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Large grazing birds and crop damage

Investigating spatial and temporal patterns to guide management practices

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Abstract

Populations of geese, swans and cranes (i.e., large grazing birds) are increasing in Europe and North America, raising conflicts between conservation and farming interests when, foraging in agricultural fields (often in the vicinity of wetlands), cause yield loss for farmers. The aim of this thesis is to increase the understanding of spatial and temporal patterns of large grazing birds and their crop damage to improve future management practices. At the national level, crop damage was found to be positively related to national estimates of bird abundance. At the regional level, crop damage followed seasonal patterns associated with vulnerable stages of crops and the crop selection by the culprit species. Seasonal patterns remained consistent over the years but differed across the country, relating to the spatial distribution of different crops and culprit species. Large grazing birds showed a clustered spatial distribution across the country with distinct hotspots of high abundance. The spatial variation in abundance of large grazing birds were largely reflected in a corresponding spatial pattern of crop damage as reported by farmers. The complexity of the system (e.g., weather dependence, opportunistic behaviour of the birds) and the coarse temporal and spatial resolution of the available data probably caused model predictions of crop damage to be characterized by large uncertainties. My results suggest that it is necessary to integrate management strategies across different spatial and temporal scales when implementing current and future management actions for crop damage prevention.

Keywords: agriculture, *Anser*, *Branta*, conservation conflicts, crop protection, *Cygnus*, *Grus*, human-wildlife interactions, wildlife damage management

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Sammanfattning

Populationerna av gäss, svanar och tranor (härefter stora betande fåglar) ökar i Europa och Nordamerika, ökningen kan orsaka en intressekonflikt mellan naturvård och jordbruk, ofta i närheten av skyddade våtmarker, eftersom fåglarna födosöker på jordbruksmark och därmed orsakar, skördeförluster för lantbrukare. Syftet med den här avhandlingen är att öka kunskapen om hur stora betande fåglar och de skador de orsakar fördelar sig geografiskt i Sverige och över tid. På nationell nivå fann jag att nivåerna av skador på grödor ökade med ökade antal av fåglarna. På regional nivå var grödoskadorna säsongsberoende, de påverkades av arternas val av grödor och hur känsliga grödorna var för skador vid den tidpunkten. Omfattning av grödoskador skilde sig över landet beroende på tillgången på favoritgrödor för respektive art samt fåglarnas utbredning i landet under säsongen. Dessa geografiska säsongsskillnader var relativt konstanta över åren. På nationell skala var fördelningen av stora betande fåglar mycket varierande, med vissa områden med mycket stora antal. Risken för grödoskador ökade i områden med höga antal stora betande fåglar. Komplexiteten i systemet (t.ex. väderberoende och fåglarnas opportunistiska beteende) och den låga upplösningen av data innebar dock att sambanden mellan antal fåglar och skador på grödor karaktäriserades av stor osäkerhet. Min avhandling visar på vikten av att integrera förvaltningsstrategier över flera skalor, både över tid och rum, för att utveckla förebyggande strategier och därmed även konflikten mellan naturvård och jordbruk.

Nyckelord: *Anser, Branta, Cygnus,* förvaltning*, Grus,* jordbruk*,* naturvårdskonflikter, skadeförebyggande, vilt

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Dedication

Pel papa i la mama,
La mama i el papa,
I en Magnus,
I en Xan

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Monträs-Janer, T., Knape, J., Nilsson, L., Tombre, I., Pärt, T. & Månsson, J. (2019). Relating national levels of crop damage to the abundance of large grazing birds: Implications for management. Journal of Applied Ecology, 56 (10), 2286-2297.

II. Monträs-Janer, T., Knape, J., Stoessel, M., Nilsson, L., Tombre, I., Pärt, T. & Månsson, J. (2020). Spatio-temporal patterns of crop damage caused by geese, swans and cranes – implications for crop damage prevention. Agriculture, Ecosystems and Environment, 300, 107001.

III. Monträs-Janer, T., Bakka, H., Knape, J., Ruete, A., Kačergytė, I., Nilsson, L., Tombre, I., Månsson, J. & Pärt, T. Species distribution models built from opportunistic presence-only data reveal seasonal potential hotspots for geese and cranes (manuscript)

IV. Monträs-Janer, T., Bakka, H., Knape, J., Ruete, A., Nilsson, L., Tombre, I., Pärt, T. & Månsson, J. Relating spatial patterns of bird abundance, crop availability and crop damage caused by large grazing birds to reveal areas of high risk of damage (manuscript).

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The contribution of Teresa Montràs-Janer to the papers included in this thesis was as follows:

I. Main author. Designed the study together with JM, TP and IT. Analyzed the data with support of JK. Wrote the manuscript with contributions from co-authors.

II. Main author. Designed the study with contributions from co-authors. Analyzed the data with support of JK and contribution from MS. Wrote the manuscript with contributions from co-authors.

