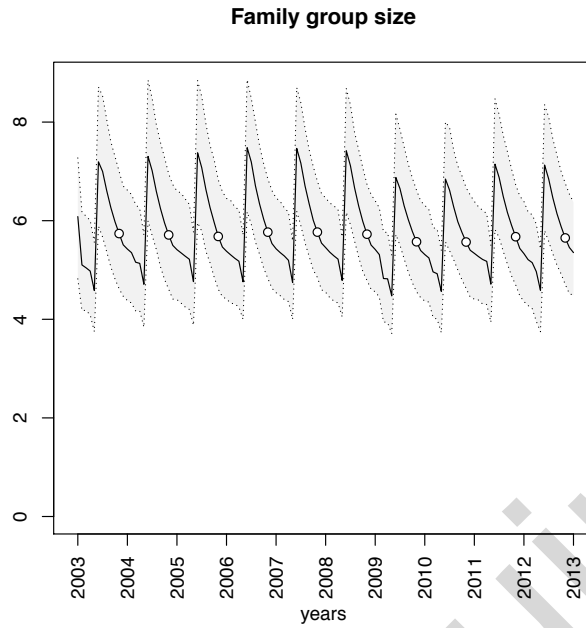
Family group size

Figure 3: Median number of individuals within family groups for the simulated populations. Empty circles are yearly values (at December 1st), the grey area between the dashed lines is the 95% CI.
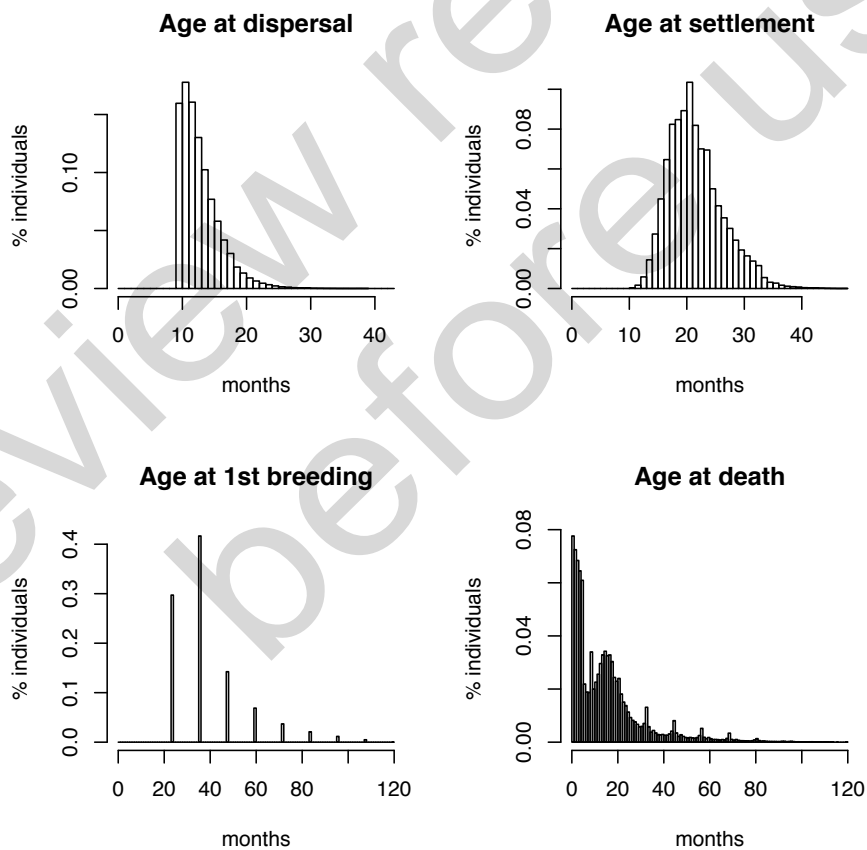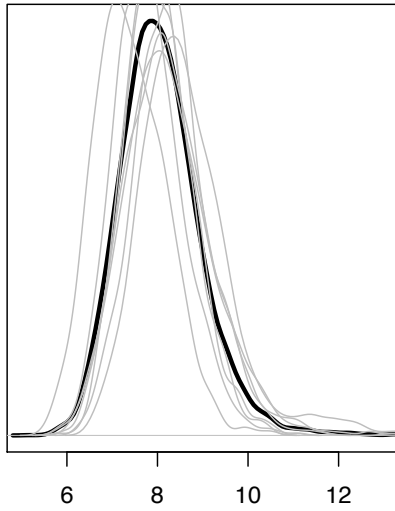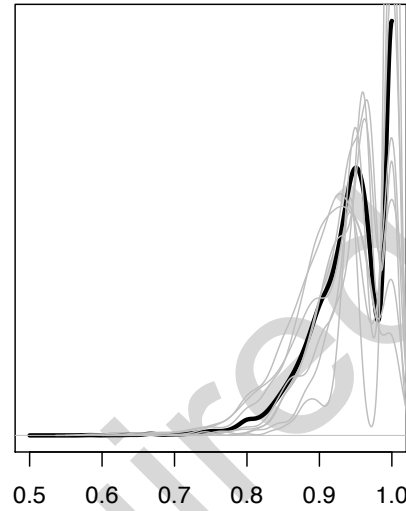

Figure 4: Distribution of age at dispersal, age at settlement, age at first time breeding and age at death in months for all individuals in simulated populations.

