# Population viability analysis of Swedish and Norwegian rock ptarmigan *Lagopus muta* populations

Degitu Endale Borecha

Høgskolen i **Hedmark**

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## Abstract

Population viability analysis (PVA) is a method of projecting the likely future state of a population or populations of a species using quantitative methods. It is principally used to determine the population(s) risk of extinction, decline, or recovery for a given period in the future based on the current demographic and environmental data of the population(s). I conducted PVA single and metapopulation models for both the Swedish and Norwegian rock ptarmigan populations by using transect count data and wing data, respectively. My objectives were to determine; (1) persistence probability of the populations in the future given current population development; (2) relative quasi-extinction risk of the populations; and (3) demographic parameters that have major impact on the population´s long term viability. My model showed that the Swedish populations are doing better than the Norwegian populations in terms of persistence probability. The hypothetical metapopulation models represented a smaller risk of quasi-extinction than the single population models. Using single population model, the rock ptarmigan population in the county of Västerbotten in Sweden showed high extinction risk. The most sensitive parameters in my models were the growth rate and environmental variation. Even though the results from my PVA models are associated with several uncertainties, I strongly recommend that the populations are in need of more attention than what they receive today.

*Key words*: grouse, least concern, PVA, Scandinavian rock ptarmigan

## Introduction

Population viability analysis (PVA) is a method of projecting the likely future state of a population or populations of a species using quantitative methods (Morris & Doak 2002, Ralls et al. 2002, Reed et al. 2002). PVAs are principally used to determine the population(s) risk of extinction, decline, or recovery for a given period in the future based on the current demographic and environmental data of the population(s) (Boyce 1992, Beissinger & Westphal 1998, Morris & Doak 2002). If the main intention of conservation is minimizing risk of extinction of a species, PVA is an important tool in assisting conservation planning and management decisions of both small and declining population(s) (Beissinger & McCullough 2002, Reed et al. 2002).

There are a number of PVA variants that are either shaped to evaluate the different features of a population(s) or limited to fit the available data type. The most frequently applied PVAs answer either the deterministic or stochastic fate of a single-population, identify sensitive parameters, compare different management options, or look at the network of metapopulation viability (Boyce 1992, Beissinger & Westphal 1998, Beissinger 2002, Morris & Doak 2002, Akcakaya et al. 2004).

The significance of the predicted PVA outputs is dependent on the quality and quantity of the demographic data that are entered into the PVA simulation. This creates various ambiguities with respect to the reliability of the PVA outputs (Lindenmayer et al. 1993a, Burgman & Hugh 2000, Reed et al. 2002), especially if the results from the PVA is intended to determine absolute extinction rather than relative probability (Beissinger & Westphal 1998, Ralls et al. 2002, Morris & Doak 2002, Beissinger & McCullough 2002).

However, there are different ways of dealing with these PVA viability issues. Exploring different simple model structures, assessing relative risks of different scenarios, limiting the prediction periods, and performing sensitivity analysis are some of the highly recommended methods which aim to improve the uncertainties associated with the available data (Grant 1986, Beissinger & Westphal 1998, Ludwig 1999, Akcakaya et al. 1999, Fieberg & Ellner 2000, Reed et al. 2002, Mills & Lindberg 2002, Morris & Doak 2002, McCarthy et al. 2003). If the demographic data is of good quality, various research has detected that PVA yield accurate predictions (Brook et al. 2000b, Ellner et al. 2002, Schodelbauerova et al. 2010).

Given all the precautions in the interpretation of the outputs, developing and incorporating a PVA as an additional management tool is essential (Lindenmayer et al. 1993b, Lindenmayer et al. 1993a, Akcakaya et al. 1999, Burgman & Hugh 2000, Ludwig & Walters 2002, Shaffer et al. 2002, Brook et al. 2002). Its importance is even greater when the intention is spotting key demographic parameters of a population at risk and/or accounting for further field work (Possingham et al. 1993, Akcakaya et al. 1999).

As compared to other grouse species, not much is known about the status of the rock ptarmigan (*Lagopus muta*) in many parts of its range (Storch 2007). Internationally, the species is considered as least concern species (BirdLife 2009, IUCN 2010). In the European Bird Directive, it is grouped under Annex II (huntable) except for two subspecies (*L. m. helveticus* and *L. m. pyrenaicus*) which are under Annex I (special conservation) (EuBirds Directive 2009). In Norway, the species is categorized as least concern (Artsportalen 2010) and not evaluated at all in Sweden.

The population dynamic of rock ptarmigan is overall poorly studied in Norway (Pedersen 1994), and the species are only monitored at Svalbard (Steen & Unander 1985, Unander & Steen 1985, Pedersen et al. 2007). In the rest of Norway, the statuses of the populations are based on hunting statistics (Haakenstad 2003, Holmstad et al. 2005, Kvasnes et al. 2010, Bolstad 2010). In Sweden, there are yearly counts in 26 monitoring areas on state-owned land since 1994 in the northern parts of the mountain range and since 1996 in the southern parts of the mountains. Beside the counts on state-owned land, the Swedish Bird Count has registered observations of rock ptarmigan since 1998. Rock ptarmigan are not managed as a separate species in Norway and Sweden and are managed in the same way as willow ptarmigan (*L. lagopus*).

There has recently been an increasing concern about the rock ptarmigans actual population status both in Norway and Sweden (Statistics-Norway 2010, Artsportalen 2010). Beside climate change, the major threat to the populations might be the sport hunting (Storch 2007, del Hoyo et al. 1994). In Norway, during peak years, > 180 000 individual rock ptarmigans was bagged (Statistics-Norway 2010) compared to Sweden where approximately between 5 – 10,000 birds are shot annually. Starting from year 2000 and onwards, the hunting statistics in Norway showed a marked decline of harvest rock ptarmigan (Statistics-Norway 2010). The same declining trends are reported from the Swedish Bird Count, which monitors bird species

at the country level each year. In both Norway and Sweden, the hunting is carried on with very little knowledge of the populations´ status.

The current discussion about the rock ptarmigan population decline in both Sweden and Norway motivated this study where I tried to determine the future viability of the populations through different scenarios. I conducted PVA models for both the Swedish and Norwegian rock ptarmigan populations (*L. m. muta*). My objectives were to determine; (1) persistence probability of the populations in the future given the current population development; (2) relative quasi-extinction risk of the populations; and (3) demographic parameters that have major impact on the population´s long term viability.

### Rock ptarmigan

Rock ptarmigan is a relatively small size game bird. It inhabits in wider latitudinal range than other grouse species (Storch 2007, Holder & Montgomerie 2008, BirdLife 2009). It populates in both arctic and alpine tundra throughout the Northern Hemisphere (Storch 2007, BirdLife 2009). Around 30 subspecies of rock ptarmigan are reported worldwide (Storch 2007, del Hoyo et al. 1994). The subspecies that inhabit the mainland of Europe and Scotland share more similarity to each other than with those that inhabit in Asia, America, and other European islands (Arnason 1972, Holder & Montgomerie 2008, Sahlman et al. 2009). Caizebgues (2003) spotted a significant similarity between Alps and Scandinavian alpine rock ptarmigan. No genetic difference has been found between Swedish and Norwegian populations (Gyllensten et al. 1985).