III. Main author. Designed the study with contributions from co-authors. Collected GIS data with support of AR. Analyzed the data with support and contributions from HB and JK. Wrote the manuscript with contributions from co-authors.

IV. Main author. Designed the study with contributions from co-authors. Collected GIS data with support of AR. Analyzed the data with support and contributions from HB and JK. Wrote the manuscript with contributions from co-authors.

1. Introduction

Human-wildlife interactions have existed throughout human history when competing for habitat and resources (Conover 2002; Nyhus 2016). Mankind has become a dominant force in nature. We have altered landscapes, changed ecosystem structures and eradicated species, all of which have resulted in a loss of biodiversity (Woodroffe et al. 2005; Waters et al. 2016). Since the 19th century, human population worldwide has increased from 1 to 7.8 billion people (United Nations www.un.org [21-July-2020]), empowering changes associated with intensification of farming, fishing, deforestation and fossil fuel combustions. Combined, these activities have had a big impact on ecosystems and ecological processes on the planet (Waters et al. 2016). As people have increasingly taken over natural habitats, interactions with wildlife have increased, sometimes causing damage to human livelihoods and unfolding into conservation conflicts (Woodroffe et al. 2005). Historically, when wildlife had a negative repercussion on human livelihoods, eradication was a common solution (Nyhus 2016). Nowadays, the need for conservation and coexistence between humans and wildlife is recognized (Mace 2014) leading to a call for knowledge of the ecological relationships and a better understanding of the mechanisms behind the impact of wildlife on human assets (Conover 2002).

One example of a drastic system change is the agricultural revolution that has reshaped agricultural landscapes worldwide since the 1960s. Following the technological advances in the mid-20th century, agriculture across the western world experienced a continuous intensification (Newton 2017) leading to extensive monocultures, at the expense of existing wetlands, through large-scale drainage (Moreno-Mateos & Comín 2010; Smart et al. 2016). About 70% of wetland habitats disappeared worldwide during this time (Davidson 2014) causing declines of biodiversity (Ma et al. 2010;

Verhoeven & Setter 2010). In light of these events, international legislations were developed in the late-20th century, to ensure restoration and protection of wetlands and wildlife (e.g., European Union Habitat Directive 92/43/EEC of 1992 or Bird Directive 79/409/EEC of 2009; Ma et al. 2010) and the number of wetland restoration projects increased (Costanza et al. 1997; Moreno-Mateos & Comín 2010).

Like other waterfowl, many populations of geese, swans and cranes (hereafter 'large grazing birds'), were declining during the first half of the 20th century due to overharvesting and habitat destruction (Fox & Madsen 2017, Lacy et al. 2015; Lefebvre et al. 2017). However, large grazing birds subsequently experienced a rapid recovery during the late second half of the 20th century, both in Europe and North America, due to increasing conservation efforts (Ebbinge 1991; Gauthier et al. 2005; Fox et al. 2017), climate change (Gauthier et al. 2005; Jensen et al. 2014; Mason et al. 2018) and the agricultural intensification (Harris and Mirande 2013; Fox et al. 2017; Lefebvre et al. 2017). In the "new" agricultural landscape, high energy forage was available all year round, due to the increased use of autumn-sown crops and fertilizers (e.g., the European Common Agricultural Policy; Stoate et al. 2001) (Fox et al. 2017, Newton 2017). Large grazing birds are opportunistic foragers (Amano et al. 2006; Chudzińska et al. 2015) and they adapted to the new situation by switching from wetlands and natural grasslands to managed agricultural land for foraging (Fox & Abraham 2017). Consequently, their carrying capacity increased (Fox et al. 2005; Fox & Abraham 2017) and several large grazing bird species exploiting agricultural habitats exhibited exponential population growth (see Fox & Madsen 2017). As a result of such increases, European populations of, for example, barnacle goose *Branta leucopsis* and greylag goose *Anser anser* as well as the American greater snow goose *Chen caerulescens* have been defined as 'superabundant' (Giroux et al. 1998; Fox & Madsen 2017) and subject to international coordinated management plans for population control (Anderson & Padding 2015; Jensen et al. 2018; Powolny et al. 2018).

