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Examensarbete i ämnet biologi
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Abstract

Successful conservation and management of Golden Eagle (*Aquila chrysaetos*) requires an in-depth understanding of its' demographic parameters. The species in Sweden is listed as Near Threatened and threats include increasing demands for renewable energy, collisions with railways, illegal persecution, and lead poisoning. Breeding performance and survival estimates can be used to increase the knowledge of the population dynamics of this apex predator. I estimated breeding performance of Golden eagles by using citizen science data from 44 territories in Northern Sweden from 1995 to 2015.Ring recovery data from the National ringing database of the Stockholm museum of Natural history, were used to estimate population and age-specific survival. Weather, voles' density and topographic variables incorporated to Generalized Linear Mixed Models (GLMMs) to explain the patterns of breeding success. In continue, fecundity and survival estimates used to structure a stage-structured Lefkovitch population projection matrix to estimate population growth, stable stage distribution and elasticities and sensitivities of the growth rate. Long term population fecundity was estimated to be 0.51 (young per pair) and breeding success it is likely to be affected by vole index, snow depth and precipitation preceding the breeding period and average temperature during the breeding. The best approximating model explained the 29% of the total breeding variance, which questions the size of the effect of habitat features and human-induced disturbance to Golden Eagles reproductive performance. Survival rates were similar with those reported in the U.S. with older individuals exhibiting higher survivorship (0.89) from the first age class (0.79). The population exhibits a positive growth rate (1.1) while elasticities and sensitivities of the growth rate indicate that the most influential transition for the population growth is the one from 3 years old to 4 years old, while individuals older than 4 years old contribute more to population growth.

1 Introduction

Knowledge of the factors affecting population dynamics of a species is fundamental for its successful conservation and management. However, estimation of species demographic parameters is not often straightforward as it depends on reliable field data. Field data collection can become difficult when species are cryptic, rare, broadly distributed, highly mobile and inhabit extreme environments (Link & Nichols, 1994; Nichols & Williams, 2006; Petit & Valiere, 2006). For instance, many species of raptors are difficult to study while their monitoring can be both costly and demanding (Dunn & Hussell, 1995; Bildstein, 2006). Nevertheless, understanding and quantifying their demographic parameters and factors affecting them is critical since raptors are apex predators and indicative of the health of the ecosystems (Sergio *et al.*, 2006, 2008). Participatory monitoring methods, whereby volunteers are involved in monitoring, can be useful for studying such species (see Devictor *et al.*, 2010; Mulder *et al.*, 2010; Singh *et al.*, 2014; Dennhardt *et al.*, 2015), as they can gather large amounts of reliable data, are cost effective and long lasting (Williams *et al.*, 2002; Good *et al.*, 2007).

Golden Eagles in Northern Sweden have been monitored by local ornithologist volunteers since the 1970s while efforts have been increased considerably the last decades (Ekenstedt & Schneider, 2007; Moss *et al.*, 2012). Inventories are made during the breeding period of the species reproductive performance (by visits in the nesting areas) and ringing of the newborn nestlings. Those monitoring programs have increased the basic knowledge of the variation in species demographic parameters in space and time while recoveries of ringed individuals are useful to monitor migrations patterns and spatial distribution of this species of high conservational concern (Fransson & Pettersson, 2001; Saurola *et al.*, 2013).

This period between the departure from the natal territories and the recruitment into the breeding population is one of the least-studied periods of the life history of golden eagles (Watson, 2010). As a consequence, a limited number of studies have attempted to determine the survival in wild of Golden Eagles (Mcintyre et al., 2006; Watson, 2010; Millsap et al., 2016).

Except from the latest studies regarding the influence of wind power installations in raptors demography (Carrete *et al.*, 2009; May *et al.*, 2010; Dahl *et al.*, 2012; Pearce-Higgins *et al.*, 2012), historically, researchers have studied the influence of food supply, weather and landscape heterogeneity on raptors reproductive performance and demography (Steenhof *et al.*, 1983, 1997, 2014; Tjernberg, 1983a; Marquiss *et al.*, 1985; Watson *et al.*, 1992; Pedrini & Sergio, 2001; Karell *et al.*, 2009; Fasce *et al.*, 2011a; Mcintyre & Schmidt, 2012; Vittorio & López-López, 2014). In Scotland, several studies have pointed that habitat loss caused by deforestation decreased habitat quality and led to lower breeding success for Golden Eagles, and abandonment of their breeding territories (Marquiss *et al.*, 1985; Whitfield *et al.*, 2001, 2007; Watson & Whitfield, 2002). In Sweden, on the other hand, forestry practices proved to have mixed effects on the population (Hipkiss *et al.*, 2014; Moss *et al.*, 2014). Clear cuts which are preferred hunting habitats, grow into the forest while old forest patches being harvested, becoming new hunting grounds but unsuitable nesting locations (Hipkiss *et al.*, 2014).

So far the mechanisms and effect of each environmental parameter on the demography of the Swedish breeding population remain poorly known. No study has determined survival of the Swedish population, apart from a recent publication of Nygård *et al.* (2016) who reports the survival of juvenile Golden Eagles in Northern Norway. As for the breeding performance, Tjernberg (1983a, 1985) along with Moss *et al.* (2012, 2014) highlighted the importance of food supply and clear cuts in the vicinity of eagles' territories, however in both studies of 1983 and 2012, prey population fluctuations explain a small percent of the breeding variance at all spatial scales. Tjernberg, (1983b) suggested the favorable weather conditions during the breeding period influence breeding, without determining the effect of a particular variable. As for the influence of wind farm installations, Hipkiss et al. (2014) focused on the conservation management, proposing the prioritization of highly productive territories over low, without exploring the effect of wind farming on breeding. However, the 85% overlap between proposed windmills and their home ranges raises (Hedfors, 2015) questions for the future effects of wind power on Golden Eagles' breeding performance.

The Golden Eagle is a long-lived, territorial and monogamous species with low reproductive rate and individuals sexually mature in the 4th or 5th year of their lives, when form pairs and establish territories (Steenhof *et al.*, 1983; Watson, 2010). According to the Swedish Environmental Protection Agency (Naturvårdsverket, 2015), the Swedish population is currently estimated at 1360 (1160-1600) individuals ranging over the boreal mountain region of northern Sweden and scattered populations occur further south but the exact population size and distribution are unknown. The species is characterized as Near Threatened (Swedish Information Center, 2016) and is listed in the Annex I of the EU Birds Directive and Habitat Directive (European Commission, 2016) of species that need special protection special conservation measures. The conservation threats include the increasing demand for more renewable energy sources, increased habitat loss effects, collisions with powerlines, railways and wind turbines in addition to illegal persecution and lead poisoning.

Due to the dynamic character of the boreal ecosystem, pairs within the same population may be found in a variety of habitats of different quality facing dissimilar possibilities of survival and reproduction (Penteriani *et al.*, 2003, 2015; Vittorio & López-López, 2014). Dissimilarities among breeding performance in different areas and years may reflect the influence of several parameters including food availability, variations in climatic conditions, topography and wind farming disturbance.

This thesis aims to improve the understanding of the Swedish Golden Eagle *(Aquila chrysaetos*) demographic parameters and population ecology. I approach this goal by exploring Golden Eagle reproduction in relation to climatic conditions, food supply, topography and wind farms while recovery data from the ringing program will be used to estimate population survival. Specifically, I aim to answer the following questions:

(i) What is the spatial and temporal pattern of breeding success in Northeastern Sweden?
(ii) What are the effects of climatic variables influence on nesting -success patterns?
(iii) Effect vole fluctuations and topography the breeding outcome?
(iv) What are the population and age-specific survival of Golden eagles based on the ring recovery data?

(v) What are the population growth rate and stable stage distribution of Golden Eagle in Northern Sweden?

2 Materials and methods

2.1 Study area

The study area extends across Sweden, where Golden Eagles have been ringed and recovered at different latitudes spanning from 56° to 69° N.

2.1.1 Breeding patterns and Productivity

For studying the breeding patterns in the study area, I selected the regions of Västerbotten, where a substantial part of the population resides (map 1). The area is sparsely populated with few towns and villages, while topography is characterized by mountain plateaus in the west and the coastline of Bothnian Gulf to the east with elevations ranging between 100 to 650 m a.s.l. It is dominated by boreal forests and young forest stands of Norway spruce (*Picea abies*), Scots Pine (*Pinus sylvestris*), Silver Birch (*Betula pendula*) and Aspen (*Populus tremula*) (Engelmark & Hytteborn, 1999). However, national parks and protected areas may contain older forest stands up to 400 years old, important for the breeding population, considering that the vast majority of Golden Eagles nests in trees approximately 370 years old (Tjernberg, 1983b). Forestry and reindeer husbandry are the dominant land use practices (Naturvårdsverket, 2015), while wind energy development increasing. Since 1996, 477 wind mills along with the extensive infrastructure, have been constructed in the study area, with plans for further expansion (Vindlov, 2016).

2.2 Golden Eagle breeding and ringing data

The majority of the original breeding data originates from the collective efforts of citizen science projects all around Sweden. From 1970 onwards, most of the study area was searched for nesting Golden Eagles by several Swedish ornithological groups (see Kungsörn Sverige, 2016; Örn-72, 2016). Occupied territories were located by observing territorial activity, court-ships, brood-rearing activity, eggs, nestlings or any other noticeable field signs (e.g. new tree branches on old nests). Any area where nesting activity was recorded for successive years was considered as a nesting territory and checked for breeding activity (Ekenstedt & Schneider, 2007; Moss *et al.*, 2012). Each territory was surveyed at least three times each year. Scheduled visits at breeding sites were organized based on species' breeding cycle. In detail, visits in the beginning of spring (February to March) were made to confirm courtship, nest building and incubation ii) visits in May were made to observe breeding attempts via the presence of incubating couple or eggs and finally iii) visits during the fledging period to investigate breeding success and ring the newborn chicks.

Each territory was characterized by a status as a) controlled (k = "kontrollerade revir" in Swedish) b) not checked (? = "okontrollerade" in Swedish) c) occupied (b = "besatt revir" in Swedish) d) failed breeding (m= "misslyckad hacking" in Swedish) and finally iv) successful, including the number of nestlings per territory.

However, not all the nests were possible to be controlled for breeding attempts through the years and it was difficult to define the number of nestlings that successfully managed to fledge. These missing data may induce bias and result in underestimation or overestimation of the productivity and breeding success of each year and territory.

Map 1. The study area of Golden Eagles breeding and survival analysis. Eagles ringed and recovered in numerous locations spanning across Sweden. Each red triangle represents a known Golden Eagle breeding territory (n= 44) in the counties of Västerbotten and Jämtland in Northern Sweden.

2.2.1 National ringing database

The bird ringing data is the outcome of monitoring programs of the Stockholm Museum of Natural History. The museum's Bird Ringing Centre is devoted into the organization, storage, and analysis of ringing and recovery reports for several bird species including the Golden Eagle (Naturhistoriska rikmuseet, 2016). Through the years, volunteers and others have collected and reported data from sites across Sweden and Europe. Our dataset included detailed information on the number of recovered and ringed Golden Eagles (both nestlings and adults) from 1906 to 2015. Additional information included ring codes, ringing – recovery year and location, and age of each individual marked and recovered. Figure 1 illustrates the basic structure of my analysis and how citizen data was used to estimate different parameters and be able to increase the knowledge regarding the breeding dynamics of Golden Eagles in Sweden.