Rock ptarmigan shows irregular fluctuation in certain locations. In some areas the population cycle happens with 3 – 5 years (Cattadori & Hudson 1999), 6 – 7 (Watson et al. 1998, Cattadori & Hudson 2000), and in others 9 - 11 years intervals (Nielsen & Petursson 1995, Watson et al. 1998, Cattadori & Hudson 2000, Nielsen 2010). From a study that was conducted in Sweden at the same study area as this project, willow grouse showed a weak 10 years cyclicity (Hörnell-Willebrand 2005).

It has been showed that alpine rock ptarmigan´s reproduction success is influenced by weather (Scherini et al. 2003, Novoa et al. 2008). The ptarmigan has one brood per year, males are territorial during the beginning of the breeding season (Watson 1965, Cotter 1999, Scherini et al. 2003, Favaron et al. 2006), and are mostly monogamous (del Hoyo et al. 1994, Bart & Earnst 1999, Cotter 1999). The latter behaviour is, at least, relatively common in Pyrenees and Alps populations of Southern Europe (Caizergues et al. 2003, Scherini et al. 2003,

Favaron et al. 2006). However, in Scotland, Svalbard, Canada, and Alaska it is recognized that occasionally it is possible to encounter bigamous (Weeden 1964, Watson 1965, Unander & Steen 1985, Watson et al. 1998, Bart & Earnst 1999, Cotter 1999), or even promiscuous birds (Unander & Steen 1985, Gardarsson 1988, Bart & Earnst 1999, Holder & Montgomerie 2008). Female rock ptarmigan breeds at age one. Yearling males can also enter the breeding pool but sometimes they are not as successful as adults ($\geq 2$ years) (Holder & Montgomerie 2008). A population predominantly has male biased sex ratio (Watson 1965, Scherini et al. 2003, Holder & Montgomerie 2008).

The life span of rock ptarmigans differ between 4 years (Caizergues et al. 2003) to  5 years (Nielsen & Bjornsson 1997). In Canada, it is recorded that banded rock ptarmigans showed a life span of 7 - 8 years (Holder & Montgomerie 2008). Some of the subspecies that live in the Arctic (Iceland, Greenland, Russia), and Italian Alps cross a very long distance (up to 1000 km) during their unpredictable migration (Gudmundsson 1972, del Hoyo et al. 1994, Favaron et al. 2006, Storch 2007). Altitudinal movement that happens with seasonal change is common in Southern Europe (Favaron et al. 2006). Nevertheless, in general, there are very few records about the species natal dispersal pattern. Some of the major natural predators of the Scandinavian alpine rock ptarmigan are gyrfalcon, and golden eagle (Nystrom et al. 2005, Nystrom et al. 2006).

## Methods

### Study area

This project analyzed data of rock ptarmigan populations from Sweden and Norway. From Norway I considered the populations of Grane, Hattfjelldal, and Vefsen municipalities which are located in Helgeland District of Nordland County, Northern Norway (see figure 1). The Swedish samples encompassed 12 municipalities that are situated within the Counties of Norrbotten, Västerbotten, and Jämtland, in Northern Sweden (figure 1, appendix 1). On average, the alpine rock ptarmigan populates on $\geq 1100$ - 1200 meter above sea level.
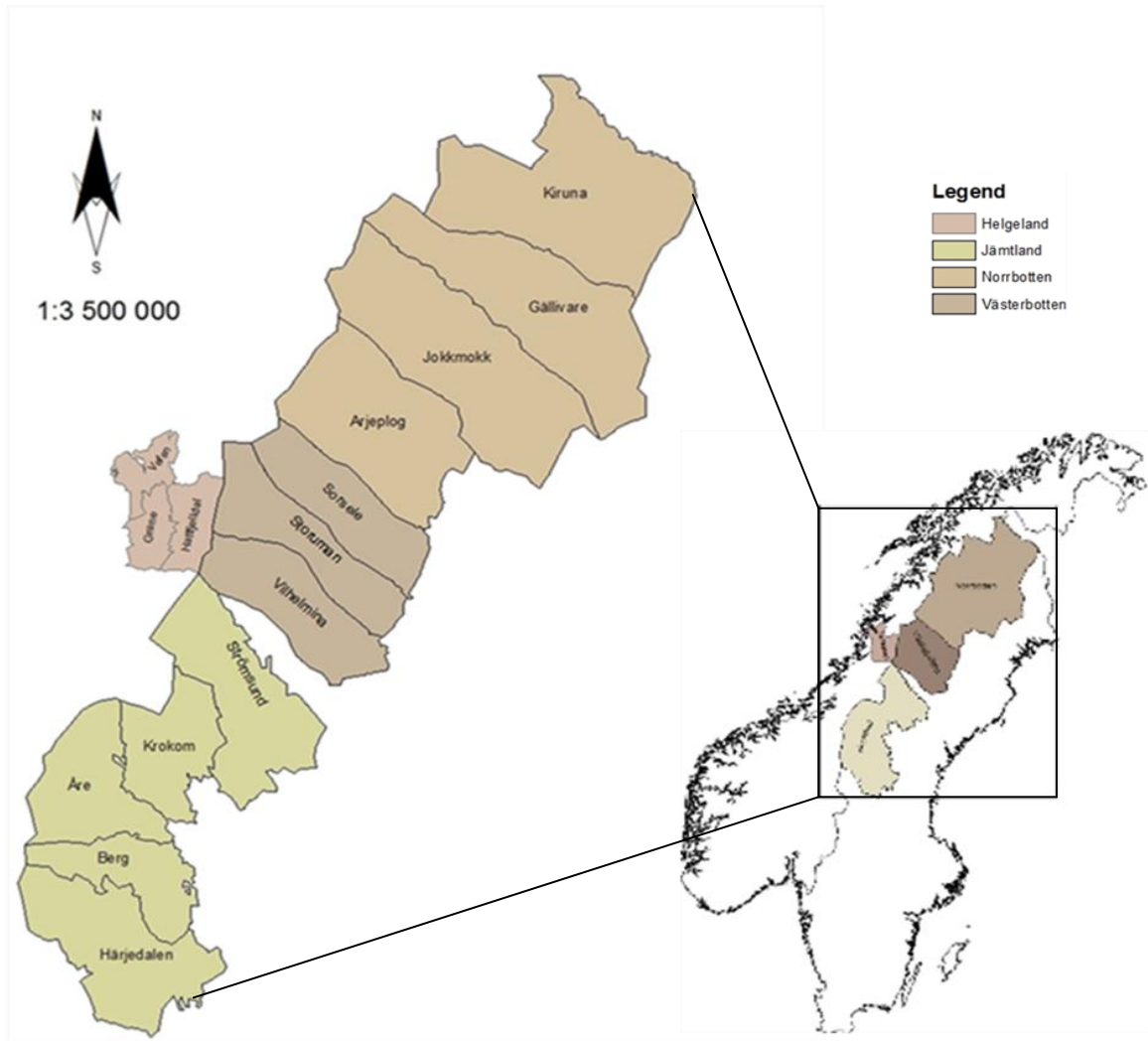
**Figure 1.** Map of the study area; the three Swedish counties and one Norwegian district. Areas in color are the counties. The names presented above stand for the municipalities that are included in the study.