Large grazing birds are social, migratory and widely distributed species. These species commonly gather in large numbers in open waterbodies and wetlands that ensure undisturbed and safe roosting grounds and reliable high-quality food in the vicinity (Jankowiak et al. 2015; Chudzińska et al. 2016; Jensen et al. 2017). Such wetlands will be visited regularly, year after year, being used as regular wintering, breeding and stopover sites (Kruckenberg and Borback-Jaene 2004; Clausen & Madsen 2015). For example, hundreds of thousands of common cranes are recorded every year at lake Der-Chatecoq, France (268,120 individuals were registered in Nov. 2019; https://champagne-ardenne.lpo.fr/). Similarly, during autumn migration, Lake Kvismaren, in central Sweden, can host up to 24,000 staging common cranes; 14,000 bean geese *Anser fabalis*; 9,000 greylag geese; 1,700 barnacle geese and 1,000 pink-footed geese *Anser brachyrhynchus* (Shah & Coulson 2018). Nature reserves (like the ones above) often assure safe and predictable roosting and foraging grounds (Madsen 1998; Rosin et al. 2012). Hence, crops and pastures in the vicinity of protected wetlands become repeatedly exposed to high concentrations of large grazing birds and to the risk of crop damage (Madsen 1998; Nilsson et al. 2019). Consequently, in agricultural landscapes, conservation conflicts and negative attitudes towards wetland restoration have arisen over the years (Dickman 2010; Eriksson et al. 2020). Conflicts between conservation and farming interests arise when birds cause direct yield loss for farmers (Tombre et al. 2013; Stroud et al. 2017). Management strategies to reduce crop damage and mitigate conflicts are developed at both the local (fields and farms) and flyway levels (Hake et al. 2010; Madsen & Williams 2012; Fox & Madsen 2017; Lefebvre et al. 2017; Mc Kenzie & Shaw 2017). At the local level, measures like scaring, provision of diversionary fields (fields where birds are left undisturbed to forage) and lethal scaring are conducted (Madsen 1998; Månsson 2017; Simonsen et al. 2016; Stroud et al. 2017). At the national level, different forms of financial compensation have been introduced to improve tolerance of grazing birds among farmers (Filion et al. 1998; Hake et al. 2010; Tombre et al. 2013; Eythórsson et al. 2017) and adaptive management plans engaging different social parties involved in the conflict have been developed (Giroux et al. 1998; Eythórsson et al. 2017; Madsen et al. 2017). At the flyway level, population control as a measure to reduce crop damage is implemented across the species' migratory ranges, e.g., the Svalbard population of pink-footed goose in Europe (Madsen et al. 2017) or the greater snow goose in North America (Lefebvre et al. 2017).

Currently, many species of large grazing bird in Europe and North America are still increasing (BirdLife International www.iucnredlist.org/ [09-June-2020]). When managing wildlife–damage conflicts, knowledge about the spatial and temporal relationships between numbers of birds and the damage they cause is essential to set acceptance levels of damage and to make informed decisions for conservation and crop protection measures (Madsen et al. 2017). Likewise, knowledge about when and where crop damage occurs, future areas at risk, species (and populations) involved, crops prone to be damaged and forecast of levels of damage are all prerequisites for designing cost-effective strategies to prevent crop damage across time and space (Forsyth et al. 2000; Conover 2002; Meisingset et al. 2018). Nonetheless, the difficulties to assess, quantify and relate crop damage to large grazing birds are compounded by an overall lack of data, leading to current knowledge gaps for preventive damage management (McNaughton 1979; van der Graaf et al. 2005; Fox et al. 2017). These days, little is known about the spatial and temporal relationships between numbers of birds and the damage they cause, especially at the national level (i.e., the level where political decisions concerning strategic management and decisions for re-imbursement are agreed; Fox et al. 2017) and at the flyway level (i.e., the level where management plans for population control are implemented). These relationships are usually just assumed to be positive and linear (McKenzie & Shaw 2017; Cusack et al. 2019). Moreover, the mechanisms driving spatial distributions of crop damage, are not yet fully understood (Fox et al. 2017) and while present areas of crop damage occurrence are known, this does not help forecasting future areas at risk as large grazing bird populations increase and expand their distributional range. However, in Sweden, the government launched a system in 1995 to compensate farmers for crop damage caused by large grazing birds (after inspection by certified inspectors). Here, information about the number of damage reports, estimated yield loss and costs for compensation for specific culprit species and damaged crop types at different times across the country, have been stored in a long-term database. This dataset provides us with an opportunity to investigate these issues.

2. Aims and Objectives

The overall aim of this thesis is to fill current gaps in the management of crop damage by large grazing birds in Sweden, at different spatial and temporal scales.

Specifically, objectives and research questions are structured as follows:

Paper I Reveal temporal relationships between national bird abundances and national crop damage levels (number of crop damage reports, estimated yield loss and costs for compensation), at the long-term (16 years: 2000 to 2015) and at the short-term (year-to-year)

Paper II Capture the spatio-temporal variation of crop damage patterns across Sweden (who causes what, when and where) at monthly basis

Paper III Identify suitable areas for large grazing birds across Sweden in terms of habitat suitability (at monthly basis), and where they can gather in larger numbers as their populations increase and expand

Paper IV Predict probability of crop damage to occur and amount of agricultural yield loss in Sweden, if populations of large grazing birds expand and establish in the new areas predicted in Paper III, by relating spatial variation of damage to spatial variation of bird abundance and crop availability