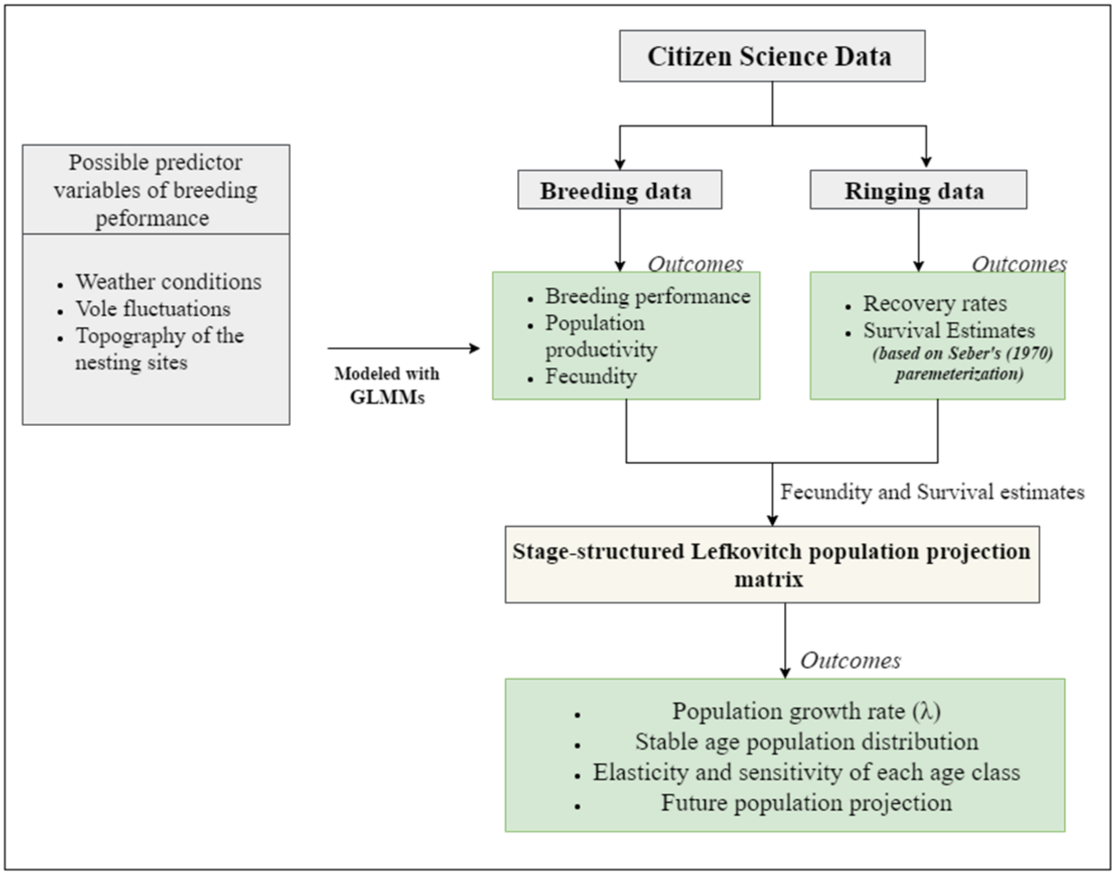


Figure 1: Flow diagram of the study methodology. Each box represents a different part of data analysis. Abbreviations are as follows: GLMMs; Generalized mixed effects models.

2.3 Data analysis

2.3.1 Reproductive performance

Reproductive performance was investigated from 1995 to 2015 at both temporal and spatial scales to facilitate an overall view on the patterns of reproductive performance both in space and time. Spatial breeding analysis, based on the fact that Golden Eagles may show a strong fidelity to well-defined nesting territories for many years (Watson, 2010) and productivity and breeding success can therefore be defined both on the basis of a territory (Brown, 1974; Marquiss *et al.*, 1985; Steenhof & Newton, 2007). As territory is defined, a specific area or the "core area" according to McLeod *et al.*, (2002), that historically contained one or more nests within the home range of the mated Golden Eagle couple.

The terminology of the reproductive parameters is based on Steenhof & Newton (2007). All the parameters calculated and their definitions are reported in table 1. Parameters estimations follow Steenhof *et al.*, (1997), Steenhof & Newton (2007) and Moss *et al.*, 2012), methodological approach. In many cases, variables were expressed as percentages in order to facilitate comparisons between territories and years. Those variables were used as an index of breeding investment of the population through space and time.

To explore the effect of different variables on the reproductive performance, breeding outcome of each effort was given a status 0 or 1 (for failed -breeding and successful breeding attempt respectively). A breeding attempt considered successful if the pair produced at least one nestling. Breeding status used as a response variable in generalize linear mixed models (GLMMs) for predicting reproductive performance in relation to several predictor variables (see statistical analysis). I considered generalized linear mixed models appropriate for my analysis because they allow me to build regression models when the distribution of the response variable is not normal (binary) and include both fixed and random effects (Zuur *et al.*, 2007; Everitt & Hothorn, 2015). Both types of models have been used from several researchers working on Golden Eagles and other raptors to explore relationships for different variables (Penteriani *et al.*, 2003; Gil-Sánchez *et al.*, 2004; López-López *et al.*, 2005; Dahl *et al.*, 2012; Vittorio & López-López, 2014; Balotari-Chiebao *et al.*, 2016; Miller *et al.*, 2016).

Most of the breeding parameters were plotted and inspected for trends and patterns both in space and time, using the package "ggplot2" (Wickham & Chang, 2016).

Table 1. List of variables that used to describe reproductive performance of the Golden Eagle population in North Sweden both in space and time. Asterisk (*) indicates that the variables were calculated both annually and spatially.

Variable	Definition
Reported reproductive parameters	Number of times a territory visited, occupied, recorded breeding attempt and successful breeding attempt. Number of young that reach the age for assessing breeding success.
Territory occupancy *	Expressed as the percentage of territories/ territory occupied in relation to known visited territories during the study period.
Breeding effort *	Expressed as the percentage of times a breeding attempt was recorded in territories/ territory in relation to known visited territories during the study period.
Breeding or nesting success *	Expressed as the percentage of times territories/territory contained at least one nestling in relation to known territories during the study period.
Average number of nestlings or average brood size	Number of nestlings produced per number of breeding attempts per territory and per year.
Productivity *	Number of nestling produced annually / spatially per 100 occupying pairs. Product of the multiplication of average number of nestlings and breeding success
Fecundity	Number of nestlings per number of occupying pairs per year assuming a 1:1 sex ratio among offspring.

2.3.2 Predictor variables of the breeding performance

2.3.2.1 Topographic data

Elevation and slope values for each nesting location were extracted from raster maps. In order to estimate the mean elevation of each territory, I created a buffer zone of 30 Km^2 using the function "gbuffer" in R package "rgeos" (Bivand *et al.*, 2016). Around each existing wind farm, 3.09 km buffers were created with the function "buffer" from package "adenhabitat" in R (Calenge, 2006, 2015). The size of the buzzer was decided in respect of recent publication, revealing that the core home range which may equate to a territory, of the Swedish population during the breeding season was estimated to range between 5 to 30 km^2 (Singh *et al.*, 2016). Slope values (in degrees) were computed from an elevation map using the function "terrain" and "extract" in R package "raster" (Hijmans *et al.*, 2016) using 4 neighboring cells to compute the slope for each location. Projection in all the maps used and created was WGS 84.

2.3.2.2 Voles population fluctuations

Based on the predictions that Golden Eagles' prey populations cycles are affected by voles' population fluctuations in Sweden (Hörnfeldt, 1978, 2004; Angelstam *et al.*, 1984; Small *et al.*, 1993) and because small game data (which are Golden Eagles main prey according to Tjemberg, 1983) were unavailable, I obtained small rodents data to represent a possible food source. Vole data for Västerbotten county, where the majority of the breeding population resides, obtained from the Swedish Environmental monitoring program of the Swedish University of Agricultural Sciences database (SLU) (data available online). Voles have been snap-trapped on a trapping grid in spring and autumn from 1971 until know in Umeå, Västerbotten county (Hörnfeldt, 2004, 2015; Hörnfeldt *et al.*, 2005). I used data of field voles (*Microtus agrestis*) and bank voles (*Myodes glareolus*) from 1994 to 2015, expressed as the numbers of individuals per 100 trap- nights. Autumn vole index preceding the breeding period and spring vole index during the breeding period used in the analysis.

2.4.2.3 Meteorological data

I obtained environmental data on temperature (^{o} C), precipitation (mm) and snow depth (m) from the Swedish meteorological and hydrological institute (SMHI) (data available online) for three weather stations (Åsele, Talliden, Glommerstäsk) located within my study area. I obtained data on monthly minimum, maximum and average temperature (^{o} C), the monthly average of precipitation (mm) and the monthly average of snow depth (m) from 1995 to 2015. Additionally, based on reported averages, I calculated the number of days below the average monthly temperature to express extreme weather conditions during in each period. These data were used to create metrological variables that characterize weather conditions for two periods for the nesting locations. The period prior to egg laying (December to February) as well as breeding and egg laying (February to April).

2.4.3 Survival

Using the ringing data provided by the Bird Ringing Center of the Stockholm Museum of Natural History, I estimated Golden Eagle's survival rates. Survival analysis used from 1990 to 2015, given the fact that recovery and ringing efforts increased rapidly during the 90s. Data was organized into a recovery matrix and annual survival rates were estimated using the Program Mark with Seber parametrization (Williams *et al.*, 2002; Cooch & White, 2015). The method for estimating survival rates using bird bands from dead individuals was given by Seber (1970) and considered appropriate for my analysis given the fact that has been used since by several researchers as a reliable method for survival estimation (Balotari-Chiebao *et al.*, 2016; Millsap *et al.*, 2016).

In program Mark, I formed sets 17 candidate models that included year and age covariates on survival and recovery probabilities. Additionally, 3 models were formulated to include linear time trends. Based on Akaike information criterion AIC_c, (Burnham & Anderson, 1998) I evaluated the candidate models and reveal the best-supported model for the analysis.

2.4.4 Population model matrix

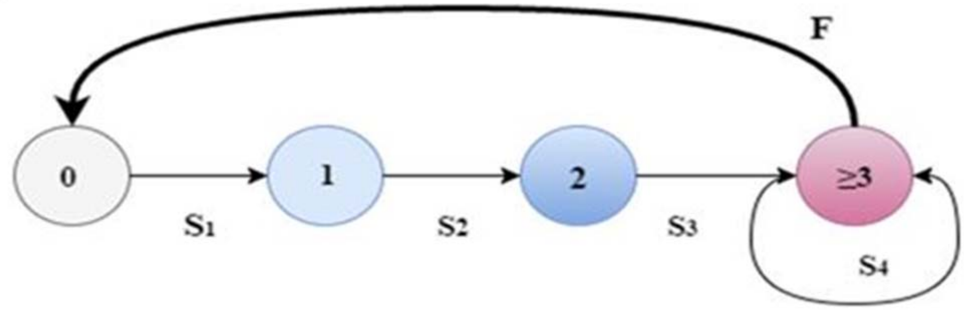
Estimation of the demographic parameters provided me the basis to move to the final part of the analysis and a build a population model matrix (figure 2). Based on the fact that Golden Eagle is a territorial monogamous species with a low reproductive rate that sexually matures around the 4^{th} and 5^{th} year of its life cycle (Steenhof *et al.*, 1983), I considered that a post-breeding stage-structured Lefkovitch matrix (Caswell, 2001) is the appropriate model for my data. The model included the age classes 0-1, 1-2, 2-3 and ≥ 3 and allowed Golden Eagles to reproduce after the third year (figure 2). It accounts survival, growth, and reproduction to describe the transitions of the population from one life stage to another. In R I conducted an analytical sensitivity analysis using the package "primer" (Stevens, 2009) in order to identify the life history stages that contribute the most to the population growth of the Golden Eagle. In R I was able to calculate a number of parameters including:
The finite rate of the population increase or growth rate (λ), which was calculated according to Caswell (2001) as the dominant eigenvalue of the matrix population model.
The stable stage distribution which is the proportion of each age stage in the total population. These proportions remain constant regardless possible changes in the value of growth rate (λ). The vector of each stage proportions is called right eigenvector of the matrix (w), while the reproductive value of each stage is called left eigenvector (v).
Sensitivities of (λ) which reveal how small changes of fecundity and survival can affect the growth rate. The sensitivity (s_{ij}) of an element in the matrix is given by the equation below.