## Data

The Norwegian rock ptarmigan data was wing data that I used as a proxy for rock ptarmigan populations of the district. The data has been documented spanning the years from 1970 to 2006 (37 years). The data contained a record of young per pair and number of individuals felled in the municipalities. The data was compiled based on hunters´ reports and adjusted for missing values. The Helgeland District was the only one that had documented the wing data of the rock ptarmigan. Therefore, I did not consider the other counties.

The Swedish data was collected through distance line transect counts. The count was performed from 1994 to 2010 (17 years) in 26 sites on state-owned land in the mountain area. The line transect count covered a combined total of 101,969 km (mean ± 2SE 7.22 ± 0.06 km

per year). In Norrbotten County, the counting started in year 1994 (17 years), while 1996 (15 years) in Jämtland, and 1998 (13 years) in Västerbotten. The lines were randomly arranged with 500 – 1000 meter distance in-between the consecutive transects. The count was performed using dogs along the transect lines in the first or second week of August. Dog handlers were carefully recruited and received training and evaluation on an annual basis. Transect lines covered all the area over 1100 meter above sea level. Besides measuring the perpendicular distance, the surveyors registered cluster size, species (willow grouse and rock ptarmigan), determined the age of the birds (yearling or adult), and took GPS records of where the birds were flushed (see Hörnell-Willebrand 2007).

I compiled basic population dynamics of rock ptarmigan from published scientific literatures (table 1), focusing on Scottish and mainland European rock ptarmigan populations´ characteristics. Where no information could be found in the literature from these areas, I used published information from arctic rock ptarmigan populations or willow grouse´s population data, as it is the most similar and sympatric species (Boyce 1992).

**Table 1.** Cocks per km$^2$, reproduction success, and mortality percent of rock ptarmigan at different locations. Key: CPP = chick per pair; CPH = chick per hen.

| Land | Reproduction success | Annual adult mortality % | Mean Spring Density (cocks/km$^2$) | Author (s) |
|------|----------------------|--------------------------|-----------------------------------|------------|
| Scotland | 3.22 - 6 CPH | | 48 – 18 ± 3 - 2 | (Watson et al. 1998) |
| Austrian Alps | | | 1.5 – 6.7 | (Nopp-Mayr & Zohmann 2008, Zohmann & Woess 2008) |
| Italian Alps | 0.08 - 5 CPH | | 0.47 -2.29 | (Novoa et al. 2008, Favaron et al. 2006, Scherini et al. 2003) |
| Svalbard | 2.4 - 9.6 CPP | | | (Steen & Unander 1985) |
| Iceland | 8.3 – 9 CPH | 54 – 63 (40) | 6.3 – 34 | (Gardarsson 1988, Nielsen 1995, Nielsen 2010) |
| Canada | | 29 – 43 | 2 - 4 | (Wilson & Martin 2010) |
| Alaska | 3.8 CPH | | | (Cotter 1999) |
| Sweden | 3.4 CPP | | | My unpublished data |

## Time series analysis

Densities were calculated with Program DISTANCE 6.2 for Windows (Thomas L. et al. 2009), for each year for all the three counties. As rock ptarmigans often occur in pair or cluster, I estimated the cluster density with conventional distance sampling. I used cluster size bias regression in which cluster size regressed on detection function, eliminating the bias that might occur when large clusters are more easily found on large distances compared to single birds. The best model was selected based on Akaike´s information criteria (AIC). For Norwegian populations, I used the wing data as the population trend.

## Software

There are a number of computer programs that are developed for PVA purposes, each holding different strengths and weaknesses (Mills et al. 1996, Brook et al. 1999, Brook et al. 2000a). Many of these software programs are generic while other are specifically shaped to fit a specific species. I reviewed the popular matrix-based generic software programs such as RAMAS (GIS/Metapop) (Akcakaya 2003), VORTEX (Lacy R.C. et al. 2009), and ALEX (Possingham & Davies 1995a) in order to find the appropriate program for my analysis.

The program VORTEX needs plenty of data which I did not have for my sample populations. Moreover, since the program follows the fate of each individual, it aborts its analysis for a population that has a large number of initial individuals and carrying capacity (Miller & Lacy 2005), which was the case for my populations. The program ALEX models only one sex (female) (Possingham & Davies 1995b, Lindenmayer et al. 1995) that I did lack as there was not a record for separate sex proportion. In addition, the ALEX software that I obtained online was out of date and could not run in Windows 7.

The literature recommends the RAMAS programs due to its more flexible way of operating than the other software applications. It is possible to run either single population or metapopulation models in RAMAS GIS/Metapop programs, and its application is proven for birds (Akcakaya et al. 2004).

However, from the RAMAS family as a whole, I could only get access to RAMAS/Ecolab. It took a lot of time to find the appropriate program that fitted the data I had. I even was in the process of ordering RAMAS/Metapop, which was deemed to be the most appropriate candidate, but unfortunately it did not arrive in time. Thus I was forced to use RAMAS Ecolab 2.0 (Akcakaya et al. 1999). This program develops very simple models and is easy to

use. However, it neglects some parameters and is not able to incorporate some options such as management scenarios.

## Parameterization

### Growth rate

To get $R_{max}$, I regressed $R_t$ on $N_t$ using the $R_t$ as response variable in SAS 9.2 (SAS 2008) and used the y-intercept of the regression as the $R_{max}$ (Akcakaya et al. 1999). To avoid correlation of $N_t$ with $R_t$, since $N_t$ appears in both dependent and independent variables, I determined $R_t$ as $R_{t\,=}\sqrt{N_{t+1}/N_{t-1}}$ (Akcakaya et al. 1999). The obtained $R_{max}$ and the corresponding slope are presented in table 2.

**Table 2.** Maximum growth rate $R_{max}$ (y-intercept), and the slope (x-intercept´) of $R_t$ on $N_t$ regression. StD R stands for the standard deviation of the growth rate.

|  | Sweden pooled | Jåmtland county | Norrbotten County | Våsterbotten County | Helgeland pooled | Grane/Vefsn Municipality | Hattfjell Municipality |
|---|---|---|---|---|---|---|---|
| $R_{max}$ | 1.882 | 1.347 | 1.603 | 0.580 | 0.936 | 1.133 | 0.878 |
| Slope | - 0.308 | - 0.119 | - 0.129 | + 0.096 | + 0.0003 | +0.0001 | +0.0002 |
| StD R | 2.08 | 0.72 | 1.52 | 0.31 | 0.45 | 0.32 | 0.54 |

### Type of density dependence

Due to lack of data I used three type of density dependence to incorporate all possible outcomes (Henle et al. 2004, Ginzburg et al. 1990, Sabo et al. 2004, Mills et al. 1996). Those are (1) contest; (2) ceiling; and (3) exponential density dependences.