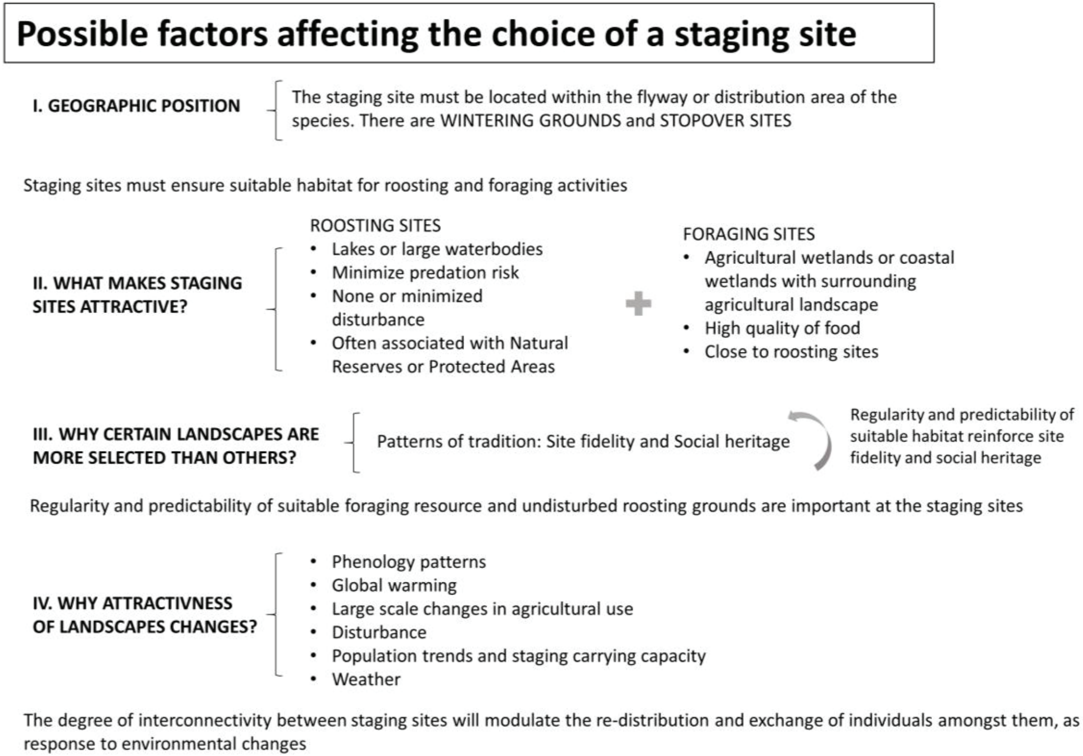
3. Study area

Geographically, Sweden ranges between 55°-70° north and 11°-25° east. It includes four climate zones (Kottek et al. 2006), five vegetation zones (Ahti et al. 1968) and eight agricultural productivity areas (Statistics Sweden 2013). The landscape of southernmost Sweden is dominated by agricultural land (i.e., crops and pastures) and holds the highest diversity of crops e.g., rapeseed, potatoes, legumes, carrots and beets with wheat, barley, hay (silage and fodder) and pastures as the main crops (Widén-Nilsson et al. 2016). The production of oil seed and sugar beets are the highest in the country here (Statistics Sweden 2013). Towards the north, forest coverage increases and agricultural heterogeneity decreases, with mowed grasslands and pastures representing approximately 70% of the agricultural land (Statistics Sweden 2013; Widén-Nilsson et al. 2016). Potatoes are cultivated throughout the country (Statistics Sweden 2013). Overall, northern Sweden has a shorter growing vegetation period compared to the south (Nilsson 2013). Nationally, the availability of different crops has not shown any distinct trend during the study period (2000 to 2015), except for barley in northern Sweden which has decreased by 50% (Widén-Nilsson et al. 2016). Market prices vary considerably amongst crops (e.g., from 2000-2015, rapeseed and potato vary between 14 – 34 euros/100 kg; barley and wheat between 8 - 17 euros/100 kg; Statistics Sweden www.scb.se) but no trends in pricing have been detected since year 2000.

4. Study species

There are five main species of large grazing birds responsible for crop damage eligible for economical compensation in Sweden (Table 1) namely common crane, barnacle goose, greylag goose, whooper swan *Cygnus cygnus* and Bean goose *Anser fabalis* (Figure 1). Swedish breeding populations (breeding pairs) are estimated at 30,000 common cranes; 4,900 barnacle geese; 41,000 greylag geese; 5,600 whooper swans and 850 bean geese (Ottosson et al. 2012). Estimates of national numbers of autumn staging and wintering individuals have increased since 2000 (Nilsson 2013; Figure 2). During mild winters, all species except common crane, may winter in southernmost Sweden (Nilsson 2013).