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family groups –> total population

family groups –> reproductions

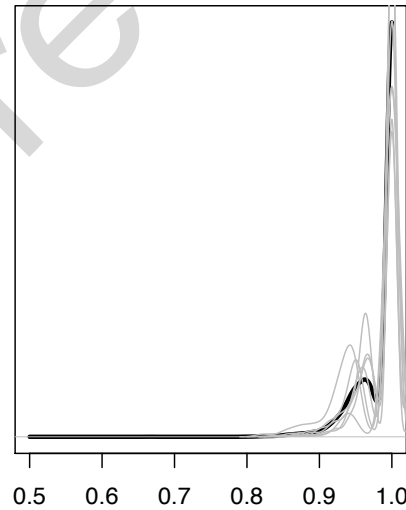8±1.08 95%CI= (6.53–10.14)

0.95±0.06 95%CI= (0.81–1)

<u>Figure 5:</u> Posterior density distribution of conversion factors for December 1st linking the number of family groups to the total number of wolves and to the number of reproductions. Black line is average from 2004 to 2013 and grey lines are average for moving 3-year windows (exact years not shown). The y axis is unit-less and indicates how likely values are on the x axis (the higher the more likely).

family groups –> total population
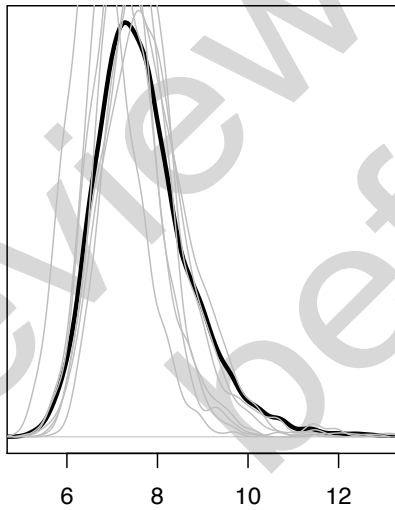
family groups –> reproductions

7.55±1.15 95%CI= (6–10.25)

1±0.05 95%CI= (0.91–1.11)

<u>Figure 6:</u> Posterior density distribution of conversion factors for March 31st linking the number of family groups to the total number of wolves and number of reproductions. Black line is average from 2004 to 2013 and grey lines are average for a moving 3-year windows (exact years not shown). The y axis is unit-less and indicates how likely values are on the x axis (the higher the more likely).

We estimate the ratio for December 1st from family groups to total wolf population size at 8.0 (95% CI = 6.53–10.14) (Figure 5 left) and the ratio from family groups to total number of reproductions at 0.95 (95% CI = 0.81–1) (Figure 5 right). We estimate the ratio for March 31st from family groups to total wolf population size at 7.55 (95% CI = 6–10.25) (Figure 6 left) and the ratio from family groups to total number of reproductions at 1 (95% CI = 0.91–1) (Figure 6 right). Many simulations have a ratio from family groups to total number of reproductions at 1, which explains the tall right tail of the distribution on Figures 5 & 6. We can use the conversion factor to calculate total population size from the number of family groups. We simply multiply the number of family groups by the distribution of estimates of the conversion factor (Figure 5 or 6 left) and obtain a distribution of population size for wolves. We therefore do not obtain a single estimate but a range of estimates that are more or less likely. The model we present gives a conversion factor for December 1st of 8.0 (95% CI = 6.53–10.14) and with 43 family groups in Sweden and Norway in 2013/2014, we would obtain a total population estimate of 344 wolves (95% CI = 281–436). Note that all values between 281 and 436 are not equally likely. We can also calculate the probability that the population is smaller or larger than certain values (Table 3). Note that Table 3 does not show the 95% CI reported in the text.

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Table 3: Population sizes estimated with the conversion factor from family groups at December 1st and associated uncertainty. For number of family groups, we show the population sizes the real population has x% chance to be smaller than. For example, if we have 43 family groups, the population has a 5% chance to smaller than 290 wolves. It has also a 95% chance to be smaller than 416 wolves, which means a 5% chance to be larger than 416 wolves.