$$sij = \frac{viwj}{<w,v>} \qquad \text{(Equation 1)}$$

Where v_i is the ith element of the reproductive value of each eigen vector, w_j is the jth element of the stage vector and <w, v> is the product of the two vectors.
Elasticities of (λ) which represent proportional contributions of each stage at the growth rate and the elements of each eigenvector (v_i, wi):

$$eji = \frac{aij\,sij}{\lambda} \qquad \text{(Equation 2)}$$

Based on derives from the sensitivity analysis, I projected the population growth of each population stage for 5 years under the assumption that demographic parameters remain stable and there is no influence of natural and anthropogenic factors.



$$\begin{pmatrix} N0, t+1 \\ N1, t+2 \\ N2, t+3 \\ N3, t+4 \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & F \\ S1 & 0 & 0 & 0 \\ 0 & S2 & 0 & 0 \\ 0 & 0 & S3 & S4 \end{pmatrix} * \begin{pmatrix} N0 \\ N1 \\ N2 \\ N3 \end{pmatrix}$$

Figure 2. Diagram of the Golden Eagle stage-structured population model. Each stage corresponds to age classes 0- 1, 1-2, 2-3 and > 3 which includes all the following age classes. S symbolizes the survival rates of each age class while F symbolizes the fecundity.

2.5 Statistical analysis

All of the statistical analysis was performed within the R environment for statistical computing (version R.3.3.2). All the variables representing Golden Eagle reproductive performance were tested against a normal distribution using the Shapiro-Wilk normality test and the function "shapiro.test" in R. I also estimated mean values, standard deviation (S.D.) and coefficient of variation (CV) (as the ratio of standard deviation to the mean multiplied by 100) for all the variables. To detect any spatial aggregation or clustering of territories based on performance and distance between them, I ran non-metric multidimensional scaling (NMDS). Statistical significance was set at $P<0.05$.

All the variables representing topographic features, weather conditions, and vole fluctuations were standardized (by subtracting mean values from raw data and dividing the difference by the standard deviation) prior to model building using the package "clusterSim" and the function "data. Normalization" in R (Walesiak, 2016). Topographic data ("elevation" and "slope") incorporated into a generalized linear model (GLMM) as fixed effects and year and territory as random effects. For the models, I used the function "glmer" from the R package "lme4" (Bates *et al.*, 2016). As response variable, I consider the breeding success, which follows a binomial distribution, so error structured assumed to be binomial and the "logit" as the link function (Crawley, 2005). Similarly, "vole index during autumn" and "vole index during spring" used as fixed effects into GLMM and territory as a random effect.
For the weather data, before the model building, I used principle component analysis (PCA) and the package "FactoMineR" in R (Husson, 2016). PCA was used to organize the data from the two different time periods and quantify interrelationships among a number of

independent variables. The main purpose of using this type of analysis was not to define relationships between the dependent (breeding) variables and independent (weather) variables but shorten the information contained in a larger set of the original data into a new smaller set of new composite dimensions (McGarigal *et al.*, 2000).

In following, weather variables incorporated into a generalized linear model (GLMM) using the same approach as described above. I build 32 of models using each weather variable and possible combinations. To select the best fitting model, I used the package "MuMln" in R and the functions "model.sel" (Barton, 2016). The significance of each variable was ranked using the AIC (Akaike's Information Criterion) (Burnham & Anderson, 1998) and contribution of each variable estimated using the function "model.avg" (Barton, 2016). The percentage of breeding variance that explained from the best supporting models was based on marginal and conditional R^{2} (Nakagawa & Schielzeth, 2013). In all of the explanatory variables, applied the significance level of $P < 0,05$. Finally, I build series of 11 models making combinations of weather, topography and prey fluctuations to find which variables explain in the best way the breeding outcome and the size of the total variance that explained.

3 Results

3.1 Breeding performance

An average 26 territories have been searched for nesting Golden Eagles in the Northern Sweden each year from 1995 to 2015 (range= 15-42, S.D. = 9.1, cv= 33.8). Through the years, an average of 21 pairs occupied breeding territories (range= 11- 34, S.D. = 7.5, cv= 36.4) among which 12 pairs breed (range =1 – 26, S.D. = 6.6, cv= 55.3) and 11 were successful (range= 1-25, S.D. = 6, cv= 57). In detail, each year 78.8% (±11.9 % S.D. cv=14.9, figure 3a) percentage of pairs occupied territories, 44.4 % (±15.6 S.D) percentage attempted to breed and 39.1 % (±15.5 S.D., figure 4b) were successful. The percentage of pairs attempted to breed and successfully raised nestlings, showed extensive variation among years (CV= 35.13– 39.7 respectively, figure 3b), while each breeding attempt resulted in 1.2 (± 0.26 S.D.) produced nestlings. Average annual productivity was 51 (±22.4 S.D.) (nestlings per year per 100 occupying pairs) however there was large interannual variation, reflecting the difference in variation between 'breeding attempts' and 'successful breeding attempts' (cv= 44.1, figure 3c). Fecundity (number of nestlings/ number of occupying pairs per year, assuming a 1:1 sex ratio among offspring (Steenhof & Newton, 2007)) was estimated as 0.51 (±0.22 S.D) and ranged between 0.0625 and 0.875.

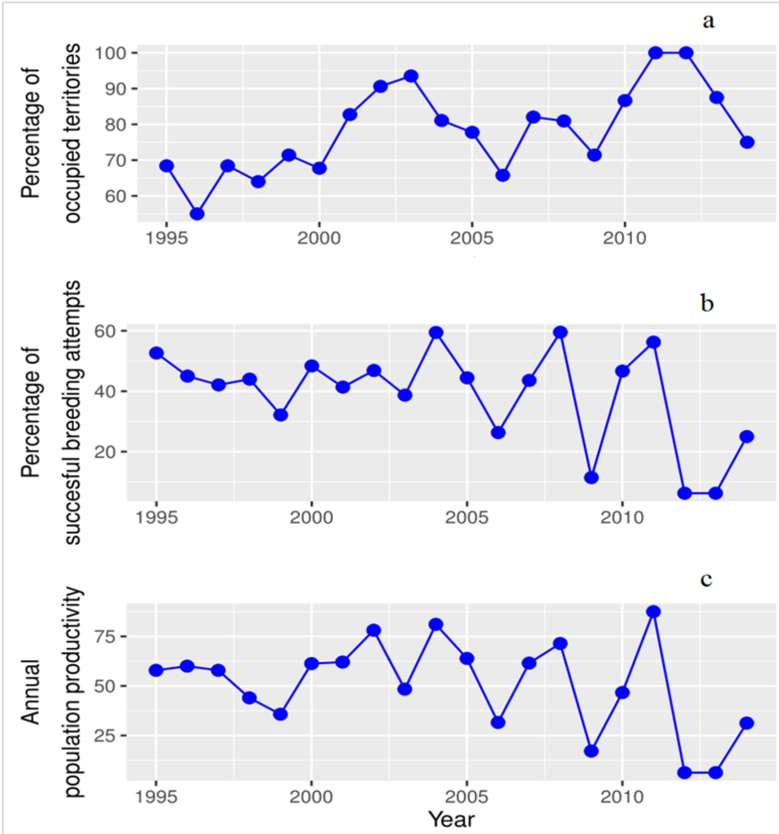


Figure 3. (a) Percentage of occupied territories, (b) percentage of successful breeding attempts, (c) annual population productivity index (nestlings per year per 100 occupying pairs) in Northern Sweden from 1995 – 2015.

During the 21 years of monitoring, each Golden Eagle territory (n=44) was examined for signs of territorial activity, occupancy or brood-rearing activity an average 13 times (range= 2-21, SD= 4.6, cv=36.4). Each territory was occupied on average 9.8 times from 1995 to 2015 (range= 1-18, SD= 4.1, cv=42.1) from which 5.9 times a breeding attempt was recorded (range= 1-14, SD= 3.2, cv=55.3). Successful breeding attempts were recorded on average 5 times (range = 0- 12, SD= 2.9, cv= 58.4).

Territories that were occupied less than 5 times during the study period were excluded from the analysis of reproductive parameters and productivity. Percentage of successful breeding attempts for each territory was 44% ± 20.2 % (range= 0-80%) and coefficient of breeding variation was 141.5 (range = 51.75- 374.17, figure 4). The average productivity of each territory was 52.8 (± 27.5 S.D.) (nestlings per 100 breeding attempts) (range= 7.14 - 113.4). From all territories, 71.7 % seem to exhibit average numbers of productivity, 15.5% exhibit high numbers and 12.8 % very low productivity. Territories that were more productive exhibited a lower variation of breeding success than the territories that were less productive (map 2) Non-metric multidimensional scaling (NMDS) based on breeding performance and distance between each territory, revealed no spatial aggregation or clustering among the nesting territories.

The highest value for reproductive parameters was found in territory GAM, with 72.7 % percentage of successful breeding attempts, 1.56 nestlings per breeding attempt and productivity of 113.4 (nestlings per 100 breeding attempts). The lowest value was found in STK with 7.14 percentage of successful breeding attempts and 1 nestling per breeding attempt (figure 4). Pattern of breeding success for all territories and years is listed as an Appendix (see figure A).