Figure 1. (A) Common crane is found all over Sweden from March to October. It breeds mainly in forested marshes, swamps and shallow bogs, using wetlands as stopover sites and foraging in the surrounding agricultural land (Månsson et al. 2013; Nilsson et al. 2016). (B) Barnacle goose peaks between April-May and September-October. It migrates and breeds mainly along the south and east coast, foraging on agricultural land (Ottosson et al. 2012; Shah & Coulson 2018). (C) Greylag goose and (D) whooper swan are mostly present in south-central and mid Sweden, with higher abundances from June-October for greylag goose and February-March for whopper swan. Both species breed in wetlands and water bodies, which they use as well as stopover sites during migration and moulting grounds, foraging across the immediate surrounding agricultural fields (Ottosson et al. 2012; Shah & Coulson 2018). (E) Bean goose crosses the country during migration, often with higher abundances in October, and only a small part of the population breeds in northern Sweden (Ottosson et al. 2012). Photos © Magnus Friberg.



Possible factors affecting the choice of a staging site

I. GEOGRAPHIC POSITION

The staging site must be located within the flyway or distribution area of the species. There are WINTERING GROUNDS and STOPOVER SITES

Staging sites must ensure suitable habitat for roosting and foraging activities

II. WHAT MAKES STAGING SITES ATTRACTIVE?

ROOSTING SITES
- Lakes or large waterbodies
- Minimize predation risk
- None or minimized disturbance
- Often associated with Natural Reserves or Protected Areas

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FORAGING SITES
- Agricultural wetlands or coastal wetlands with surrounding agricultural landscape
- High quality of food
- Close to roosting sites

III. WHY CERTAIN LANDSCAPES ARE MORE SELECTED THAN OTHERS?

Patterns of tradition: Site fidelity and Social heritage

Regularity and predictability of suitable habitat reinforce site fidelity and social heritage

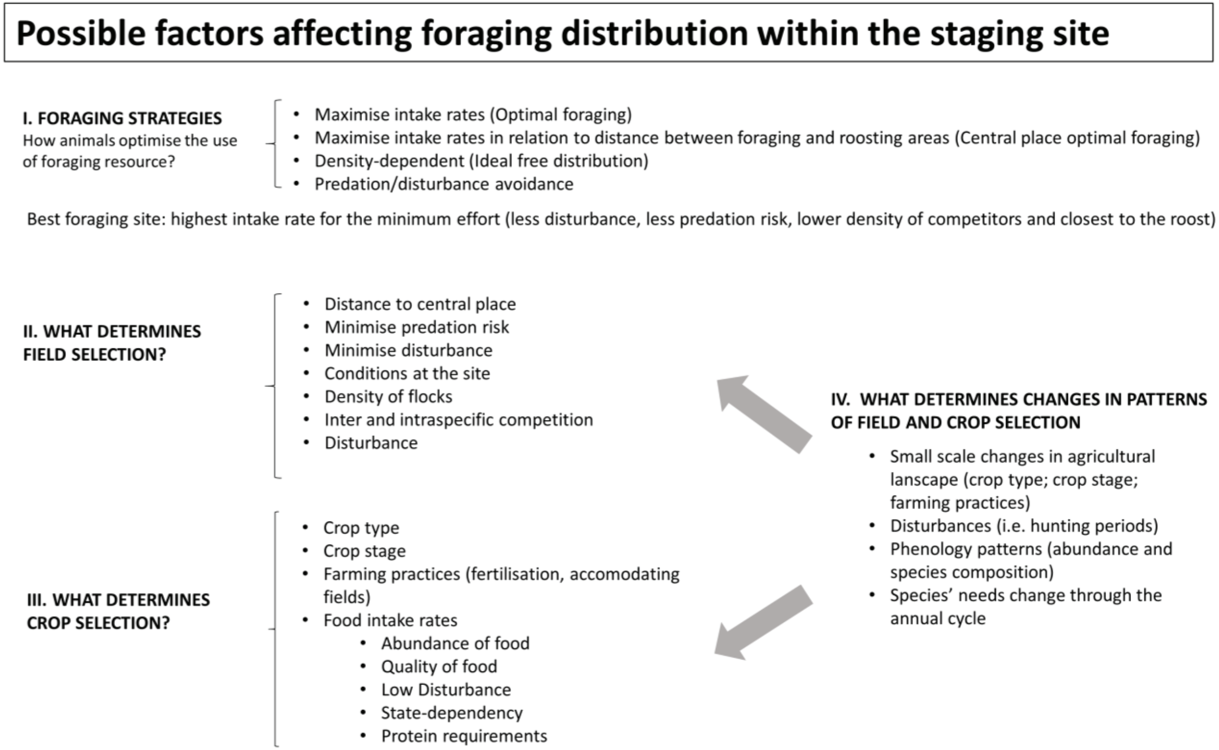
Regularity and predictability of suitable foraging resource and undisturbed roosting grounds are important at the staging sites