If we have this number of family groups:	Population has a 5% chance to be smaller than:	Population has a 10% chance to be smaller than:	Population is equally likely to be smaller or larger than:	Population has a 90% chance to be smaller than:	Population has a 95% chance to be smaller than:
21	142	147	168	194	203
22	148	154	176	203	213
23	155	161	184	212	222
24	162	168	192	221	232
25	168	175	200	230	242
26	175	182	208	240	251
27	182	189	216	249	261
28	189	196	224	258	271
29	195	203	232	267	280
30	202	210	240	276	290
31	209	217	248	286	300
32	216	224	256	295	309
33	222	231	264	304	319
34	229	238	272	313	329
35	236	245	280	323	338
36	243	252	288	332	348
37	249	259	296	341	358
38	256	266	304	350	367
39	263	273	312	359	377
40	270	280	320	369	387
41	276	287	328	378	396
42	283	294	336	387	406
43	290	301	344	396	416
44	297	308	352	405	425
45	303	315	360	415	435
46	310	322	368	424	445
47	317	329	376	433	454
48	323	336	384	442	464
49	330	343	392	452	474
50	337	350	400	461	483
51	344	357	408	470	493
52	350	364	416	479	503
53	357	371	424	488	512
54	364	378	432	498	522
55	371	385	440	507	532
56	377	392	448	516	541
57	384	399	456	525	551
58	391	406	464	534	561
59	398	413	472	544	570
60	404	420	480	553	580

Sensitivity analysis

We run a sensitivity analysis by varying parameters across a range of biologically plausible values and assessing how growth rate, conversion factor to population size and conversion factor to number of reproductions vary (Figures 7, 8, 9). We also show how the relative model fit to data varies by calculating the sum of squares of the difference (i.e. the Euclidian distance) between the simulations and the data (for family groups, reproductions and pairs) and dividing it by the shortest possible distance to scale it from 1. This relative fit is important as it illustrates that how changing parameters make the model less good at replicating the Scandinavian wolf population trajectory and should be carefully considered when looking at how changing parameters affect conversion factors.
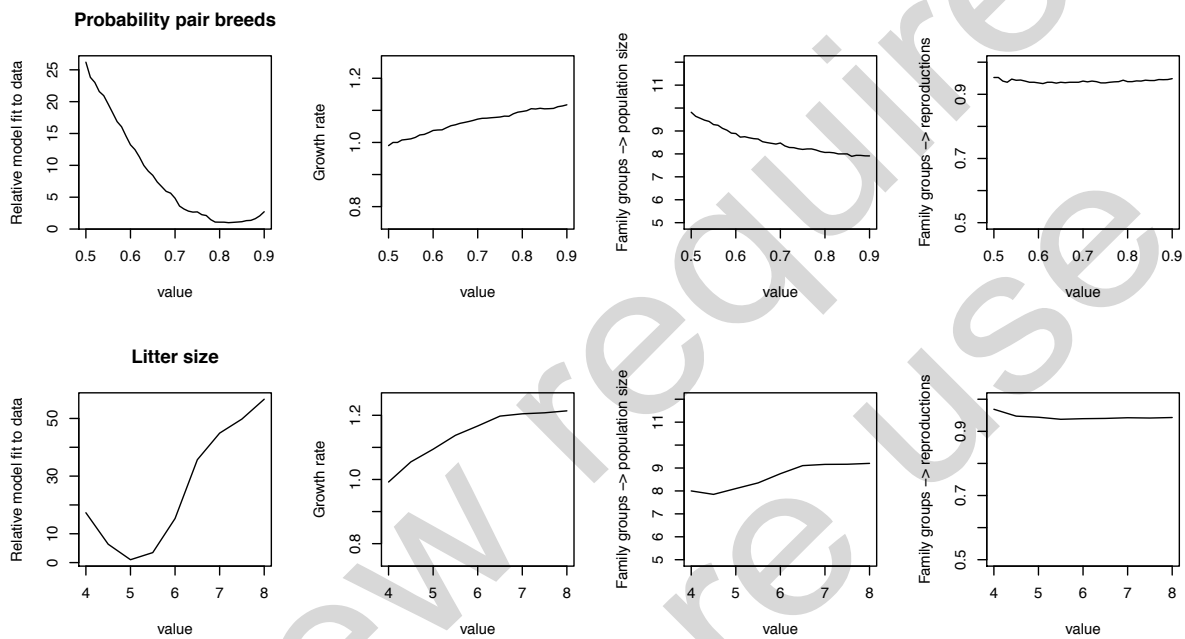