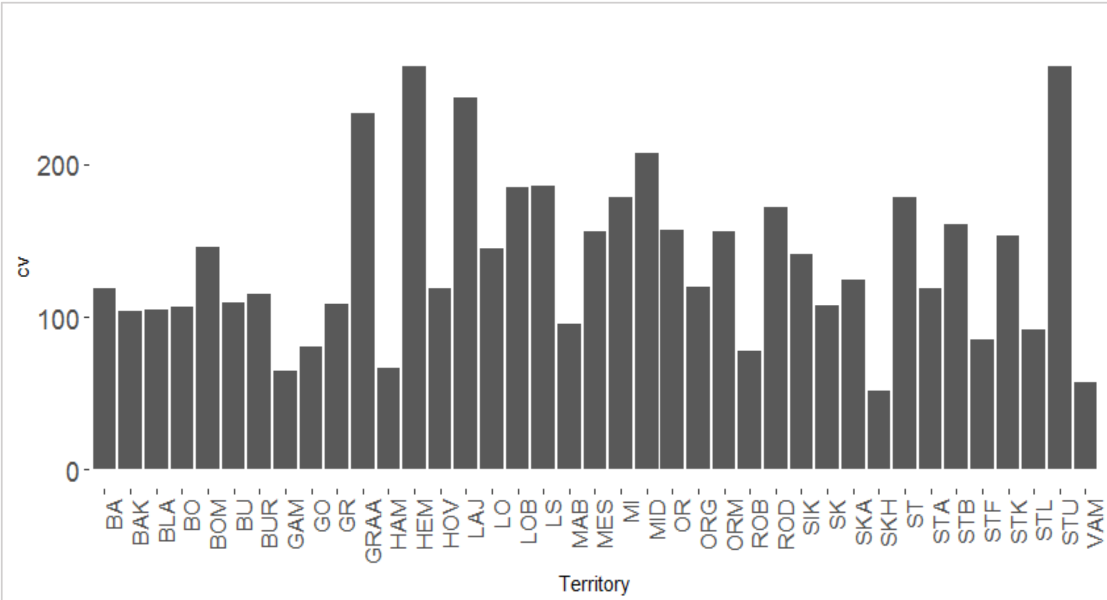
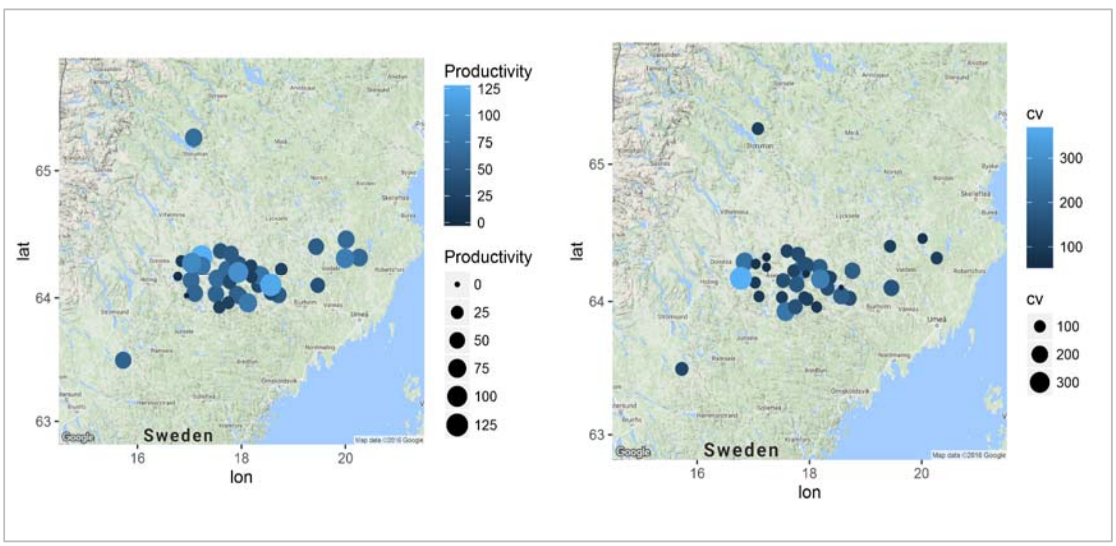


Figure 4. The coefficient of variation of breeding success (CV) for reported nesting territories from 1995 – 2015 in Northern Sweden. The coefficient of variation calculated as the ratio of standard deviation (σ) to the mean number of successful breeding attempt (μ) multiplied by 100.



Map 2. Maps for the study area and the breeding territories (n=39) in Northern Sweden. Each point represents a breeding territory, while size and color the magnitude of productivity (on the left) and coefficient of variation (cv) of breeding success (on the right).

3.2 Effects of the predictor variables on breeding performance

3.2.1 Topographic features

Average value of slope in the Eagles' territories (n=39) was 11.2^o (ranged= 2.29^o -29.29^o, se= 9.16), while mean ground elevation was 361.1 m a.s.l (range= 243.1 – 525. 6 m a.s.l., se= 1.23). Values, incorporated into a generalized linear mixed effects model (GLMM) with binomial response variable (breeding success was coded as 1 {successful} or 0 {unsuccessful}), and territory ID and year as random effects. I found no evidence that topography can predict the breeding outcome (table 2), while according to Z values elevation and slope have similar effects.

Table 2: Generalized linear mixed effects model results, showing predictors of breeding success of Golden Eagles, for different values of topographic features in Northern Sweden (breeding attempts= 540, number of territories = 39). Asterisk (*) indicates significant p-values (< 0.05) and numbers denote the parameters estimates.

Fixed effects	Estimate	SE	Z value	P value
Topographic features				
Intercept	-0.57	0.23	-2.5	0.01 *
Elevation	0.04	0.16	0.23	0.82
Slope	0.03	0.14	0.20	0.83
Random effects	Variance	SD		
Territory	0.65	0.81		
Year	0.40	0.64		

3.2.2 Vole population fluctuations

Estimated vole index (number of voles per 100 trap-nights) ranged from 0.1 to 3.16 in spring (mean = 0.97, SD= 0.78) and from 0.43 to 10.76 (mean= 1.18, SD = 2.79) in autumn, from 1995 to 2015 in Västerbotten county (see figure B Appendix). Vole numbers in spring were highest in 2007, decreased sharply in 2012 and remained low the following year (see figure B Appendix). Similarly, during autumn voles peaked in 2007 and exhibited annual lowest in 2012 (figure 5). On the contrary, highest number of occupied territories recorded in 2012 and lowest in 1995 (figure 5). According to regression analysis, percentage of occupied territories during the breeding period was unrelated with the number of voles preceding the breeding period (t=0.59, P=0.55).

To explore the effect of vole index on breeding success, as described above, the number of voles during spring and during the autumn of the preceding breeding year, incorporated into a generalized linear mixed effects model (GLMM) with binomial response variable (breeding success was coded as 1 {successful} or 0 {unsuccessful}), and territory ID as a random effect. I found evidence that breeding outcome is not significantly associated with the number of voles during the spring (table 3) but is significantly associated with the number of voles in the autumn preceding the breeding season (table 3). According to R^2, vole indices explained 15.1 % of the total variance. Results can be compared to Moss *et al.*

(2012) results, who reported a significant association between number of voles in previous autumn and annual population production (F= 6.30, P=0.021).

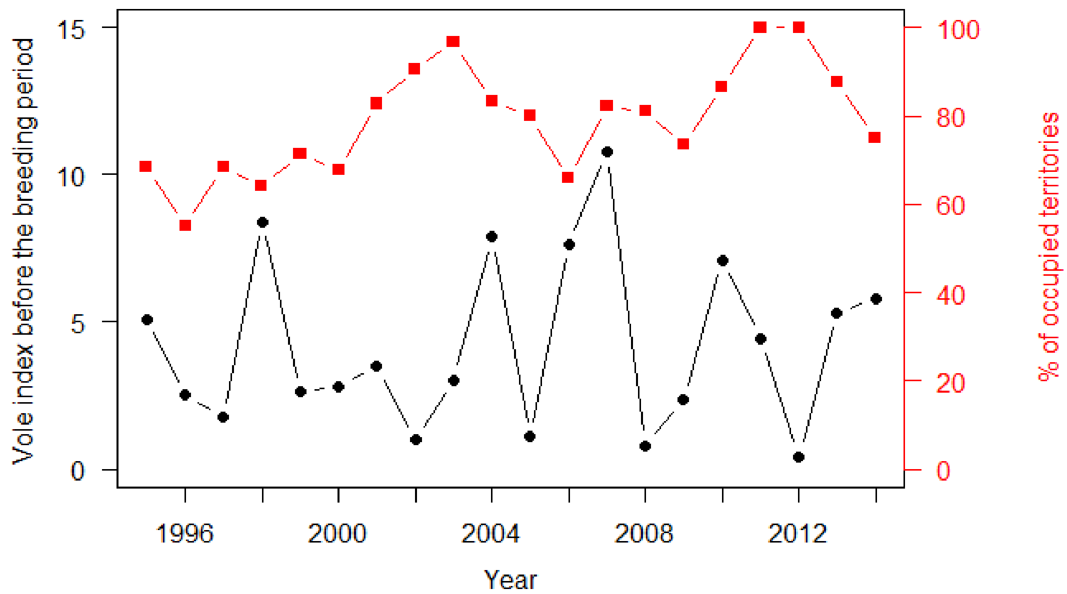


Figure 5. The number of voles per 100 trap nights (black line) during autumn before the breeding season in Västerbotten County and percentage of occupied territories from 1995 to 2015 (red line) in Northern Sweden.

Table 3: Generalized linear mixed effects model results, showing predictors of Golden Eagles breeding success for different values of vole density, during and preceding the breeding period in Västerbotten County in Northern Sweden (breeding attempts= 540, number of territories = 39). Asterisk (**) indicates significant p-values (< 0.001) and the numbers denote the parameters estimates.

Fixed effects	Estimate	SE	Z value	P value
Prey availability				
Intercept	-0.50	0.15	-3.25	< 0.01 **
Vole autumn density	0.23	0.09	2.50	< 0.01*
Voles spring density	0.09	0.09	0.89	0.38
Random effects	Variance	SD		
Territory	0.50	0.70		

3.2.3 Meteorological variables

Annual means of climate variables for two time periods were selected to represent weather conditions during the breeding season (February to April) and preceding the breeding season (December to February). Detailed information of mean values and standard error of climatic variables is listed in the Appendix (see table A). PCA analysis of all weather data revealed that the first two axes explained the 48 % of the total variance while highest variance contribution exhibited the average temperature preceding the breeding season (PB_avtmp) and minimum temperature during the breeding season (B_mintmp) (figure 6). The cumulative proportion of variance revealed that 12 of the 14 weather variables contained 99.9 % of the total variance which suggests that a global model slightly over fits the data and cannot be used (Burnham & Anderson, 1998).

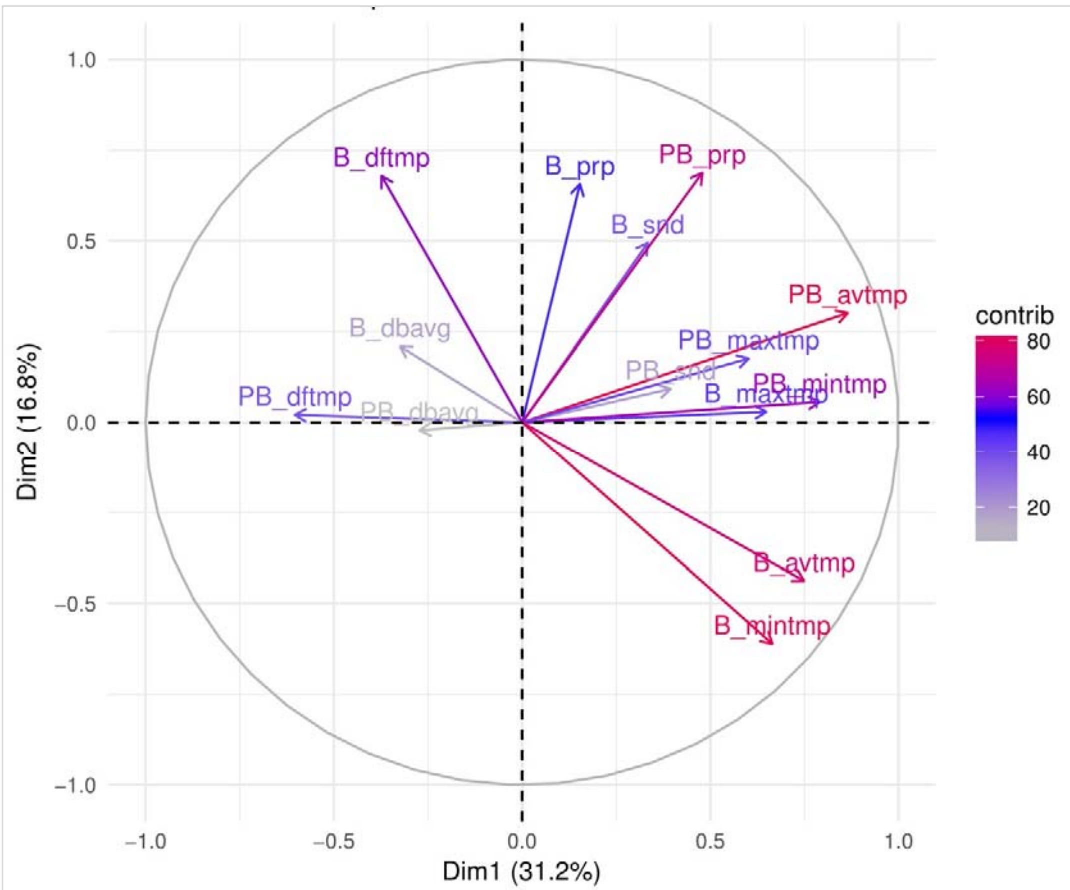


Figure 6: Variables factor map based on the principal component analysis (PCA) of weather variables during two periods. Preceding the breeding season (December to February {PB}) during the breeding period (February to April {B}). Variables are indicated by different names with first two letters indicating the period. Variance is symbolized using solid lines with arrows. Abbreviations are as follows: dftmp = difference between minimum and maximum temperature; prp = precipitation; snd= snow depth; max= maximum temperature, dbavg=number of days below the average temperature; avtmp= average temperature; mintmp = minimum temperature.