IV. WHY ATTRACTIVNESS OF LANDSCAPES CHANGES?

- Phenology patterns
- Global warming
- Large scale changes in agricultural use
- Disturbance
- Population trends and staging carrying capacity
- Weather

The degree of interconnectivity between staging sites will modulate the re-distribution and exchange of individuals amongst them, as a response to environmental changes

Box 1. Possible factors determining attractiveness of a staging site for large grazing birds (Figure from Montràs-Janer 2016; references: Madsen 1998; Warren et al. 1992; Béchet et al. 2003; Kruckenberg & Borback-Jaene 2004; Gauthier et al. 2005; Tombre et al. 2008; Baveco et al. 2011; Rosin et al. 2012; Jankowiak et al. 2015; Chudzińska et al. 2015, 2016; Teitelbaum et al. 2016; Fox et al. 2017; Jensen et al. 2017).



Possible factors affecting foraging distribution within the staging site

I. FORAGING STRATEGIES
How animals optimise the use of foraging resource?

- Maximise intake rates (Optimal foraging)
- Maximise intake rates in relation to distance between foraging and roosting areas (Central place optimal foraging)
- Density-dependent (Ideal free distribution)
- Predation/disturbance avoidance

Best foraging site: highest intake rate for the minimum effort (less disturbance, less predation risk, lower density of competitors and closest to the roost)

II. WHAT DETERMINES FIELD SELECTION?

- Distance to central place
- Minimise predation risk
- Minimise disturbance
- Conditions at the site
- Density of flocks
- Inter and intraspecific competition
- Disturbance

III. WHAT DETERMINES CROP SELECTION?

- Crop type
- Crop stage
- Farming practices (fertilisation, accomodating fields)
- Food intake rates
    - Abundance of food
    - Quality of food
    - Low Disturbance
    - State-dependency
    - Protein requirements

IV. WHAT DETERMINES CHANGES IN PATTERNS OF FIELD AND CROP SELECTION

- Small scale changes in agricultural lanscape (crop type; crop stage; farming practices)
- Disturbances (i.e. hunting periods)
- Phenology patterns (abundance and species composition)
- Species' needs change through the annual cycle

Box 2. Possible factors affecting foraging distribution of large grazing birds within the staging site. (Figure from Montràs-Janer 2016; references: Macarthur & Pianka 1966; Fretwell & Lucas 1970; Schoener 1979; Bélanger & Bédard 1989; Chisholm & Spray 2002; Nolet et al. 2002; Baveco et al. 2011; Rosin et al. 2012; Madsen et al. 2014; Chudzińska et al. 2015, 2016; Jankowiak et al. 2015; Jensen et al. 2017; Simonsen et al. 2016; Teitelbaum et al. 2016; Fox et al. 2017).

5. Methods

5.1 Swedish crop damage dataset

In this thesis, I have made full use of the unique Swedish crop damage dataset. This dataset is based on data collected by the County Administrative Boards (CABs). It was initiated in 1995, when the Swedish government launched a system to compensate farmers affected by crop damage caused by large grazing birds. Since then, farmers suffering from crop damage due to foraging geese, swans and cranes can report the damage to the CABs, who immediately send an authorized inspector to the field to certify the damage, identify the culprit species, the damaged crops and estimate the loss of yield (i.e., kilos of biomass loss) using a standardized methodology (for details see Månsson et al. 2011 and Paper I). Yield loss due to other wildlife species or causes such as flooding or drought, is deducted from the total loss (Månsson et al. 2011). Once the damage is certified and registered by the authorized inspectors, the CABs compute the economical compensations according to the annual market prices.

The species included in the compensation scheme are bean goose, barnacle goose, brent goose *Branta bernicla*, greylag goose, greater white-fronted goose *Anser albifrons*, mute swan *Cygnus olor*, whooper swan and common crane. Crop damage caused by Canada goose *Branta canadensis* is not compensated for since conditional shooting is allowed for this non-native species throughout the year (i.e., farmers can shoot geese on fields where they cause damage, outside the hunting season).

I have used three indicators of crop damage levels namely, damage reports (number of approved reports of crop damage), yield loss (estimated loss of biomass) and compensation costs (economical compensations paid by the CABs to the farmers).

5.2 National indices of bird numbers

In Paper I, I have explored national relationships between bird abundance and damage levels. To do so, I have used the annual national autumn counts for geese and swans (Nilsson & Haas 2016), conducted in the vicinity of roosting sites and designed to cover all main stopover sites (Nilsson 2013). I have also used the autumn migratory counts of common cranes, conducted at their four major autumn stopover sites (Lundin 2005; Nilsson et al. 2016). Both these counts are viewed as estimates of national numbers, i.e., population indices (Nilsson 2013).