Figure 7: Sensitivity of model outputs for reproduction parameters (probability a pair breeds and litter size): relative fit of the model to data (1st figure from the left), sensitivity of growth rate (2nd figure from the left), sensitivity of conversion factor to population size (3rd figure from the left) and sensitivity of conversion factor to number of reproductions (4th figure from the left). Model relative fit is the best (value closer to 1) for the model parameters (see Table 2).
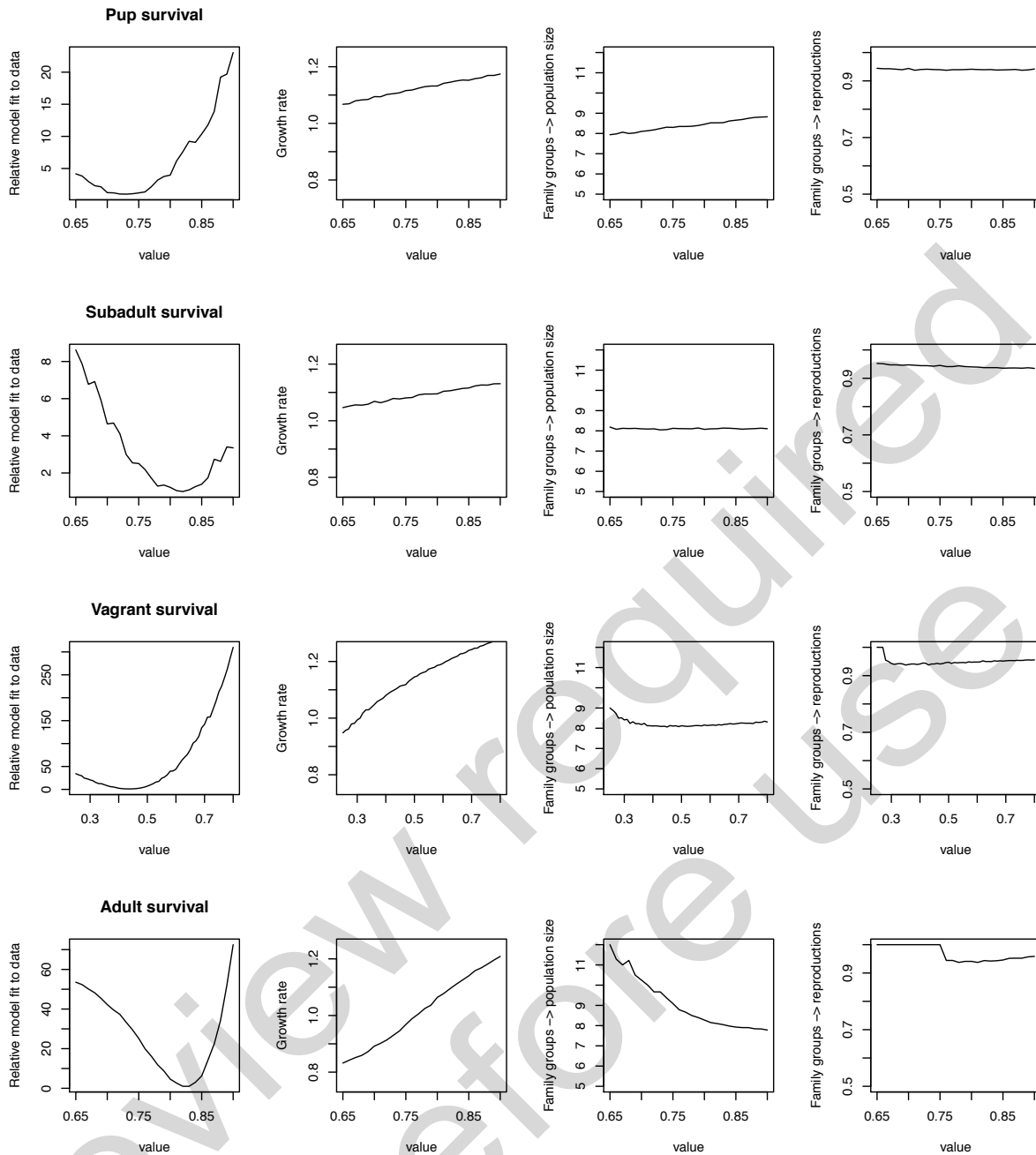
Figure 8: Sensitivity of model outputs for pup, subadult, vagrant and adult survivals: relative fit of the model to data (1st figure from the left), sensitivity of growth rate (2nd figure from the left), sensitivity of conversion factor to population size (3rd figure from the left) and sensitivity of conversion factor to number of reproductions (4th figure from the left). Model relative fit is the best (value closer to 1) for the model parameters (see Table 2).
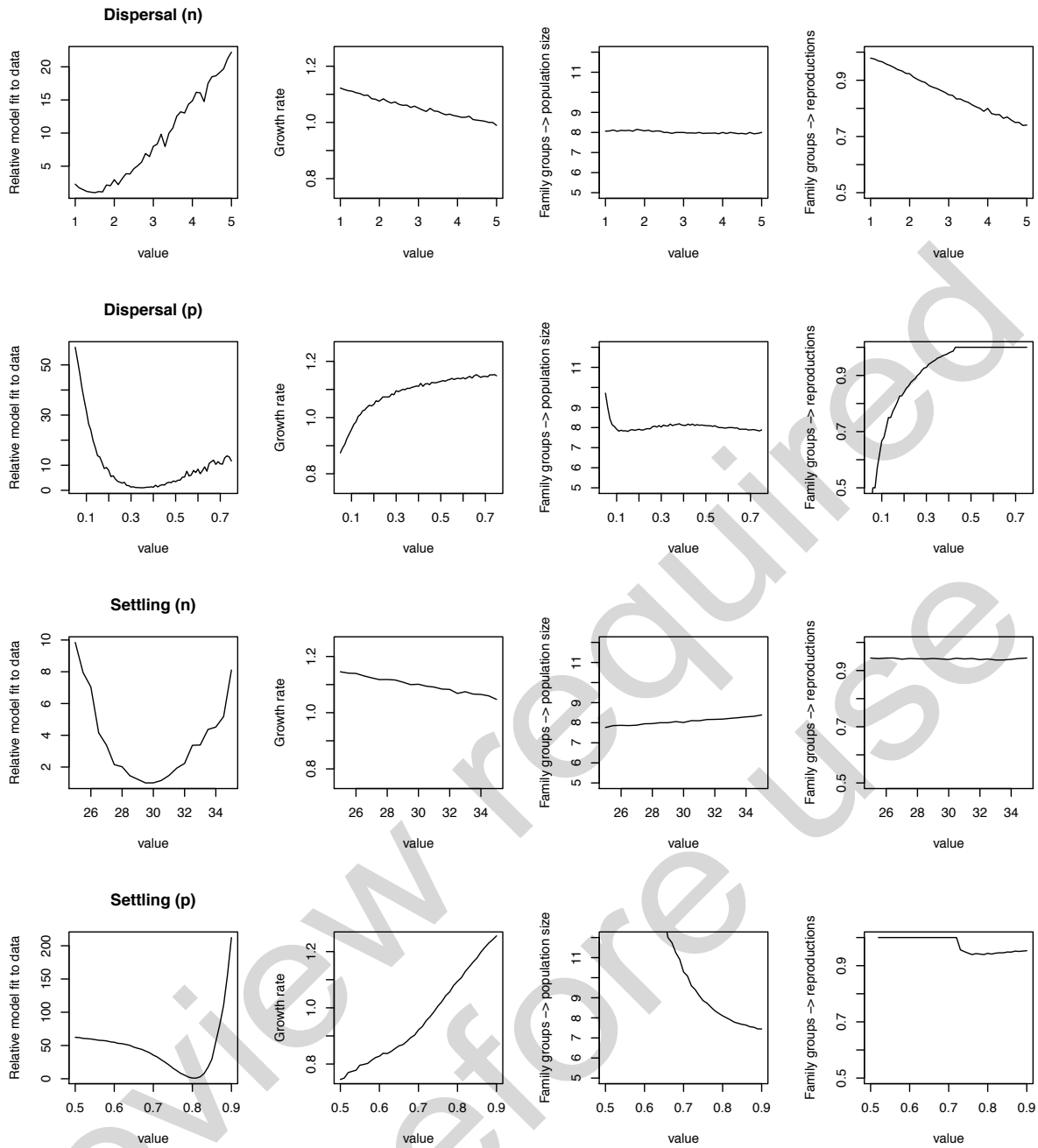
Figure 9: Sensitivity of model outputs for dispersal and settlement parameters (size and probability of negative binomial distributions): relative fit of the model to data (1st figure from the left), sensitivity of growth rate (2nd figure from the left), sensitivity of conversion factor to population size (3rd figure from the left) and sensitivity of conversion factor to number of reproductions (4th figure from the left) Model relative fit is the best (value closer to 1) for the model parameters (see Table 2).