The variables of the two periods, incorporated to generalized linear mixed effects models as explanatory variables with binomial response variable (breeding success was coded as 1 {successful} or 0 {unsuccessful}) and territory as a random effect. For the two periods during and preceding breeding season, variable selection was performed using Akiake's Information Criterion approach and the final model was selected using a model average function. The most parsimonious model included variables from both periods and according to conditional R^2, it was able to predict the 24 % of the total variance of the breeding outcome (Nakagawa & Schielzeth, 2013) (table 4). Among the weather variables the highest effect, according to z value exhibited snow depth and precipitation before the breeding and average temperature during the breeding period (table 5).

Table 4. Best weather models ranked by AICc, containing climatic variables as predictors of the outcome of breeding performance of Golden Eagles in Northern Sweden. Most parsimonious model is shown in bold.

Model	**LogLik**	**df**	**AICc**	**Delta AICc**	**Weight**	**R^2**
27	**-333.44**	**14**	**695.68**	**0**	**0.99**	**0.24**
10	-344.49	8	705.26	9.58	0.01	0.17
16	-344.88	8	706.02	10.34	0.01	0.18

Table 5: Generalized linear mixed effects model results, showing predictors of Golden Eagles breeding success for different weather variables during and preceding the breeding period in Västerbotten County in Northern Sweden (breeding attempts= 540, number of territories = 39). Variables with the highest effect are shown in bold. Asterisk (***) indicates significant p-values (< 0.001), asterisk (**) indicates significant p-values (< 0.01) and the numbers denote the parameters estimates.

Fixed effects	**Estimate**	**SE**	**Z value**	**P value**
Weather data during (B) and preceding the breeding (PB)				
Intercept	-0.57	0.17	-3.39	< 0.01 ***
Maximum temperature (B)	-0.22	0.53	-0.41	0.68
Difference between maximum and m inimum temperature (B)	0.51	0.38	1.34	0.17
Snow depth (B)	0.17	0.17	1.00	0.31
Average temperature (B)	**0.56**	**0.17**	**3.23**	**<0.01****
Maximum temperature (PB)	-0.47	0.46	-1.02	0.30
Precipitation (PB)	**-0.80**	**0.22**	**-3.58**	**<0.01*****
Difference between maximum and m inimum temperature (PB)	0.30	0.43	0.69	0.48
Average temperature (PB)	0.74	0.73	1.02	0.30
Snow depth (PB)	**0.68**	**0.18**	**3.62**	**<0.01*****
Number of days below the average temperature (PB)	0.16	0.12	1.37	0.16
Random effects	**Variance**	**SD**		
Territory	0.60	0.77		

Having identified the relationship between breeding success topography, vole population fluctuations, and weather, I develop a series of alternative mixed effects models including different combinations of the three categories of the explanatory variables. Based on the ranking of AICc and AICc weights, the highest probability of being the best model explaining Golden Eagles' breeding success, had the model 8 (table 6) which included all the explanatory variables (table 7). The model was able to explain the 29 % of the total breeding variance (table 6).

Table 6. Best models ranked by AICc, containing the variables explain the outcome of breeding performance of Golden Eagles in Northern Sweden. Most parsimonious model is shown in bold. W, P and T are abbreviations for weather, prey and topographic respectively Asterisk (*) indicates

Model	intercept	W	P	T	LogLik	df	AICc	Delta AICc	Weight	R^2
08	**-0.68**	*	*	*	**-312.71**	**20**	**665.43**	**0**	**0.991**	0.29
10	-0.49		*	*	-332.74	6	675.96	10.53	0.005	0.19
05	-0.52	*		*	-332.15	11	677.16	11.73	0.003	0.18

Table 7: Generalized linear mixed effect model results, of the best model in table 6 showing predictors of Golden Eagles breeding success for different variables during and preceding the breeding period in Västerbotten County in Northern Sweden (breeding attempts= 540, number of territories = 39). Variables with the highest effect are shown in bold. Asterisk (***) indicates significant p-values (< 0.001), asterisk (**) indicates significant p-values (< 0.01) and the numbers denote the parameters estimates.

Fixed effects	Estimate	SE	Z value	P value
Model 27				
Intercept	-0.68	0.17	-3.29	< 0.01 ***
slope	0.04	0.14	0.29	0.77
elevation	0.02	0.16	014	0.88
Voles index autumn	0.39	0.20	1.953	0.05
Voles index spring	0.20	0.14	0.28	0.13
Maximum temperature (B)	-0.29	0.58	-0.49	0.61
Difference between maximum a nd minimum temperature (B)	0.79	0.43	1.82	0.06
Snow depth (B)	0.20	0.18	1.13	0.25
Average temperature (B)	**0.39**	**0.18**	**2.09**	**0.03**
Maximum temperature (PB)	0.43	0.63	0.68	0.49
Precipitation (PB)	**-0.79**	**0.21**	**-3.68**	**<0.01*****
Difference between maximum a nd minimum temperature (PB)	-0.41	0.53	-0.77	0.43
Average temperature (PB)	0.05	0.15	0.33	0.74
Snow depth (PB)	**0.50**	**0.19**	**2.659**	**<0.01*****
Number of days below the average temperature (PB)	0.05	0.15	0.33	0.74
Random effects	**Variance**	**SD**		

Territory	0.65	0.80

3.3 Survival

Ringing efforts of the Bird Ringing Center of the Stockholm Museum of Natural History, between 1918 and 2015, resulted in 2562 ringed Golden Eagles and 205 recovered individuals (table 8). Ringing included both nestlings and fledged eagles, however, the 90% (n= 2317) of ringed individuals were nestlings. Recovery rate is calculated to be 8.6 % (n= 205), higher than the recovery rates reported by the U.S Fish and Wildlife Service and lower than that reported by the Finnish Ministry of Environment (5.6% and 33.2 % respectively) (Saurola *et al.*, 2013; Millsap *et al.*, 2016). The age of the oldest recovered individual was estimated to be 21 years old, which is younger than the published data (32 years old) (Fransson & Pettersson, 2001). Most of the dead individuals were found in Sweden (n=179) while recoveries were also reported in Norway (n= 10), Finland (n=3), Denmark (n= 2) and Russia (n=1).

Table 8: Recovery statistics for Golden Eagle in Sweden from 1918 to 2015.

Total number of ringed individuals	2562
Number of ringed nestlings	2317
Number of ringed fledged individuals	135
Total number of recovered individuals	205
Recovery rate (N^o recovered/ N^o not recovered)	8.6 %
Oldest Eagle recovered	21
Second Oldest Eagle	19

The proportional recovery rate (number recovered/ number not recovered) declined with age (figure 7), was greater for the first age classes (0 to 2 years old) than all other age classes (t_{21} = 3.527, P=0.001). Cumulative proportion of recoveries since the ringing event indicated that 51 % of the Golden Eagles will die 2 years after ringing, 81.9% by 8 years and 95.2% 14 years post ringing. According to the logistic regression analysis in the age of 22 only 0.8% of golden eagles will be alive (Estimate= 0.24±0.016, t=14, figure 8).

I estimated the survival rates using the recovery data from 1990 to 2015. The data set included 2.095 ringed individuals and 158 recoveries. The recovery rate from 1990 to 2015 was 8.2%. Using the dead recovery model with Seber parameterization in Program Mark (Cooch & White, 2015), I evaluated 17 candidate models that included age, time, linear and logit time trends in survival (table 9) with constant and non- constant recovery probability. The general model showed an adequate fit to the data (Bootstrap GOF, p= 0.83) and since there no indications of overdispresion, $\hat{c}$ was set to 1.00. Based on Akaike information criterion the most parsimonious model included 4 age classes and constant recovery probability. According to the model, survival gradually increased from 0.79 in the hatching year to 0.89 after the third year (figure 9, table 10). Table 10 illustrates the survival estimates for each age class with 95% confidence intervals. Overall mean survival from 90s to 2015 was estimated to be S= 0.86 and SE=0.0169 (representing total variance) and recovery rate was 0.1.

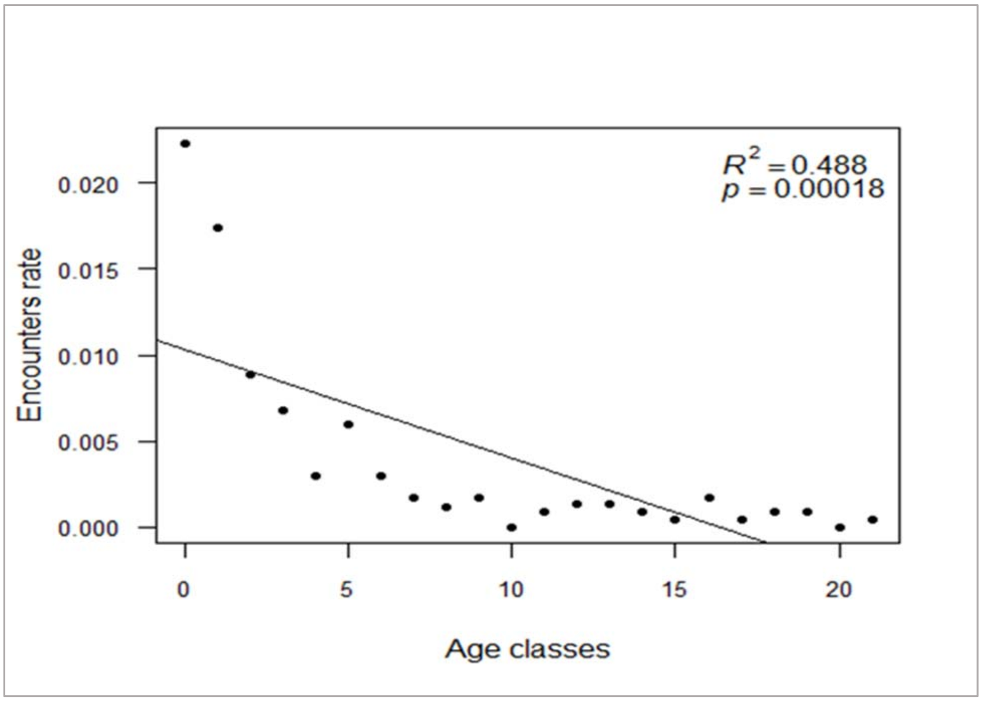


Figure 7. Proportional recovery rate (No individuals recovered/ No individuals not recovered) by age class of Golden Eagles ringed as nestlings between 1918 to 2015. The rate is higher for individuals in the two first age classes.