I used contest density dependence due to the territorial behaviour of the rock ptarmigans (Favaron et al. 2006, Scherini et al. 2003, Cotter 1999, Watson et al. 1998), which is one of the major characteristic of the contest density dependence type (Akcakaya et al. 1999, Burgman et al. 1993). Ceiling is a type of contest density dependence that has a property of allowing the population to grow exponentially until the point of carrying capacity (Akcakaya et al. 1999). I decided to use this density dependence type for two reasons. First, because of the territorial behaviour of the rock ptarmigan that this density variant shares with the contest type, and second related to how most of the PVA models operate. I fitted the ceiling density dependence because it is the most used density dependence type in many PVA simulations, regardless of the type of species (Akcakaya et al. 2004, Henle et al. 2004). I used the exponential density dependence to check the likelihood of the populations´ persistence in an ideal situation (Ginzburg et al. 1990, Sabo et al. 2004, Mills et al. 1996).

## Carrying capacity (K)

I determined the maximum individuals in the study area based on the available literature and my own interpolations (table 1 & appendix 1). I compared the number of cocks per km$^2$ in Scotland, the Alps, Iceland, Svalbard, and Alaska. Deriving carrying capacity based on habitat area might lead to overly optimistic estimations (Reed et al. 2002, Brook et al. 1997), thus I calculated the possible carrying capacity (number of pairs) of the study sites with respect to the total area size ≥1200 meter above sea level, excluding all infrastructure areas and water bodies.

Pairs usually occupy larger territory than a single cock (Favaron et al. 2006, Unander & Steen 1985). This larger territory preference (Unander & Steen 1985) probably contains the required landscape combinations. So I took an arbitrary K which was 10 pairs per km$^2$ or 1 per 10 hectare (appendix 1).

The area sizes were calculated by Triangulated Irregular Network (TIN) model with ArcGis 10 for Windows from maps that were obtained from the ESRI online dataset (ESRI 2010), the SLU (Swedish University of Agricultural Sciences) database, and from Evenstad Campus.

## Initial abundance

Initial abundance for Helgeland was determined as half of the calculated carrying capacity (appendix 1). I multiplied this by two because I wanted to get the number of individuals but not of pairs, which means that the initial abundance and carrying capacity are equal. For the Swedish populations, I took the abundance of year 2010 obtained from the Program DISTANCE. Thus, my PVA starts from year 2010. I used the sum of the initial abundance of the subpopulations as initial population size of the metapopulations. This might underestimate the population when the possible floaters and territorial unpaired cocks were not included (Scherini et al. 2003, Unander & Steen 1985, Gardarsson 1988, Cotter 1999).

## Dispersal

An important part of the population dynamics of birds is dispersal rate and distances moved (Greenwood & Harvey 1982, Arcese 1989). However, there are very limited information about dispersal and movement of rock ptarmigan. In Northern Norway, coast to inland dispersal of juvenile hens were noted (Holmstad et al. 2004), but it is not clear how long distance they dispersed. A maximum natal dispersal distance of 17.7 km (Bech et al. 2009) has been recorded in the Alps for female rock ptarmigan. Through genetic structure study, up to 170 km (Caizergues et al. 2003) was also reported in the same area. However, the latter distance might not represent one-time step dispersal, as genetic changes take generations to

modify. Results from Svalbard (Unander & Steen 1985), Iceland (Nielsen & Bjornsson 1997, Gardarsson 1988), and Scotland (Watson et al. 2000) show that juveniles have less return rate to their birth place. In Canada females disperse more than males (Cotter 1999), which seems to be a typical behaviour for ptarmigan species (del Hoyo et al. 1994).

The program RAMAS Ecolab does not make any assumption regarding the stage/age wise dispersal, so I fitted dispersal with the assumption that only juvenile disperse. I used 17.7 km as an average natal dispersal distance when this distance was closer to juvenile distances of willow grouse in Sweden (Hörnell-Willebrand & Smith 2005), and probably more realistic in Scandinavia compared to longer distances. I decided to treat both male and female juveniles as having equal dispersal distance, since I preferred to take the female dispersal distance for a conservative estimate. I used 60 km ($\approx$3*17.7) as the maximum dispersal distance.

I estimated dispersal rate from the reproduction success (3.4 chicks per pair, see table 1). I assumed that all pairs had the same reproduction success, and all individuals in the population reproduce. Based on that, the populations were composed of $\approx$ 2:3 adult to juvenile ratio. I assumed that each population might encompass three juveniles per pair. If all the juveniles disperse, then the maximum dispersal rate is 0.67 (2/3).

### Correlation

I used $C_{ij}$ = a*exp (-D /b) formula (Akcakaya 2004, Akcakaya et al. 1999) to calculate a correlation value that the subpopulations might have within 100 km distance; in which $C_{ij}$ stands for the correlation value of i and j populations, D for distance, and "a" and "b" are the function´s parameters. I set parameter "a" to one and calculated the corresponding "b" value for correlation value of pair subpopulation at a time using their distance. The Norwegian metapopulation (the two municipalities) had a correlation figure of 0.83 at 100 km distance, which showed strong correlation. The correlation value of the second metapopulation i.e. the three Swedish counties and Helgeland (Norway) at 100 km distance was roughly 0.66, which also indicated medium environmental correlation of the areas.

### Mating and survival rate

I used the Swedish willow grouse´s adult survival rate, which was approximately 40% (Smith & Willebrand 1999). This is close to the reported 38% August to Spring survival rate of rock ptarmigan (del Hoyo et al. 1994). I did not explore the effect of hunting mortality as I keep an assumption that it is compensatory mortality. I did not fit any mating possibilities because the computer program does not have the option and I do not know what type of assumption it has.

## Simulation scenarios

### *Sweden*

I ran two types of models; stochastic hypothetical metapopulation and single population models (La Montagne et al. 2002, table 3). The metapopulation was constructed based on the respective counties/district´s populations. I developed two metapopulations; one that included Helgeland as part of the three Swedish counties, the other one included only the three Swedish counties. In these models each of the counties were considered to be a subpopulation of a metapopulation. The former model which encompassed Helgeland District was based on the assumption that if the Swedish counties share individuals, it is also possible that this district might also be part of the metapopulation due to its proximity (figure 1). However, I developed the second metapopulation out of the three Swedish counties to cross-check the population status and avoid bias based on data source (as the Swedish one was based on distance line count while the Helgeland District was based on wing data). The single population model was based on each counties´ populations and the country´s overall population.

I did not use the municipalities as subpopulation because each municipality gave very small individuals/density during the density calculation in program DISTANCE. The count on state-owned land in Sweden was focused on estimating willow grouse densities, and estimates of rock ptarmigan from this count would probably be biased low. To increase the sample size, I pooled each county and estimated average density for each county per year.

### *Norway*

Due to the difference of collected data between the countries, I treated the Norwegian data alone. I constructed two models using the Norwegian data in the same way as with the Swedish data; stochastic single and metapopulation (table 3). Instead of county I considered the municipalities as metapopulation. The single population model was based on the overall wing data of the district. The hypothetical metapopulation enclosed two populations; Hattfjelldal, and Vefsn/Grane municipalities from Helgeland. I used the Vefsn and Grane municipalities together as one population, rather than separately, because their data were pooled together by the local management authority.