For the second part of the assignment we run simulations to calculate how the number of monitored family groups influences the precision of estimates of the mean litter size. We started by checking that litter size in winter is Poisson distributed. We then run Monte Carlo sampling of a given number of Poisson values. We calculate how the mean of these values differ from the rate (= 4) of the Poisson distribution (Figure 10).
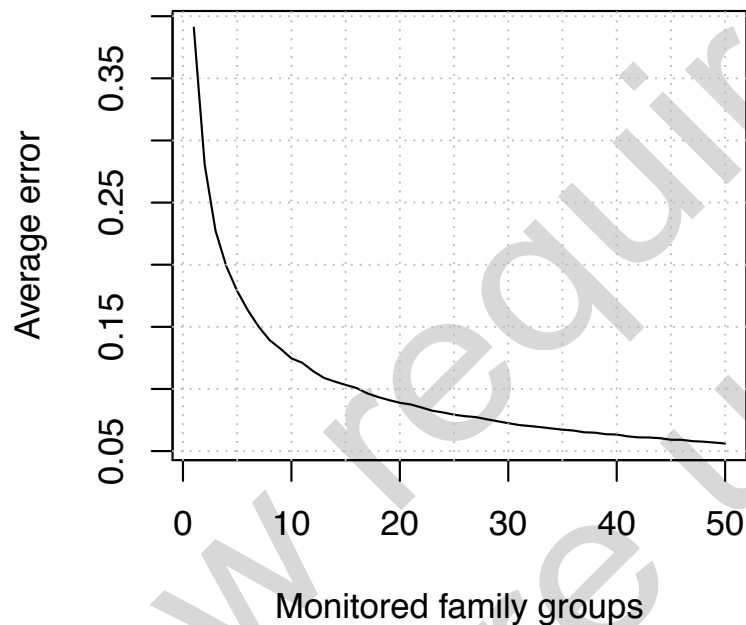

Figure 10: Left: Average error (deviation from the mean in %) when estimating mean litter size from a given number of family groups.

We find that having an average error of 10% in estimating litter size (i.e. deviating from the mean by not more than 10%) required monitoring at least 15 family groups (Figure 10). Having an average error of 5% would require sampling a lot more family groups (>50) while accepting an error of 20% requires only sampling 4 family groups.