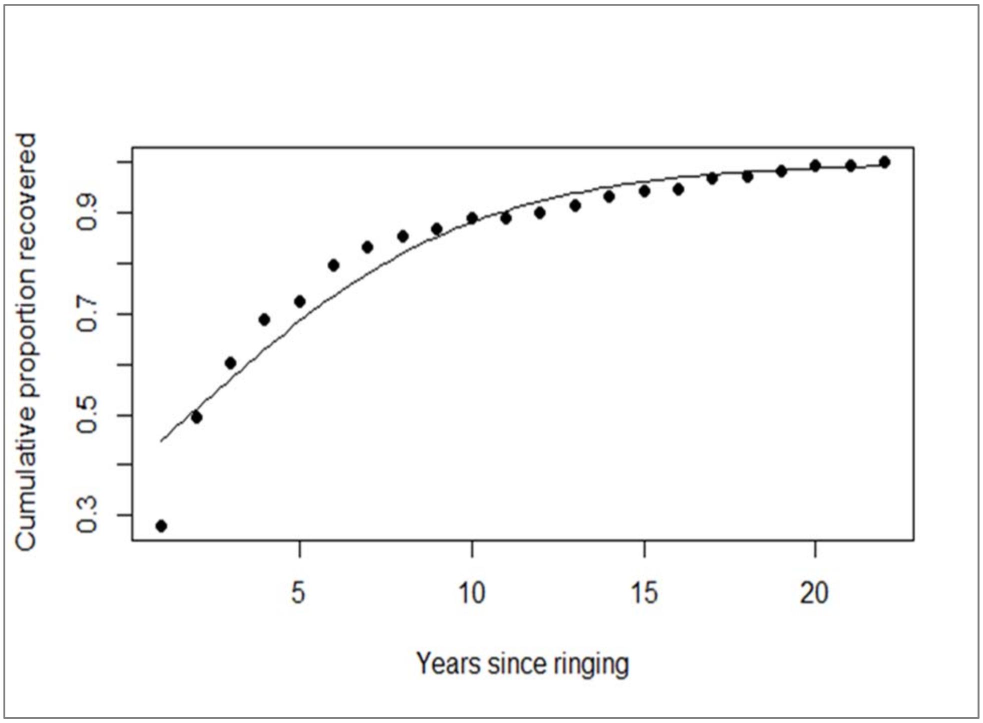


Figure 8. Curve based on prediction from a logistic regression model of the cumulative proportion of recoveries in years since the first ringing occasion. Maximum age predicted from the model (p= 0.994, Age = 22).

In order to see the magnitude of within and among year variation I ran a variance component analysis of the overall data, parameterized for a linear trend. Output of the analysis is illustrated in figure 10. The estimate of the intercept was β_1= 0.91 and the slope of the decline over time was (β_2= -0.003474). The Golden Eagle population even though exhibited high overall survival rate, through the years, there is evidence of a gentle decrease line (figure 10). Survival estimates for each year are listed in the Appendix (see table B).

Table 9. Details of candidate models ranked in ascending order of the Delta AICc values. The models evaluated to the survival and recovery probabilities of golden eagles, based on ringing recoveries from 1990 to 2015. The data analyzed using the Seber parameterization in Program Mark.

Models	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Number of Parameters**
S(age4)r(.)	**1.785,76**	**0**	**0.41**	**1**	**5**
S(age3)r(.)	1.786,83	1.06	0.24	0.58	4
S(age5)r(.)	1.787,74	1.98	0.15	0.37	6
S(age6)r(.)	1.788,53	2.77	0.10	0.24	7
S(.)r(.)	1.790,33	4.57	0.04	0.10	2
S(Clogit)r(.)	1.791,028	5.263	0.03	0.07	7
S(age4)r(t)	1.797,922	12.15	0	0	30
S(.)r(t)	1.803,519	17.75	0	0	27
S(t)r(.)	1.804,135	18.37	0	0	27

S(age2 + t/-)r(.)	1.818,385	32.62	0	0	28
S(linear)r(t)	1.825,739	39.97	0	0	25
S(age2 + t/t)r(.)	1.831,887	46.12	0	0	52
S(t)r(t)	1.838,937	53.17	0	0	49
S(age3 + t/t/.)r(.)	1.843,317	57.55	0	0	53
S(trend) r(.)	1.845,289	59.52	0	0	2
S(mean) r()	1.851,503	65.73	0	0	25
S(age4 + t/t/t/.)r(.)	1.871,253	85.48	0	0	75

The most parsimonious model (based on ĉ= 1) appears in the first row and is shown in bold. Notation characters are as follows: S= survival; r= recovery probability; t = time dependence; age= the age covariate and number indicates each age class. Clogit= not strictly linear structure of survival; linear=linear structure; trend=simple linear trend; mean=mean survival. Symbols are as follows: = constant over time; + = additive effect; / = separates different age classes

Table 10. Estimates of the annual survival rates for Golden Eagles from 1990 to 2015 based on the results of the most parsimonious model in table 9.

Annual Survival	Estimate	SE	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Hatching Year	0.79	0.029	0.71	0.85
Second Year	0.81	0.036	0.73	0.88
Third Year	0.87	0.030	0.78	0.92
After Fourth Year	0.89	0.022	0.82	0.94
Recovery rate	0.101	0.012	0.084	0.134

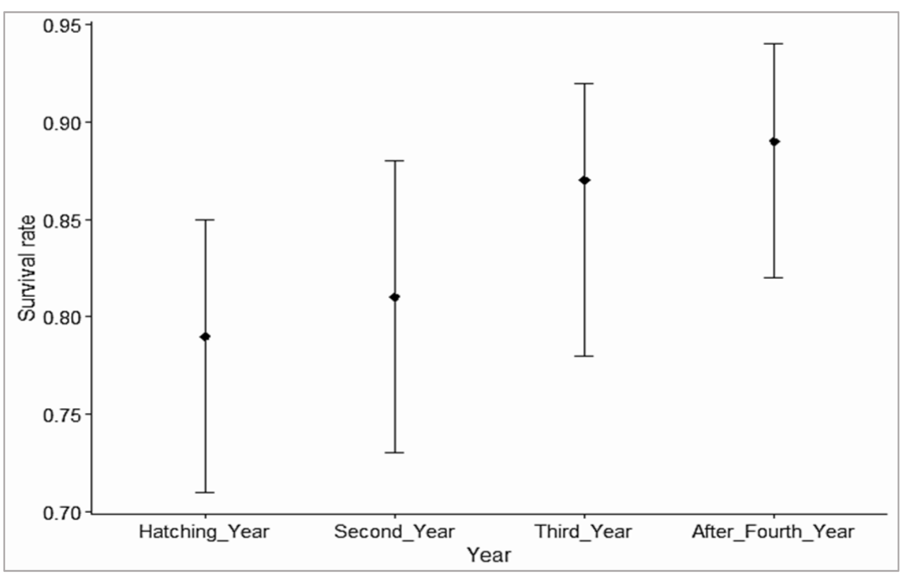


Figure 9. Plot of the survival estimates for Golden Eagle with confidence intervals for four age classes according to model estimates in table 10.

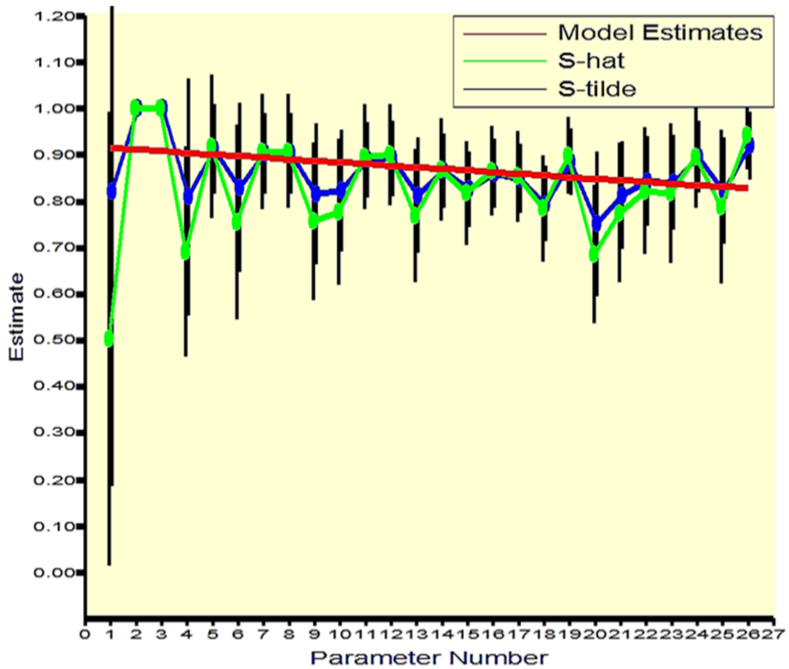


Figure 10. Plot of the survival estimates (S-hat) from 1990 to 2015 (green line), the "shrinkage" estimates (S-tilde) (blue line) and the mean survival estimate β=0.86 (red line). Shrinkage estimate is derived by the survival estimates by the removal of sampling variation. Parameter number corresponds to each year of survival analysis (see Appendix Table B).

3.4 Population projection matrix

Using derived estimations of general survivorship from entire Sweden (table 10) and mean fecundity of the population in Northern Sweden (see part of Golden Eagle breeding performance), I paremeterise a post-breeding stage-based, Lefkovitch matrix model (matrix 1) (Lefkovitch, 1965; Caswell, 2001). Based on the population matrix, the asymptotic finite rate of increase (λ) of Golden Eagle was estimated as 1.1 which indicates growth in the population.

Stable age population structure that emerged from the matrix, revealed that if the projection matrix does not change over time (demographic rates (S, F) remain constant), the Golden Eagle population will eventually be composed of 22.71 % individuals one-year-old, 16.27% two-years-old, 11.96 % three-years-old, and 49.06 % over four years old (figure 11).

Sensitivity and elasticity of each transition revealed that that the most importance transition exhibited by Eagles is S_3 (table 11), surviving from stage 3 to stage 4. Elasticities of the three first age classes appears to be equally important (table 11). The same proportional change in any of the three first age class (S_1, S_2, S_3) will result in approximately the same change in growth rate, while changes of survival after the four years of age will have a much higher effect on population growth. Those values provide a proportional change of demographic rates under the assumption that the population is at equilibrium face (Caswell, 2001) and there is no influence of natural phenomena and other anthropogenic factors.

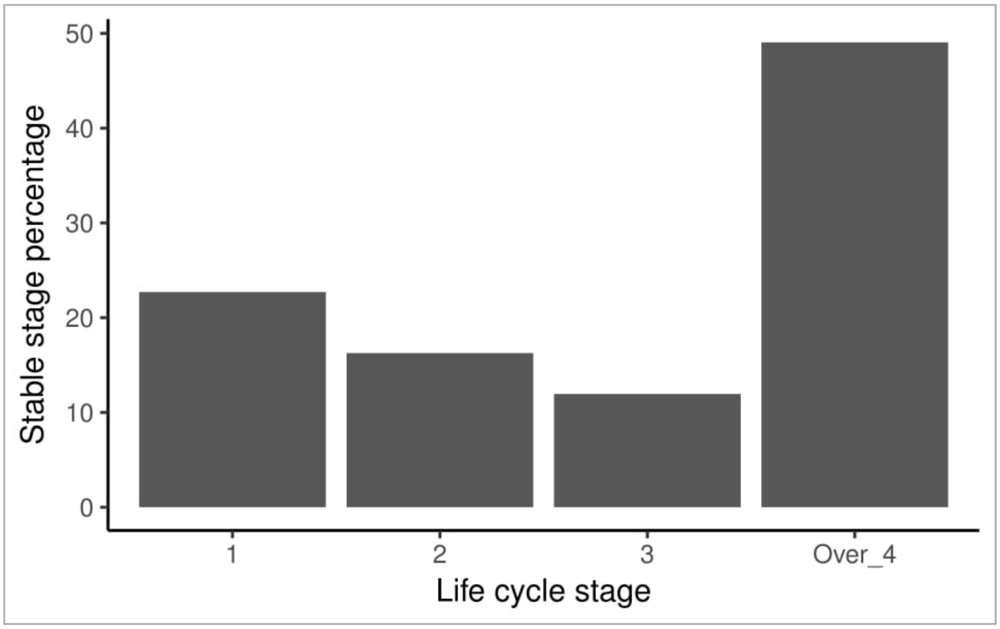


Figure 11. Percentage of each life cycle stage of Golden Eagle population that emerged from the matrix 1, if demographic rates (S, F) remain constant over time.