5.3 Swedish Species Observation System

In Paper III, I have investigated monthly spatial distributions of species abundance in Sweden, at a fine spatial resolution (100 km^2). To do so, I have used data from the citizen science platform 'Swedish Species Observation System' (SSOS; Artportalen https://artportalen.se; SLU Artdatabanken) (Leidenberger et al. 2016) a Swedish open access website for anyone to report observations of Swedish flora and fauna. The use of opportunistic data opens possibilities for large spatial and temporal scale studies (Schmeller et al. 2009). However, the use of such non-standardized presence-only data (i.e., information of absences is not provided) requires addressing some statistical issues to avoid biased results, namely 1) non-uniform observation intensity and 2) unknown detectability of the species (Guélat & Kéry 2015, Guillera-Arroita 2017, Coron et al. 2018).

5.4 Satellite imagery

Nowadays, there are many available sources of satellite data, covering extensive spatio-temporal ranges at different spatial and temporal resolutions (Rushton et al. 2004). In Paper III, I have taken advantage of the accessibility of such sources of data (i.e., MODIS and Swedish Corine land cover) to investigate monthly spatial distributions of species abundance in Sweden, in relation to land cover, Enhanced Vegetation Index and snow cover, i.e., habitat suitability. In Paper IV, I have used the estimated bird abundances from Paper III to predict crop damage across Sweden. Because crop damage depends not only on the species abundance but also on the available foraging resources (Conover 2002), I have used the crop availability dataset elaborated by Widén-Nilsson et al. (2016) to incorporate foraging resource availability into the models.

5.5 Modelling data with temporal and spatial dependency

In this thesis, I have studied relationships across time and space and therefore run temporal and spatial statistical models (Paper I, III and IV). When data is collected within a temporal and/or spatial framework, the data points are not independent from each other (Turner & Gardner 2015). This means that the risk of finding statistical significance when it does not exist, increases, i.e., uncertainties may be underestimated (Turner & Gardner 2015). To avoid that, temporal and spatial autocorrelation need to be accounted for in the models.

In Paper I, I have investigated relationships between national bird abundance and national damage levels, across 16 years of data and at year-to-year basis. To account for temporal autocorrelation across 16 years of data, I have assumed that regression residuals followed a random walk process 'Rw1' (as described in Zuur et al. 2017). To analyze inter-annual fluctuations, I have included a 'drift term' into the random walk, which allows examining the year-to-year association between the response and the covariate when trends in both variables are accounted for.

In Paper III, I have investigated monthly spatial distributions of species abundance across the country in relation to environmental covariates. To analyze this georeferenced data, I have divided Sweden in 4,865 grid cells (each one of 100km^2), defined the spatial dependency through a neighborhood structure of eight neighbors or grid cells (as in Blangiardo & Cameletti 2015) and incorporated a Leroux Model to account for spatial autocorrelation (Leroux et al. 2000).

In Paper IV, I have investigated how monthly spatial patterns of species abundance from Paper III, linked to spatial patterns of expected probability of crop damage to occur and agricultural yield loss across Sweden. To account for the seasonality of the data, I have incorporated 'month' as a random intercept (i.e., where each grid observation is nested within each month).

5.6 Models, Bayesian approach and INLA for Bayesian inference

When analyzing data, we first need to think of a coherent model to investigate the data. In Paper I, I have fitted Negative Binomial Generalized Linear Mixed Models (GLMM) to study relationships between national bird abundance and damage levels across time. In Paper III, I have used Poisson GLMM to develop Species Distribution Models (see below) and investigate monthly spatial distributions of species abundance across Sweden, and the use of staging sites in relation to habitat suitability. In Paper IV, I have run Logistic Regression Models for binary outcomes (Bernoulli distribution) to predict probability of crop damage across Sweden, and Log-normal Mixed Linear Models to predict amount of yield loss, in relation to spatial distributions of bird abundance and crop availability (see related papers for details).

All modelling analysis in Paper I, III and IV has been approach from a Bayesian point of view. There are two main advantages in taking this approach (in contrast to the frequentist or 'classical' approach, see Appendix 1 for further information). First, Bayesian methods allow us to develop complex models, like the spatial and temporal hierarchical models I have used (where dependency structures in the data need to be captured), without the need for simplification (Blangiardo & Cameletti 2015). Second, Bayesian methods offer the possibility to account for the uncertainty around the parameter estimates and the model predictions, as well as the capability of dealing with missing data (Blangiardo & Cameletti 2015) (see Appendix 1 for details).