We can also calculate how many family groups need to be monitored every year to be able to detect a change in litter size from one year to the next. This depends on the level of changes that we aim at detecting. If we aim at detecting an annual change of group size of 0.1 wolf, we need a very high number of family groups. However, aiming at detecting a change of 1 wolf required monitoring 15 family groups if an error rate of 10% is acceptable (Figure 11).

Figure 11: Probability of not detecting a change of 1.0 (grey line), 0.5 pup (continuous line), 0.25 (dashed line) and 0.1 wolves (dotted line) between years in mean litter size as a function of the number of monitored family groups.

Discussion

<u>Conversion factors</u>

We have used an individual-based population model to calculate a conversion factor from one population component to total population size. We have done this by simulating the population growth from an initial population in 2003/2004 up to 2013/2014. All transitions in the model (e.g. probability to survive to next month, to disperse, or to find a partner) are based on the occurrences of these events recorded for the radio-marked animals. The model is therefore strongly dependent on the assumption that the radio-marked wolves are representative for the population. The total sample size of radio-marked wolves is 154 individuals representing a total of 197 "wolf years" and corresponds to a little more than 10% of all wolves that have ever lived in this population, which is a relatively good representation. However, the representation of "wolf years" is much lower than the one estimated for all wolves that have ever been alive during this time period in Scandinavia. Also, the territorial wolves are over-represented in the radio-data, while the other social categories are less well represented.

A potential caveat with the use of the model is that the radio-data have been collected during the whole study period 1999-2014 whereas the model will be used for predicting population structure ahead. It is therefore an inherent assumption that the demographic parameters have not changed substantially over time and that the relative proportion between different social categories are representative for the current population. We have in an earlier report demonstrated a decrease in poaching after 2006 (Liberg et al. 2012). Although poaching might have rebounded to higher levels again, the assumption of constant demographic parameter values may result in biased model results as compared to the true contemporary population. If the model is not continuously updated with new data from radio-marked and DNA-sampled individuals, this problem may grow with time. For example, if the population in the near future will be exposed to a regulating harvest, it is possible that this will have effects on the relative proportions of different social groups of wolves, and thus also on the conversion factors for estimating the total population size and number of reproductions from the number of family groups found during monitoring.

The only monitoring data used to directly infer a parameter in the model is litter size in early winter (for first time breeders) which was used to estimate survival of pups from birth to winter, based on ratio in litter sizes at birth and in early winter. However, this parameter has a relatively small effect on the ratio between number of family groups and reproductions (see Figure 7), which supports the conclusion that circular dependence between model and monitoring data will not seriously affect model results. The relatively good fit between model results and monitoring data in Figure 1 is encouraging, although it does not imply the model perfectly represents the dynamic of the wolf population. In particular, the fit between the model and monitoring data for specific years and especially for the last two years is less good and may suggest the model does not capture the current dynamics in the population.

In the simulations of population size the time step used is one month. Because the population is subject to a birth pulse during spring when the population size is at its annual highest and

that mortality is a continuous process occurring during the whole year, this results in population trajectories of an undulating form of the annual dynamics for the various components of the wolf population (Figures 1, 2, 3). Thus, the number of individuals peaks directly after breeding (all new pups are born on May 1st in the model), and then drops off gradually due to the continuous mortality until the reproduction event next year. Therefore the number of family groups and reproductions (note that in this report the term "reproduction" is used in the same way as in the monitoring reports, i.e. actually meaning "reproducing unit", normally a family group in which there has been a reproduction that specific year) also peak at May 1st, because at that date many pairs become breeding family groups. After this date both the number of family groups and reproductions slowly drops because some of them cease to fulfill the criteria of being a family group (minimum three animals sharing a territory and at least one of them territory marking), due to mortality and dispersal. The number of pairs however, drops instantly at the reproduction event, because a large number of pairs then transform into reproducing family groups. During summer following reproduction the number of pairs slowly builds up again due to new pairs forming (mainly from dispersing subadults) continuously during the year, until next year´s breeding event.

The conversion factors presented here are based on the ratio of family groups to total population size and to the number of reproduction respectively, during the whole simulation period. The simulated populations at December 1st (which is the date that best will correspond to earlier brutto-estimates of population size from monitoring) gave a ratio from family groups to total wolf population size of 8.0 (95% CI = 6.53–10.14) (Figure 5 left) and to the number of reproductions of 0.95 (95% CI = 0.81–1) (Figure 5 right). The conversion factor for family groups to reproductions did not deviate much from the average ratio of 0.96 ± 0.05 pseudo SD of these two social groups as received from monitoring data from the period 2003/2004-2013/2014. However, the conversion factor from family groups to total population size was substantially smaller than the previous average estimates of 9.55 ± 0.61 pseudo SD (2003/2004-2010/2011). This means that the median estimate of the simulation-based model converts to a 17% smaller total population size as compared with previous monitoring data. The underlying reason for this difference is not obvious and may have multiple causes. Very simply expressed it could be due either to earlier overestimations of the true population size from monitoring (observation error), or to an inappropriate structure of the population model, or to insufficient information in the input demographic parameters (as compared to the current population) used in the model or to a combination of all these factors.