By using the estimated number or Golden Eagle individuals in 2015 (Naturvårdsverket, 2015) and based on stable age distribution results (matrix 1). I projected the population growth of each age class for 5 years (figure 12) without incorporated influence of anthropogenic and environmental factors.

$$\begin{pmatrix} N0, t+1 \\ N1, t+2 \\ N2, t+3 \\ N3, t+4 \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0.51 \\ 0.79 & 0 & 0 & 0 \\ 0 & 0.81 & 0 & 0 \\ 0 & 0 & 0.87 & 0.89 \end{pmatrix} * \begin{pmatrix} 311 \\ 223 \\ 163 \\ 662 \end{pmatrix} \qquad \text{(matrix 1)}$$

Table 11. Matrix elements, values elasticities and sensitivities

Element	Value	Elasticity	Sensitivity
F	0.51	0.122	0.1222
S_1	0.79	0.122	0.1702
S_2	0.81	0.122	0.2316
S_3	0.87	0.122	0.2934
S_4	0.89	0.512	0.0875

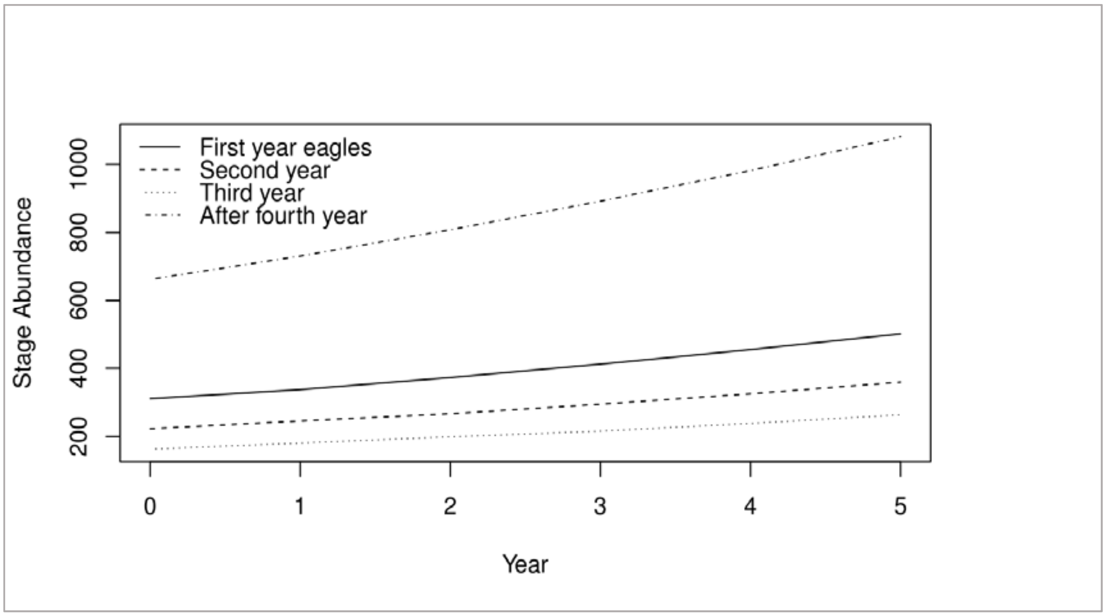


Figure 12. Projected population growth in 5 years separated from each population stage of Golden Eagles in part of the population from the eastern part of Västerbotten, Northern Sweden under the assumption that demographic parameters remain stable.

4 Discussion

Using citizen science data, aimed to provide new details on Golden Eagle population ecology in Sweden. I used Golden Eagles' breeding data from Northern Sweden, provided from regional ornithological groups, to explore how breeding performance fluctuates through space and time. Additionally, those data used to develop a number of predictive models of the potential breeding outcome and explore if topography, vole populations fluctuations and weather can predict the outcome of reproduction. I also demonstrate a formerly undocumented aspect of Swedish Golden Eagle population ecology, providing an insight on survival rates, stable age distribution, elasticities, and sensitivities of each age class using ringing data provided by the National museum of Stockholm.

My results showed that breeding performance of Golden Eagles in Northern Sweden exhibited high variation both at spatial and temporal scales from 1995 to 2015. Long term fecundity was 0.51 (young per pair) while 71.7 % of the breeding territories exhibited an average productivity of 52.8 ± 27.5 (nestlings per 100 breeding attempts). I found that vole density, snow and precipitation preceding the breeding period and average temperature during the breeding had significant effects on the breeding outcomes. Vole population fluctuations, weather and topography explained 29% of the total variation in the data, which indicates that additional parameters may affect the breeding outcome, and not included in the analysis (e.g. habitat features, forestry activities and other anthropogenic factors). Based on the ringing data, mean survival of the Swedish population from 1990 to 2015 was estimated to be 0.86 of older individuals exhibiting higher survivorship (0.89) from the first age class (0.79). Stable age distribution of the population indicates that the population consists in 22.71 % one-year-olds, 16.27% two-year-olds, 11.96 % three-year-olds, and 49.06 % over four years old individuals. The population exhibits a growth rate of 1.1, while changes of the survival of individuals after the four years will have a much higher effect on population growth.

Several studies have examined Golden Eagle reproductive performance in a variety of geographical areas and conditions. However, different parameters and definitions have been used in each study to describe the breeding demography, and for that reason, comparisons must be interpreted with caution. Long-term fecundity of Golden Eagles in my study area (0.51 young per pair) was similar but lower than those reported in other studies of the Swedish population. Moss *et al.*, (2012) reported 0.64 young per territory while Tjernberg (1983a) reported 0.68 nestlings per occupied territory. However, it should be mentioned that my results are limited to a given dataset and not representative all known nesting territories in Northern Sweden. Similarities have been found with studies in other countries. Specifically, in Finland Fasce *et al.*, (2011) reported that Golden Eagles produced on average 0.42 young per surveyed pair; (Millsap *et al.*, 2016) in the continental U.S. observed on average of 0.54 young per occupied nesting territory; Pedrini & Sergio, (2001) report 0.59 fledged young per pair in the Italian Alps; and Mcintyre & Schmidt, (2012) reported that population production was 0.4 fledglings per occupied nesting territory in Denali National Park in Alaska.

According to the spatial analysis, 71.7 % of the territories seem to exhibit average productivity, 15.5% high and 12.8 % very low. High-quality territories produced more nestlings through time and exhibited less variation in breeding success. Multidimensional scaling revealed no spatial aggregation between territories, while generalized linear models revealed that topography did not predict the breeding outcome. This can be explained by the fact that Sweden and study area, in particular, are not characterized by extreme variation in topographic features. As other studies have pointed, territory quality is correlated with habitat diversity, with the best territories being the most or least diverse, and landscape heterogeneity to be more likely to affect territory quality and productivity (Penteriani *et al.*, 2003; Navarro-López & Fargallo, 2015). Importance of landscape characteristics, revealed by Moss *et al.*, (2014), who using Golden Eagles nesting observations in Northern Sweden, revealed that proportion of clear cuts can have a significant effect on the home range of Golden Eagles which affect food supply thereby affecting the breeding outcome. According to a recent publication regarding habitat selection, topography can have a significant effect on habitat selection (Singh *et al.*, 2016). A supplementary analysis is needed to explore how different landscape characteristics and forestry activities determine the productivity of a territory and how those can be incorporated into the management of Golden Eagles in Northern Sweden.

As in other studies of Golden Eagles (Tjemberg, 1983; Watson *et al.*, 1992; Bates & Moretti, 1994; Steenhof *et al.*, 1997; McIntyre & Adams, 1999; Moss *et al.*, 2012; Schweiger *et al.*, 2015), prey availability was an important factor influencing breeding success in Northern Sweden. Increased food availability during the breeding period is vital because females produce and incubate their eggs. My findings support that reproductive outcome was tied closely to vole index (number of voles per 100 trap nights) in autumn and less related to vole index in spring. Vole index explained 15.1 % of the breeding success variation. This finding is consistent with those of (Moss *et al.*, 2012), who found that population production was significantly related to indices of primal prey and vole abundance in the previous autumn. Unfortunately, population data from other prey species were not available and did not use in my analysis.

However, the number of occupied territories was unrelated to vole abundance. This is consistent with (Watson *et al.*, 1992; Steenhof *et al.*, 1997; Moss *et al.*, 2012), who found that unfavorable conditions (low prey availability) do not limits the number of territorial birds that attempted to breed. This result also contrasts with older predictions and theories behind raptors fluctuations (Galushin, 1974; Tjemberg, 1983) which suggested that raptors are in synchrony with prey numbers. Based on the fact that Golden eagle is a long – lived species (21 years old was the oldest ringed individual recovered), there is little breeding pressure, individuals prefer to occupy territories even if prey numbers are low and breeding might fail (Newton, 2010).

Based on the data available, in general, reproductive output was influenced by prey availability preceding the breeding period and weather. Among the climatic variables, snow depth and precipitation preceding the breeding season and average temperature during the breeding season had highest influence on breeding success (see table 5). This is consistent with Watson, (2010) who states that "variation in breeding performance can be accounted for differences in food supply and weather conditions preceding the breeding season or the previous winter, with weather moderating the direct link between breeding success and food supply". Tjernberg (1983b) studied nesting patterns of Golden Eagle and observed that precipitation might have negative effects on breeding outcome because high amounts of water can make tree nests heavier and susceptible to damage. Greater support is needed from the surrounding branches which increase with the age of the tree. Apart from the climate preceding the breeding season, the average temperature during breeding also influenced eagle reproduction. Average temperature during brood rearing was positively related to the probability of a successful breeding attempt. Lehikoinen *et al.*, (2010) examining the effects of climate in four boreal nocturnal raptors found that increasing temperature and snow depth directly affects the timing of the breeding, presumably by affecting the number of voles. Hörnfeldt, (2004) argues that winter severity may negatively affect vole numbers by increasing predation and causing decreased food availability when food hiding places are not accessible due to the snow. It is evident that weather might have direct effects on reproduction and indirect influencing prey abundance and behavior. According to models, weather conditions preceding the breeding season and average temperature during the breeding season, along with differences in vole density and topography accounted for the 29% of the breeding variation. Weather conditions along with food supply form a mechanism that has direct effects on breeding success, a finding also supported by the several researchers working with Golden Eagle through the years (Steenhof et al., 1997; Watson, 2010; Mcintyre & Schmidt, 2012).

However, the low R-square of the statistical model for variables predicting breeding performance indicates that there are more variables that are significantly affecting the breeding outcome and not included in this study. For instance, we cannot rule out that possible lead exposure influenced breeding performance because it may have affected the ability of birds to hunt and obtain food for them and the new born nestlings (Helander *et al.*, 2009).