**Table 3.** Summary of the model scenario including some of the parameter´s value.

| Parameter | Value |
|---|---|
| Maximum growth rate | Table 2 |
| Initial population size | Appendix 1 |
| Survival rate | 0.40 |
| Correlation | 0.83; 0.66 |
| Dispersal rate | 0.67 |
| Maximum dispersal distance | 60 km |
| Average dispersal distance | 17.7 km |
| Carrying capacity (K) | 10 pairs/km$^2$, appendix 1 |
| Density dependence type | Contest, ceiling, exponential |
| Models | |
|     Metapopulation | Sweden vs Helgeland; Sweden; Helgeland |
|     Single population | Swedish counties (3); Sweden pooled (1); Helgeland´s municipalities (2); Helgeland pooled (1) |

## Sensitivity analysis

I analysed ± 10 % changes of (1) maximum growth rate; (2) survival rate; (3) dispersal distances; (4) dispersal rate; (5) initial population; (6) carrying capacity; (7) initial abundance; and (8) standard deviation of the growth rate (explains environmental stochastic). This analysis was done to identify which parameters had the most effect on the long term persistence of the ptarmigan.

I did two representative models; one metapopulation and one single population. I did the analysis by changing one parameter at a time while keeping the other parameters constant. The sensitivity was weighted up by the proportion change of expected minimum population size (EMP); $S = \Delta EMP/EMP$ (McCarthy & Thompson 2001). I used a model without change (the best estimate) as a base model to compare the parameters changes with. I run each models five times and took an average of their EMP. Ceiling density dependence type was used to test for all of the parameters.

## Viability

Viability of a modelled population is measured as the probability of quasi- extinction and or expected minimum population size. Quasi-extinction risk is expressed as the likelihood of the population declining to an arbitrary small population size; zero being a minimum abundance representing extinction (Ginzburg et al. 1982). Expected minimum population (EMP) size is the smallest population abundance that a model simulation gives. This abundance can be used to measure the risk of different scenarios by presenting a proportion change of the smallest expected population size to the initial population size (McCarthy & Thompson 2001).

I used both these viability output methods for my PVA models´ results. I used EMP to measure the sensitivity analysis while quasi-extinction for the PVA. For the PVA results, I recorded probability of extinction, and 20% and 50% decline of initial population size within the next 30 years. However, I paid more attention to the probability of extinction, and the 20% decline from the initial population abundance. For the sake of evaluating the predicted risk state, I compared my PVA results with the standard measures (criterion E) of World Conservation Union (IUCN). IUCN classify risk of a species as "vulnerable" if a PVA results indicate > 10% extinction within 100 years, "endangered" if it shows > 20% probability of extinction within 20 years or five generations, whichever is longer, and "critically endangered", if the PVA result indicates > 50% extinction in 10 years (IUCN 2001, Mace & Lande 1991).

The simulation ran 1000 replications and projected for the next 30 years (approximately six years life span of the ptarmigan times 5 years generation period). The smaller the prediction period the better the reliability of the PVA outputs (Saether & Engen 2002, Beissinger & Westphal 1998), although both long and short projections might give the same outputs.

# Results

## Persistence probability of the populations

### The Swedish populations

I explored the persistence probability of the populations for the next 30 years through demographic stochastic models. The probabilities of the models´ populations going extinct and falling below 20% and 50% of the initial population size, at least once during the next 30 years as shown in figure 2 and appendix 2. All models showed < 3% extinction probability except for Västerbotten County´s single population model, which became 100% extinct (appendix 2). As compared to the single populations, the metapopulation models showed a lower extinction risk (figure 2, 4 and appendix 2).

The single population model that represented the whole rock ptarmigan population of Sweden illustrated > 30% probability of a 20% decline from the initial population size regardless of what kind of density dependence were chosen. The highest risk of falling below 20% of initial population size for the hypothetical Sweden metapopulation model was 15%. The metapopulation that I developed out of both Swedish and Norwegian populations had < 30% of probability 20% decline (figure 4). Norrbotten´s rock ptarmigan population model demonstrated higher chance of 20% decline for the next 30 years compared to the Jämtland under the contest density dependence type, 76% and 50% probability respectively.

### The Norwegian populations

None of the Norwegian populations´ models became extinct although the single population models illustrated high risk of extinction except Vefsn/Grane´s model (figure 3, appendix 2). The single population model that represented Helgeland District had 32 – 34 % probability of extinction in the coming 30 years regardless of type of density dependence. The hypothetical metapopulation showed < 3% extinction risk. On the municipality level, Hattfjelldal single population model had relatively higher probability of extinction compared to Vefsn/Grane, 77– 79%, and <2% respectively (appendix 2). All the Helgeland population models showed 55 – 100% probability of falling below 20% of the initial population abundance at least once in the next 30 years regardless of whatever density dependence the population was modelled with. However, the Vefsn/Grane single population model showed an exceptional low risk in all aspects.
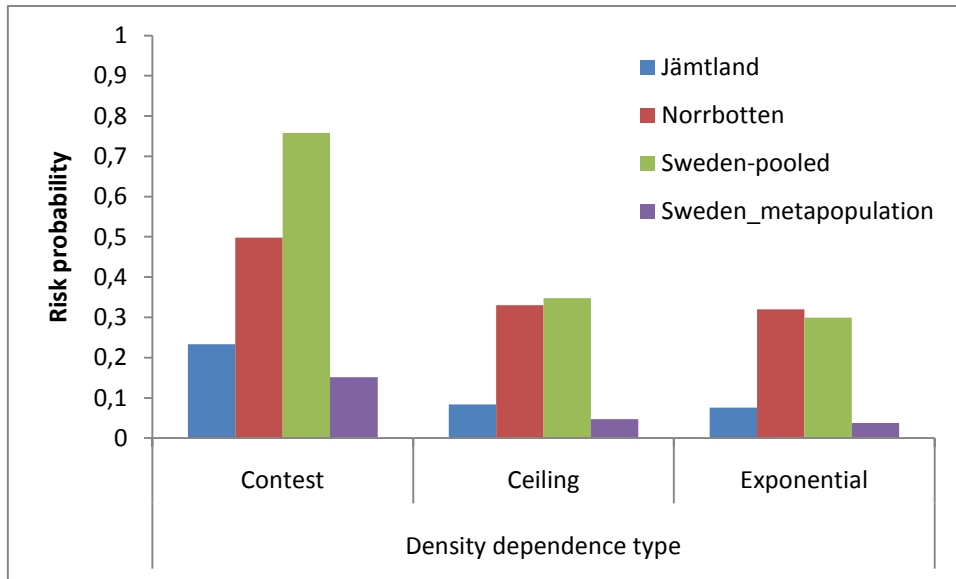
**Figure 2.** Probabilities of the Swedish rock ptarmigan populations in the three northern counties falling below 20 % of initial population size at least once during the next 30 years.
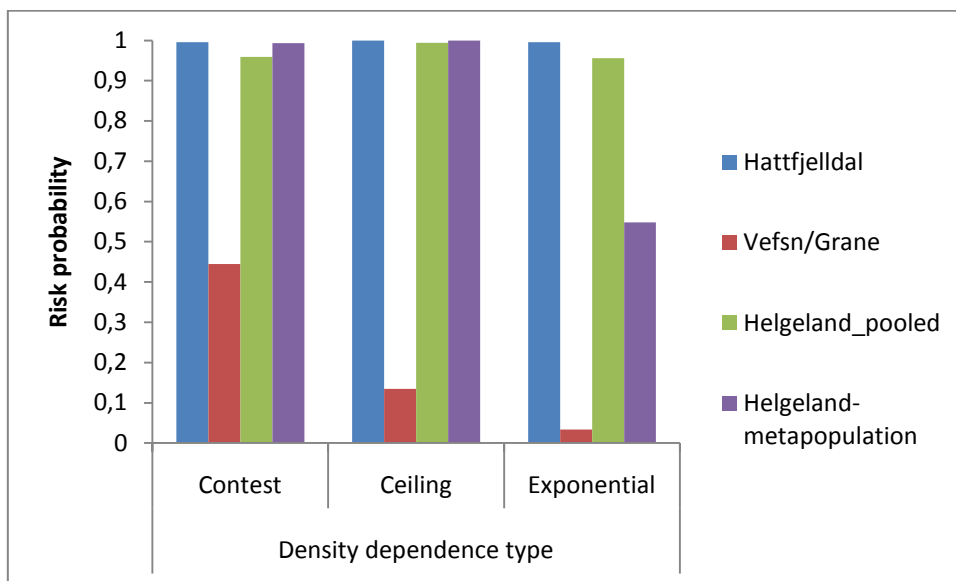