The total population has been monitored directly in the field during only five years (1998/99-2002/03). In the period 2003/04-2010/11, total counts continued in Norway, but in Sweden the total number of individuals was counted only in family groups and pairs whereas the number of vagrants and stationary single wolves was calculated each year based on their proportion of the total population (17 – 23 %) during the three monitoring seasons of 2000/2001–2002/2003 (Wabakken et al. 2007). After 2010/2011, total count of individuals even in family groups and pairs was abandoned in Sweden, while Norway continued to perform total counts. Therefore the total number of individuals in the entire Scandinavian wolf population after 2010/2011 was calculated from the ratio between the number of reproductions and the total number of individuals as found during the three seasons

2000/2001-2002/2003. Estimates of total population size has therefore for a long time been based on conversion factors. There is at present no possibility to validate these conversion factors, but considering that they are based on only three years of data it is likely that they may contain some kind of error of unknown size. It is also possible that the demographic structure, i.e. proportions between different social components (family groups, pairs, vagrants) of the population have changed over time. Also important, the conversion factor used during the three last years for estimating total population size in Scandinavia had a very wide range estimates (Svensson et al. 2014). For example, in last year´s (2013/2014) monitoring report it resulted a in a population size range of 316–520 individuals. A calculation of the population with the new conversion factor (8.0 * 43 = 344) is within this span, albeit near the lower end. Note that previous population estimates included dead wolves.

We cannot expect any model to give a perfect match to the real world. One could consider the relatively good fit with monitoring data on number of family groups, reproductions and pairs, and claim it looks as the present wolf population model mirrors reality reasonably well if we consider the total modelling period. However, the model fits 3 dependent exponential trajectories (family groups, reproductions and pairs), and a proper model fit does systematically imply the model is correct. It is also important to examine other outputs of the model, such as the age of particular events in the life of individuals (see Figure 4) and contrast it with data from radio-marked animals (again assuming they would be representative).

During the work in this assignment, we have made a large number of changes to the model to improve it, but the conversion factor between family groups and number of individuals has stayed rather stable. This is confirmed by the sensitivity analyses which show that the model is rather robust to practically all input parameters. However, some of the input parameters are based on rather weak data, e.g. probabilities for vagrants to settle and pair. This informs us that these are aspects where we would benefit from more telemetry data. Some structural assumptions of the model were more difficult to validate and it is here that the model deserves further attention before it can be considered as validated and management ready. We have struggled in modeling the dynamic of vagrants from when they disperse to when they settle and pair. First, these animals are under-represented in the radio-marked individuals, so what we can learn from them is rather limited and may not apply to all vagrants. For the mechanism through which a vagrant becomes territorial and breeder, we have made "best guesses" and have assumed that vagrants at a certain age replace missing breeders or meet other vagrants to form pairs. This age is estimated by the model through Pattern Oriented Modelling so that the model fits the data the best. However, in the model this mechanism assumes settlement and pairing are synchronous, which they may not be in reality. Having settlement and pairing as separate events increases the number of parameters (we would need parameters for each event) and therefore increases the difficulty for the model to fit the data (there may be plenty of combinations of parameters that gives good model fit without being biologically meaningful). It is unfortunate that such a critical mechanism (settling and pair formation) is poorly known and this precludes to have a model as realistic and robust as one could wish.

It is also important that the conversion factor for population size produced by this model has a very wide confidence interval that overlaps a large part the confidence interval from the monitoring conversion factor that has been used so far. It is highly probable that the true average ratio between number of family groups and total number of individuals are somewhere within this overlap. At present there is no method to find out exactly what is the true conversion factor, but a continued collection of demographic data (telemetry, DNA) is likely to improve accuracy of the model.

Finally, one should bear in mind that it is somewhat unrealistic to believe that a true population size estimate of any species and even more from an elusive species such as the wolf could be estimated from either a monitoring program or from a demographic population model. Errors will become larger the larger the population is growing and the larger the disturbances (e.g. harvest: unknown and complex consequences on social structure, fate of remaining individuals, etc.) occur in the population. Our work is therefore an attempt to update our knowledge about the conversion factor using new data and quantify in a more robust way the uncertainty around this parameter. Although it shows a surprisingly good fit with monitoring data on number of family groups, reproductions and pairs, it is still possible that the model does not produce correct estimates of the ratio between family groups and total number of individuals.

The model applies to whole Scandinavia, and is not appropriate for applying on single counties or other smaller geographic areas. This is mainly because stochastic factors that might deviate for what is typical for the whole population will have larger impact, the smaller area the model is applied to, which will result in much larger confidence intervals (less predictive power). There might also exist systematic differences (habitat, dominating prey species, human density, survival and reproduction) between different sub-areas (e.g. Sweden versus Norway, or north-western Svealand versus Västmanland/Uppland) that make it inappropriate to apply the model to these smaller units. Because the model is based on average demographic parameters collected from the total Scandinavian wolf range, if for some reason information on total number of individuals, or some other parameter in a specific smaller area is required, it has to be solved by performing more intensive monitoring for that particular area. This will of course increase costs, but might still be considered worthwhile for a specific purpose (e.g. for planning, preparing and/or evaluating some special local/regional management action).