Annual survival of Golden Eagles in Sweden was lower for the first-year individuals (0.79) and higher for the individuals older than three years old (0.89). Recovery rates of ringed individuals indicate that 0-1 and 1-2 age classes experience the largest proportional decrease in survival. My result is similar with Millsap *et al.* (2016) estimation of Golden Eagle survival across the Western U.S. who reported that older individuals had higher survivorship (0.87) from the first age class (0.70). On the contrary, Nygård *et al.*, (2016) reported lower survival for the juvenile Golden Eagle in Norway (0.58) and stated that individuals hatched in the interior of the country exhibited higher survival than those in the northernmost islands. Causes of death for the recovered individuals were unknown and it was impossible to be able to determine if mortality is natural or human caused. Naturally, it is highly possible that Eagles aged 1 to 2 years old not to have the same foraging efficiency as older age classes and die from starvation (Watson, 2010), something that is supported by my results given the fact that 50% of the recovered individuals aged between 1 to 2 years old. However, Golden Eagles in Sweden face several threats of human-induced mortality which includes collisions with power lines, trains, and automobiles to lead poisoning and human persecution. It was interesting to see that according to Nygård *et al.*, 2016) illegal hunting was the number one cause of mortality of juvenile Eagles in Northern Sweden.

Stable age distribution of the Golden Eagle in Sweden states that the highest number of individuals are aged more than 4 years old while less is the number of juveniles aging three years old. According to the elasticities of the population matrix, the most influential transition is the one from 3 years old to 4 years old and sexually maturity while the most influential stage in determining growth rate is the stage older than four-year-old. According to the Swedish parliament, Sweden aims for a population of minimum 150 breeding pairs per year (Riksdagen protokoll 2013/14:43). In order to maintain a viable population, and secure a stable or increasing growth rate, it is important to protect individuals that forming pairs and establish territories or are old enough to reproduce and reduce effects of several causes like collisions and lead poisoning that pose a threat for their survival and breeding success. However, with the resent decisions of the Norwegian parliament for change the legislation regarding Golden Eagles, which will result in more than 200 individuals to be killed (see Norsk Ornitologisk Forening, 2016), is a question how the population dynamics of Swedish population also will be affected.

5 Conclusion

Based on a limited dataset of citizen- science data, Golden Eagle's reproductive performance in the Northern Sweden fluctuates both in space and time. Breeding success seems to be affected mostly by weather and vole density and topography does not appear to affect the breeding outcome. All the studied variables managed to predict the 29% of the total breeding variance which questions the size of the effect of habitat features and human-induced disturbance to Golden Eagles reproductive performance. Survival rates of the Swedish population were similar with those reported in the U.S., with older individuals exhibiting higher survivorship from the first age class. The population exhibits a positive growth rate with 49% of the individuals aging over 4 years old. The most influential transition for the population is the one from 3 years old to 4 years old, while individuals older than 4 years old contribute more to population growth since they are sexually mature and are being able to reproduce. The knowledge gaps regarding the factors that may drive nest- success patterns and the ongoing increase of human-based influences, lead to the conclusion of the importance of additional analysis and immediate attention to determine the size of the effect of human disturbance into the Swedish Golden Eagle population ecology and how those affect management goals and decisions.

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7 Appendix

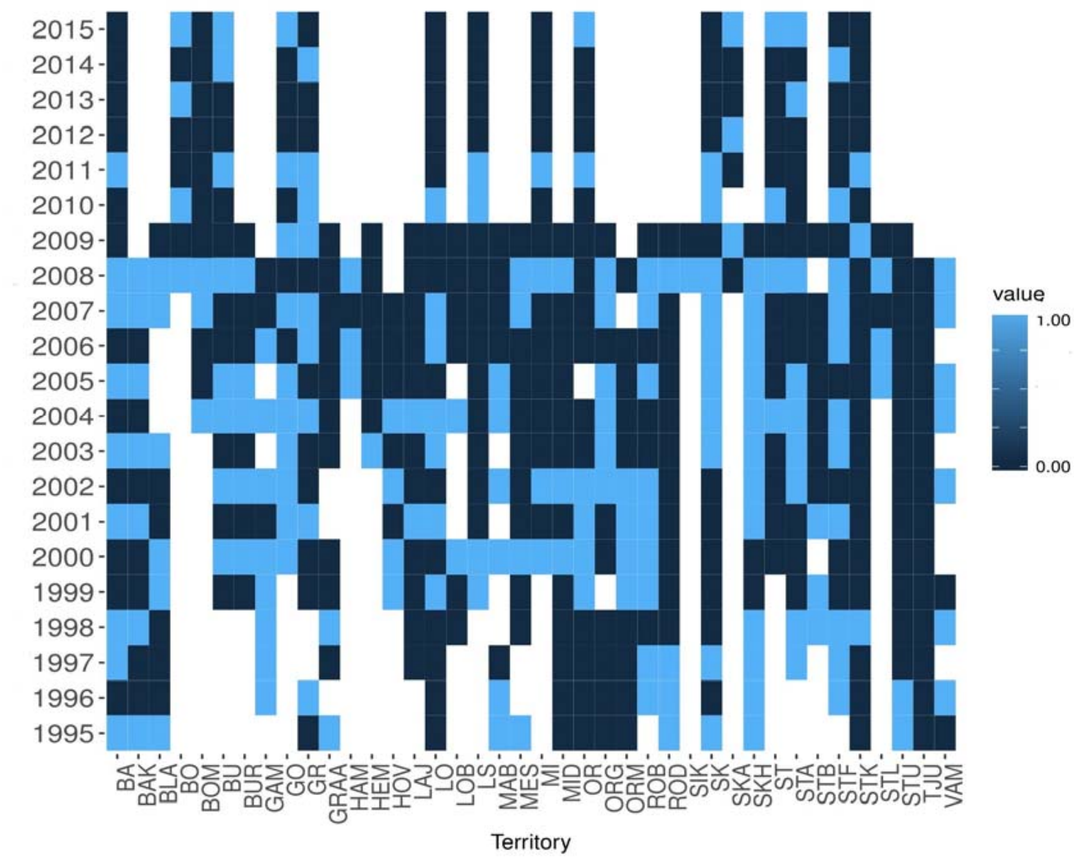

Figure A. Patterns of breeding success from 1995 to 2015 for reported nesting territories (n=39) in Northern Sweden. Dark blue color indicates failed breeding attempt while light blue successful breeding attempt.

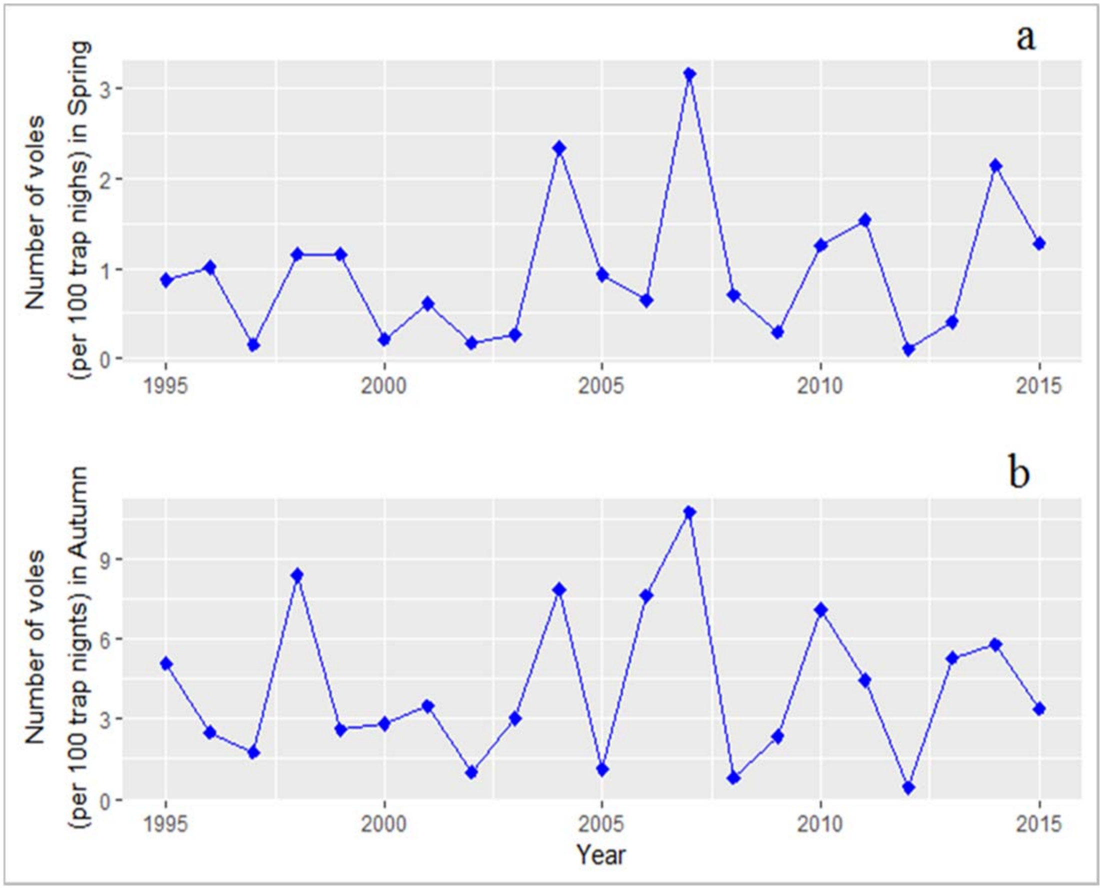

Figure B. The number of voles per 100 trap nights (bank voles (Myodes glareolus) and field voles (Microtus agrestis)) in (a) spring and (b) autumn from 1995 to 2015 in Västerbotten County, Northern Sweden.

Table A. Mean values and standard error of the climatic variables used to describe weather conditions from 1995 to 2015 in Västerbotten county in Northern Sweden.

Variable	**Mean**	**St. error**
December – February		
Days below average	13.99	1.01
Average temperature	-9.45	2.34
Snow depth	186.10	0.11
Min temperature	0.57	3.76
Max temperature	-25.69	1.60
Difference between max and min temperature	1.34	3.32
Snow days	27.02	15.14
Precipitation	42.32	11.55
February April		
Days below average	13.95	1.06
Average temperature	-4.56	1.96
Snow depth	0.73	0.20
Min temperature	-15.21	2.99
Max temperature	3.73	1.48
Difference between max and min temperature	18.94	2.75
Snow days	186.10	15.14
Precipitation	33.34	10.39

Table B. Survival estimates (S-hat) and shrinkage estimates (S-tilde) from 1990-2015. Shrinkage estimate is derived by the survival estimates by the removal of sampling variation. Parameter number corresponds to each year of survival analysis.

Parameter	Year	S-hat	SE (S- hat)	S-tilde	SE (S -tilde)
1	1990	0.50	0.24	0.78	0.06
2	1991	1	0	1	0
3	1992	1	0	1	0
4	1993	0.69	0.11	0.78	0.05
5	1994	0.91	0.07	0.89	0.04
6	1995	0.75	0.10	0.81	0.05
7	1996	0.90	0.06	0.89	0.04
8	1997	0.90	0.06	0.89	0.04
9	1998	0.75	0.08	0.80	0.05
10	1999	0.77	0.08	0.81	0.05
11	2000	0.89	0.05	0.88	0.04
12	2001	0.89	0.05	0.88	0.04
13	2002	0.76	0.07	0.81	0.04
14	2003	0.86	0.05	0.86	0.04
15	2004	0.81	0.05	0.82	0.04
16	2005	0.86	0.04	0.85	0.03
17	2006	0.85	0.05	0.84	0.03
18	2007	0.78	0.05	0.79	0.04
19	2008	0.89	0.04	0.88	0.03
20	2009	0.68	0.07	0.76	0.04
21	2010	0.77	0.07	0.82	0.04
22	2011	0.82	0.07	0.85	0.04
23	2012	0.81	0.07	0.85	0.45
24	2013	0.89	0.05	0.90	0.03
25	2014	0.78	0.08	0.83	0.04
26	2015	0.94	0.03	0.92	0.02

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