**Figure 3.** Probabilities of the Norwegian rock ptarmigan populations in the three municipalities of Helgeland District, Nordland County falling below 20% initial population size at least once during the next 30 years.
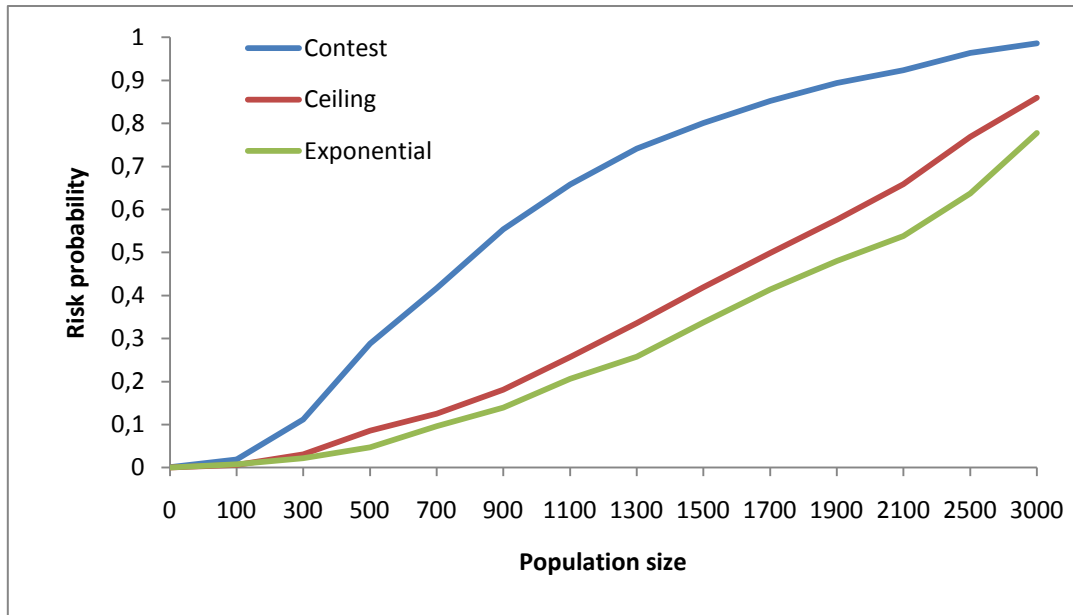
**Figure 4.** The quasi-extinction risk probability of the metapopulation (the three Swedish counties and Helgeland District) under the three density dependence types for the next 30 years.

## Sensitivity analysis

Except carrying capacity, average dispersal distance, and an increase in dispersal rate, the metapopulation was sensitive to change of all the parameters with reference to the direction of changes (table 4). The single population model was sensitive to change of all the parameters except carrying capacity. However, both models were most sensitive to an increase of maximum growth rate, and a decrease of standard deviation. A 10% increase of maximum growth rate brought 4.9 sensitivity changes on the metapopulation and 17.5 on the single population model. For a 10% decrease in standard deviation the metapopulation and single population models showed 1.9 and 4.0 sensitivity, respectively. An increase in initial population size increased the viability of the single population model. However, the change did only produce slight non-directional changes in the metapopulation model.

**Table 4.** The results of ± 10% sensitivity analysis of the Swedish metapopulation and Jämtland County single population models using Expected Minimum Population size (EMP) as proportion of the initial population abundance. The +/– represents for the ± 10% changes.

| | Metapopulation of Sweden | | | Jämtland single population | | |
|---|---|---|---|---|---|---|
| | EMP | Sensitivity | Rank | EMP | Sensitivity | Rank |
| **Base model** | **0.110** | | | **0.004** | | |
| | | | | | | |
| Changes relative to the base model | | | | | | |
| Maximum growth rate (+) | 0.650 | 4.90 | 1 | 0.069 | 17.50 | 1 |
| Maximum growth rate (-) | 0.000 | -1.00 | 3 | 0.000 | -1.00 | 4 |
| Standard deviation (+) | 0.030 | -0.72 | 4 | 0.000 | -1.00 | 4 |
| Standard deviation (-) | 0.319 | 1.90 | 2 | 0.019 | 4.00 | 2 |
| Survival rate (+) | 0.137 | 0.24 | 7 | 0.006 | 0.50 | 5 |
| Survival rate (-) | 0.095 | -0.14 | 9 | 0.002 | -0.50 | 5 |
| Carrying capacity (+) | 0.110 | 0.00 | 12 | 0.004 | 0.00 | 6 |
| Carrying capacity (-) | 0.118 | 0.07 | 11 | 0.004 | 0.00 | 6 |
| Initial abundance (+) | 0.099 | -0.10 | 10 | 0.009 | 1.50 | 3 |
| Initial abundance (-) | 0.095 | -0.14 | 9 | 0.000 | -1.00 | 4 |
| Dispersal rate (+) | 0.118 | 0.07 | 11 | | | |
| Dispersal rate (-) | 0.068 | -0.38 | 5 | | | |
| Maximum dispersal distance (+) | 0.125 | 0.14 | 9 | | | |
| Maximum dispersal distance (-) | 0.087 | -0.21 | 8 | | | |
| Average dispersal distance (+) | 0.103 | -0.07 | 11 | | | |
| Average dispersal distance (-) | 0.103 | -0.07 | 11 | | | |
| Correlation (+) | 0.160 | 0.45 | 6 | | | |
| Correlation (-) | 0.087 | -0.21 | 8 | | | |

## Discussion

### The Swedish populations showed better viability

I made both single population and hypothetical metapopulation projections for both the Swedish and Norwegian rock ptarmigan populations to determine their quasi-extinction probabilities. The simulations of the different Swedish models illustrated that the populations are doing well, which at least did not qualify them to be "endangered" for the next coming 30 years. However, at county level, it was clear that the Västerbotten population had a unique trend, where the model indicated that it had a 100% probability of extinction in the coming 30 years. In literal sense, this probability risk puts the population under the "critically endangered" class of the IUCN red list (IUCN 2001). I think, this quasi-extinction risk probability of the population model might be observed due to two reasons. First, one must consider that models show the true features of the population and thus this risk might be a true scenario. Second, on the other hand, I cannot exclude the possibility that the study sites – more specifically that the transect count locations, were not probably representative enough to capture the trend of the population at the county level.