Using the conversion factor to estimate population size at any time during the year is not straightforward if there are protective or license hunts that may remove whole family groups and other animals. For example, suppose that 10 vagrant animals would be removed in October–November in a protective hunt, then our conversion factor from family groups to total population size at December 1st would not hold because the number of family groups would not be changed (only vagrants were killed) while population would have been reduced by 10 animals. Alternatively, if 5 family groups are removed, it does not necessarily mean that we need to update population size by multiplying the conversion factor by this reduced number of family groups, because no vagrants have been killed. A continuously updated monitoring of wolf numbers would in fact require updating the model every month with a

detailed data on the composition of harvest and no general simple rule can be proposed for this. A rough estimate of population size at March 31st might be obtained by calculating population size at December 1st from the conversion factor and family groups at that date, applying a natural decline rate (how much population declines during winter due to baseline mortality rate, the model estimates this at 0.9) and then removing the legally (protective+license) hunted wolves.

<u>Needed sampling effort of family groups</u>

We calculated how many groups would need to be sampled to properly estimate average litter size (Figure 10) and to detect a particular change of litter size (Figure 11). We found that quite a few groups would need to be monitored to be able to detect a true change in average litter size. This is due to the fact that litter sizes are integer (e.g. they can be either 2, 3 or 4 but not 3.1 or 4.3) and this results in that large sample sizes is needed to detect any real change in the mean litter size. Because the calculated sample sizes were already large enough, we did not include observation error (for example counting 6 wolves when there in fact were 7 in that group) in this estimate of required sample size, as doing so would increase the sample size needed further.

We find it important that the monitoring does not only give measures of how large the population is, but also gives a measure of reproduction. Reproduction is together with mortality the most important parameter in the demography of wildlife populations. To manage a threatened population like the Scandinavian wolf without having any information about the reproduction is to work without a valuable piece of information. It will make it almost impossible to analyze reasons for possible future changes in the growth rate of the population. We have in the introduction argued why measuring reproduction is so important for understanding the effects of inbreeding. Reproduction in terms of litter size is presently our only quantitative measurement of inbreeding depression, and is likely to remain so for some time. But there are many other possible problems for the status of the wolf population that can appear in the future, where information on reproductive parameters will prove indispensable. We argue that to consciously renounce from obtaining information on reproduction is a risky way to manage the wolf population. As long as the research on radio-telemetry continue, this will produce some information on reproduction from visits at dens with the aid of radio-marked animals, but here annual sample sizes are likely be very small (<5 annually), unless the effort (and funding) for radio-marking increases dramatically. Therefore the only available method to get enough large samples for calculating litter size with a reasonable effort is by counting the number of individuals in family groups on snow during winter.

A slow but continuous change in litter sizes over ten years would not need the same amount of annual sampling as a comparison between two groups. An alternative to intensify monitoring in a selected number of territories each year would be to have a more intensive (>40 territories) monitoring effort being made at certain intervals, such as for example every fifth year, or in years which have exceptionally good snow conditions. This model could also be combined with more intensive tracking and sampling in a smaller number of territories each year. Large scale intensive monitoring during some specific years over large areas may also be used as controls to estimate if all family groups are monitored or if there is an

observation error in the number of family groups monitored. This effort should be directed towards areas where one or two wolves have been counted. Although large sampling efforts seem to be needed to verify changes in mean group size it is important to consider that statistical techniques may develop in the near future so as to improve the predictive power for any given sample size. We therefore recommend that at least 15 wolf territories are sample more intensively every year. Most likely 3 of those territories will annually be intensively monitored in Norway due to the current Norwegian goal of monitoring all wolves in the field. This sampling effort should be directed to both first time breeders and to family groups where reproduction previously has been recorded (family groups may here include subadults) and also consider variation in the level of inbreeding among sampled groups.

<u>Future challenges</u>

The model presented in this study (and its conversion factors) are based on the present situation of the wolf population. However, conditions might change in the future that affect population demography and structure. For example, these changes may include different harvest regimes affecting the proportions between different categories of wolves. Also, pack size is highly variable among wolf populations and is one of the main mechanisms by which wolf populations may differ in total size (Fuller et al. 2003). Variation in survival, reproduction and age at dispersal may all be mechanisms that affect differences in pack size. These parameters may be related to factors such as type of main prey and population density, and may therefore change in the future as the population is growing or expanding in range. A population expansion to new regions with different prey species or other habitat related factors might therefore impact on the demography of the population. It has not been possible to include such potential changes in the present model but it is important to be aware of the limitations of the current model for future use. A regular updating of demographic parameter from radio-marked wolves is therefore important.

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