Compared to the results from modelling the Swedish rock ptarmigan populations, it is not clear how the Norwegian population models will develop. If I take the results literally, the Helgeland populations fit the "critically endangered" criterion, and especially the Hattfjelldal Municipality population was at high risk. And it seemed that the Vefsn/Grane population had a stronger contribution to the stabilization of the extinction risk of the Helgeland metapopulation model. This is because the population model of Vefsn/Grane showed relatively lower extinction and decline risks. When the populations were treated as a metapopulation, the decline/extinction risks of these populations were restored. If the populations had a real metapopulation dynamics, therefore, all the populations had better persistence probability, which might be the contribution of the Vefsn/Grane population.

This high risk of quasi-extinction observed in the Norwegian rock ptarmigan populations might partially be explained by the quality of the wing data. Probably the harvest report might not be a proxy estimate of the population for different reasons. Hornell-Willebrand et al. (2006) and Willebrand et al. (2011) showed that hunting statistics is biased and therefore may not be used as a representative sample of population abundance or change. This is because the harvests are an output of hunters' effort which by itself is influenced by different factors (Hornell-Willebrand et al. 2006, Willebrand et al. 2011). Nevertheless, a few reports from

Scotland found that harvest statistics were reliable representative measures of population abundance (Cattadori et al. 2003). Although it is not known how much of these factors affect the Norwegian hunters, at least their harvest reports depend on their attempt of delivering the harvest wing to the management authority. Therefore, these uncertainties make this prediction unreliable.

These predictions were based on very simple model structures which excluded many factors, such as the sport hunting on private land in Sweden and in all other areas except my study sites in Norway, predators, climate changes, landscape variations, and mating system. These factors might have big contribution on explaining the reason for populations´ size decline or even help to provide more reliable predictions. Developing simple models, such as deterministic models, is recommended if there is not enough data (Beissinger & Westphal 1998, Morris & Doak 2002). However, these type of models probably underestimate the quasi-extinction probability of the model population as it obviously exclude even more of the factors that affect the viability of the populations (Akcakaya et al. 1999, Morris & Doak 2002, Boyce 1992). Stochastic models are recommended models for social birds like rock ptarmigan because they are more realistic, although they might overly increase the extinction risk prediction (Doxa et al. 2010).

If hunting contributes as an additive mortality cause compared to my assumed compensatory management, for example, my prediction might have a different outcome (Akcakaya et al. 2004). An additive mortality could not be explored in the software I used (RAMAS Ecolab) because this program did not encompasses this option, as it is developed for simple PVA analysis. The same goes for the mating system which was indicated as an important viability parameter (Bessa-Gomes et al. 2003). This is especially true for the rock ptarmigan population which has a mixed monogamous to polygamous mating system.

The models showed lower extinction rate under ceiling and exponential density dependence, with the lowest under exponential density dependence. Though some research indicated that ceiling density dependence increases the extinction risk probability as compared to the other density types (Traill et al. 2007, Ginzburg et al. 1990), it was not observed in my analysis, though there was a slight indication of it in the Norwegian models (appendix 2).

The lowest extinction and population size decline results observed under exponential density dependence does not mean that exponential density dependence did underestimate the extinction risk; rather it might be a good conservative estimate. Although this density

dependence type represents an ideal density type in many circumstances, reports indicated that the density type does explain the wild population pattern (Mills et al. 1996, Sabo et al. 2004). For example Sabo et al. (2004) wrote that exponential density dependence gave > 75% correct prediction regardless of the type of the real density type that the wild population had. Sabo et al. (2004) states that, however, these scenarios might not work for populations that are declining > 50% of initial abundance and food regulated populations. As I do not know the real population abundance of the Norwegian rock ptarmigan population, the predicted 50% decline from the initial population size might not help me to compare this result with their finding. However, I think the ptarmigan populations are not regulated by food but by predators. This can be explained by reference to the rock ptarmigan populations of Iceland where the populations dramatically started to decline after exotic predators were introduced (Nielsen & Willebrand, unpublished data).

## Sensitivity analysis

I singled out the Jämtland County´s single population model for the parameter´s sensitivity analysis because it was the only single population model that had above zero expected minimum abundance under the density dependence model. Among the metapopulation models, I used the Swedish metapopulation due to its better quality data which opposed the indirect estimate of the Norwegian population that was gained from the hunt statistics.

The sensitivity analysis gave an apparent image that growth rate plays a crucial role in the viability of the ptarmigan population models. However, this finding could not pinpoint whether it is the adult, juvenile, or only the fecundity that contribute to the growth. Even though a +10% change in survival rate brought a +50% viability difference on the single population model, it was not as strong as an increase in growth rate produced, which had +1750% difference from the base model. That means the other parameter of the population were most sensitive to the change of the growth rate. For the base model, I used an average survival rate of Swedish adult willow grouse. In Iceland, it is found that adult survival explained the major fluctuation of rock ptarmigan (Gardarsson 1988). If the adult survival had a major contribution, I think I might have got different results than this one. The simplicity of the model and absence of data restricts further explanation for this sensitivity result. But I do not think these sensitivity results are so small that they should be neglected (Reed et al. 2002, Morris & Doak 2002), although the growth and survival rates are linearly interlinked (Morris & Doak 2002).

Next to maximum growth rate, standard deviation, which explains environmental variation, was the second most sensitive parameter in both the single and metapopulation models. Environmental stochastic is a probability that produce a variation on reproduction and survival rate of the population due to an influence of weather, predator influence or other similar factors (Miller & Lacy 2005, Akcakaya et al. 1999). In my model, I did not include any of these factors. The model had an assumption that the standard deviation of the maximum growth rate reveals the impact of how these factors influence the population. However, from the research that have been conducted on the same data that I currently used for the Norwegian data, there was no relationship observed between weather and rock ptarmigan chick production (Haakenstad 2003). But this finding contradicts other studies that found strong relationship between these factors (Morris et al. 2008, Boyce et al. 2006, Chirakkal & Gerber 2010). One possible explanation for the current sensitivity result is probably a result of the influence by the predators and the hunting.

The other important image that could be observed from the sensitivity analysis was the feasibility of the hypothetical metapopulation model. The representative hypothetical model showed sensitivity in the decreased dispersal rate and maximum dispersal distances (table 4). This can be an indication that the populations exist as a metapopulation rather than a single population. Based on this, if the populations have real metapopulation dynamics, then all the populations have safer persistence probability because all the metapopulations showed lesser quasi-extinction risks than the single populations. This scenario also decrease the portrayed less persistence viability of the Norwegian single populations. However, for some reason the increase or decrease in carrying capacity did not brought any change on the quasi-extinction probability to none of the population models.

## Reliability of the outputs

The significance of the predicted PVA outputs are dependent on the quality and quantity of the demographic data that are entered into the PVA simulations. This creates various ambiguities with respect to the reliability of the PVA outputs (Lindenmayer et al. 1993a, Burgman & Hugh 2000, Beissinger & McCullough 2002). Therefore, the results from my PVA models should only be used as guidance for future management, and to identify what type of data to collect in future studies of the species.

I made many assumptions. Due to the limited data, I could not perform the traditional prediction validation method, which is usually done by dividing the data into two, and

projecting the other half to check the second half (Brook et al. 2000b, Brook et al. 1997, Morris & Doak 2002). I also could not include the uncertainty or confidence intervals of the prediction (Ralls et al. 2002), since the software (RAMAS/Ecolab) did not produce this for the quasi-extinction probability results. Therefore, the extinction risks should not have to be taken literally.

However, it is assuring to bear in mind that the Swedish population models` prediction is probably a better estimate for two reasons. First, I believe that the line transect data was long enough to capture the major growth rate fluctuation. Brook and Kikkawa (1998) reported that 15 years of demographic data did not bring any significance to the PVA prediction change from the one that were conducted with 25 years of count data for Capricorn silvereye birds (Brook & Kikkawa 1998). The smallest transect count data series of the Swedish populations was 15 years, which made it good enough to give insight into the real population fluctuation, as the expected rock ptarmigan fluctuation in the area is 10 years (Hörnell-Willebrand 2005).

Second, the projection period, for the coming 30 years, was small enough to make reliable estimates of the rock ptarmigan with respect to its life span. Although it was on orchids, Schodelbauerova et al (2010) evidenced accurate PVA prediction for 8 years generation periods (Schodelbauerova et al. 2010). In my analysis I assumed five generation periods.

## Management implications

I did not found any information in the scientific literature of previous studies using PVA on rock ptarmigan that I could compare my results with. I rather preferred to emphasize the relative risks of the model population instead. My results are full of uncertainties, as I made several assumptions. But I tried to explore as different scenarios and model structures as possible with the available data and the given software. So it could be considered as best estimate that could be obtained from the available data.

I believe that the count data from Sweden was long enough to capture some of the possible population fluctuations and reflected the approximate trend. Although I did not include the risk posed by hunting, it is possible that the harvest rate might explained some of the risk of the populations´ decline in a better way (Storch 2007).

The viability analysis of the single population reflected a different quasi-extinction risk. This might be an indication that these populations need a different management system at a "population" level, which is at the administration level under the current assumption. The

models showed that the Västerbotten population was under the highest quasi-extinction risk probability. This is either because of the real risk that the population is facing in the wild or that the sample sites were not representative enough to capture the trend of the population of the area. My results indicated that more information is needed in Västerbotten, and my recommendation is thus to increase the number of count sites.

Brooke et al (2008) assessed the transfer rate of threatened species under the IUCN categories and found that species classified as least concern gets less attention compared to the species that are identified to have higher extinction risk. This leads to a biased management practice as conservation offers more benefit to the species that have less risk of extinction compared to the species with higher risk (Brooke et al. 2008). The explanation for this is that the species classified as least concern often will end up being threatened if no efforts are put in the management system to rectify this state of affairs. Using PVA as a support for the management of species is not a common practice in many places, even if this is slowly changing however (Morris et al. 2002).

Even though the results from my PVA models are associated with a high level of uncertainties, I strongly recommend that the populations need more attention than what they receive today. Increased monitoring efforts by increasing numbers of study sites on the state-owned land in Sweden, and Norway in general, where no regular counts are made, is my first recommendation. By analysing the existing information, I have identified what types of data that is in need of being collected in future studies. Information on adult survival and mortality causes, breeding success and factors that influence this, as well as dispersal distances and frequencies will be crucial to know in order to be able to manage rock populations in a sustainable way in the future.

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# Appendixes

**Appendix 1.** The counties´ and municipalities´ land area size ≥1200 m above sea level and the calculated corresponding carrying capacity and initial abundance of the ptarmigans.

|  | Municipality | ≥ 1200 area/ km$^2$ | Carrying capacity (K) | Initial abundance |
|---|---|---|---|---|
|  | Vefsn/Grane | 12.79 | 10 x 12.79 = 127.9 | 128 |
|  | Hattfjelldal | 109.89 | 10 x 109.89 = 1098.9 | 1099 |
| **Pooled Helgeland** |  | 122.67 | 10 x 122.67 = 1226.7 | 1227 |
|  | **County** |  |  |  |
| **Jämtland** | Jämtland | 328.99 | 10 x 328.99 = 3289.9 | 538 |
| **Norrbotten** | Norrbotten | 3025.20 | 10 x 3025.2 = 30252 | 765 |
| **Västrebotten** | Västrebotten | 240.94 | 10 x 240.94 = 2409.4 | 12 |
| **Pooled Sweden** |  | 3595.13 | 10 x 3595.13 = 35951.3 | 2322 |

**Appendix 2.** Probability of quasi-extinction, and 20% and 50% decline from the initial population size for all the model scenarios. The results in the table are expressed in %.

| Probability | Sweden | | | Norway (Helgeland) | | |
|---|---|---|---|---|---|---|
|  | **Density dependence type** | | | **Density dependence type** | | |
|  | Contest | Ceiling | Exponential | Contest | Ceiling | Exponential |
|  | **Jämtland** | | | **Hattfjelldal** | | |
| **20 %** | 23.3 | 8.4 | 7.6 | 99.6 | 100.0 | 99.6 |
| **50 %** | 64.0 | 29.9 | 26.9 | 100.0 | 100.0 | 100.0 |
| **Exinction** | 0.1 | 0.0 | 0.0 | 77.2 | 78.8 | 78.5 |
|  | **Norrbotten** | | | **Vefsn/Grane** | | |
| **20 %** | 49.8 | 33.0 | 32.0 | 44.5 | 13.5 | 3.4 |
| **50 %** | 77.1 | 53.7 | 50.6 | 92.6 | 70.1 | 17.2 |
| **Exinction** | 2.9 | 2.1 | 0.0 | 1.8 | 0.1 | 0.0 |
|  | **Västerbotten** | | | **Helgeland-pooled** | | |
| **20 %** | - | - | - | 95.9 | 99.4 | 95.6 |
| **50 %** | - | - | - | 98.1 | 100.0 | 98.9 |
| **Exinction** | 100.0 | 100.0 | 100.0 | 32.5 | 33.7 | 31.5 |
|  | **Sweden-pooled** | | | **Helgeland-metapopulation** | | |
| **20 %** | 75.8 | 34.8 | 29.9 | 99.3 | 100.0 | 54.8 |
| **50 %** | 94.8 | 58.3 | 46.4 | 99.9 | 100.0 | 84.7 |
| **Exinction** | 1.3 | 0.9 | 0.8 | 2.7 | 0.5 | 0.3 |
|  | **Sweden-metapopulation** | | | **Sweden-Norway-metapopulation** | | |
| **20 %** | 15.1 | 4.7 | 3.8 | 28.8 | 8.0 | 5.1 |
| **50 %** | 49.1 | 19.8 | 15.3 | 72.4 | 31.6 | 25.8 |
| **Exinction** | 0.0 | 0.0 | 0.0 | 0 | 0 | 0.0 |