For all models in Paper I, III and IV, I have used the advantages of using the Integrated Nested Laplace Approximation (INLA) for Bayesian inference (Rue et al. 2009) and the R-package R-INLA (www.r-inla.org) for model execution (Rue et al. 2017; Bakka et al. 2018). INLA is a method for approximate Bayesian inference for Latent Gaussian Models (Rue et al. 2009), such as the Generalized Linear Models, mixed-effects models and spatial and temporal models used in Paper I, III and IV. It has higher computational-cost-efficiency and allows incorporating spatial and temporal dependency with higher flexibility than other Bayesian methods, like the commonly used Markov Chain Monte Carlo (Blangiardo & Cameletti 2015; Zuur et al. 2017), especially when, as here in this thesis, the modelling involves large spatial datasets, over large geographical ranges and for multiple species (Blangiardo & Cameletti 2015, Zuur et al. 2017).

5.6.1 Species Distribution Models

In Paper III, I have aimed to investigate seasonal use of staging sites by large grazing birds across Sweden as populations increase and expand. Therefore, I have developed monthly Species Distribution Models (SDMs) to infer distributions of species abundance across the country. SDMs, also known as Habitat Suitability Models, are empirical methods that relate species' observations to environmental characteristics (Guisan et al. 2017). Nowadays, they are widely used as decision-making tools in conservation, wildlife management and ecological forecasting (Araújo et al. 2019; Titeux et al. 2020). Their purpose is to improve ecological and evolutionary insights of species' distributions and predict these distributions across the landscape. Paper IV is an example of SDMs' application to wildlife damage management, where I have used the estimated bird abundances from Paper III to predict probability of crop damage and yield loss across the Swedish agricultural land, incorporating as well the spatial availability of crop types in the models.

5.7 Cluster Analysis and Generalized Additive Models. Capturing spatial and temporal patterns in the crop damage dataset

In Paper II, I have investigated spatio-temporal patterns of crop damage and how they differed across Sweden, in relation to regional differences in crop types and species causing damage.

Agglomerative Hierarchical Cluster analysis is a non-supervised learning technique, commonly used in many fields (e.g., machine learning, pattern recognition or exploratory data mining) to identify homogeneous groups within heterogeneous data (Carvalho et al. 2009). The idea is to group a set of objects in a way that, objects in the same group (or cluster) will be more similar to each other than to objects belonging to other clusters. It is a bottom-up approach, starting with each object (or data point) being its own cluster and merging them using the appropriate linkage method. There are different linkage methods, and their use will depend on what we want to answer. For example, in Paper II, I have first applied the ‘complete-linkage method’ to lump individual locations of crop damage by geographical proximity. Then, I have applied the ‘Ward’s linkage method’ to join the clusters from the first clustering analysis, to identify regions with similar patterns of monthly crop damage.

Generalized Additive Models (GAMs) seek to model the response variable by a linear combination of independent variables, each of them on the form of a smoothed function (Wood 2004). The interest of a GAM relies on these smooth functions, commonly used to reveal non-linear relationships between covariates and response variables, and to undercover patterns (Wood 2004). In Paper II, I have used GAMs to reveal seasonal patterns of crop damage occurrence, as well as their consistency and tendency across the years. In Paper IV, I have used the same method to reveal seasonal patterns of yield loss and bird phenology and their consistency across the years.

6. Results and Discussion

6.1 Large grazing birds and crop damage in Sweden. A brief overview

During the period 2000 to 2015, the inspectors of the Swedish County Administrative Boards registered 2,194 damage reports, resulting in 34,500 metric tonnes of yield loss and 3.4 million euros due for compensation. About 90% of all damages were caused by common cranes, barnacle and greylag geese, with the remaining 8% by whooper swans and bean geese (Table 1). Crop damage in Sweden increased since year 2000, with all three crop damage level indicators (damage reports, yield loss and compensation costs) showing similar annual patterns (Figure 2).

Table 1. Number of damage reports, yield loss (metric tonnes T) and compensation costs (euros) (percentages in parentheses) for the main species of large grazing birds causing crop damage in Sweden from 2000 to 2015. The category 'others' includes Canada goose, mute swan, greater white-fronted goose, brent goose and unidentified geese.

	Common crane	**Barnacle goose**	**Greylag goose**	**Whooper swan**	**Bean goose**	**Others***
Damage reports	976 (34.2)	804 (28.2)	772 (27.1)	114 (4.0)	106 (3.7)	79 (2.8)
Yield loss (metric tonnes)	11,620 (33.7)	11,531 (33.5)	9,157 (26.6)	774 (2.2)	902 (2.6)	460 (1.4)
Compensation costs (x1000 euros)	1,136 (33.8)	1,154 (34.3)	738 (22.0)	144 (4.3)	93 (2.8)	97.5 (2.9)

*Canada goose = 197 T and 11,500 euros; mute swan = 8 T and 2,600 euros; greater white-fronted goose = 105 T and 60,200 euros; brent goose = 21 T and 2,400 euros; unidentified = 129 T and 20,500 euros. Source: Montràs-Janer et al. 2019.

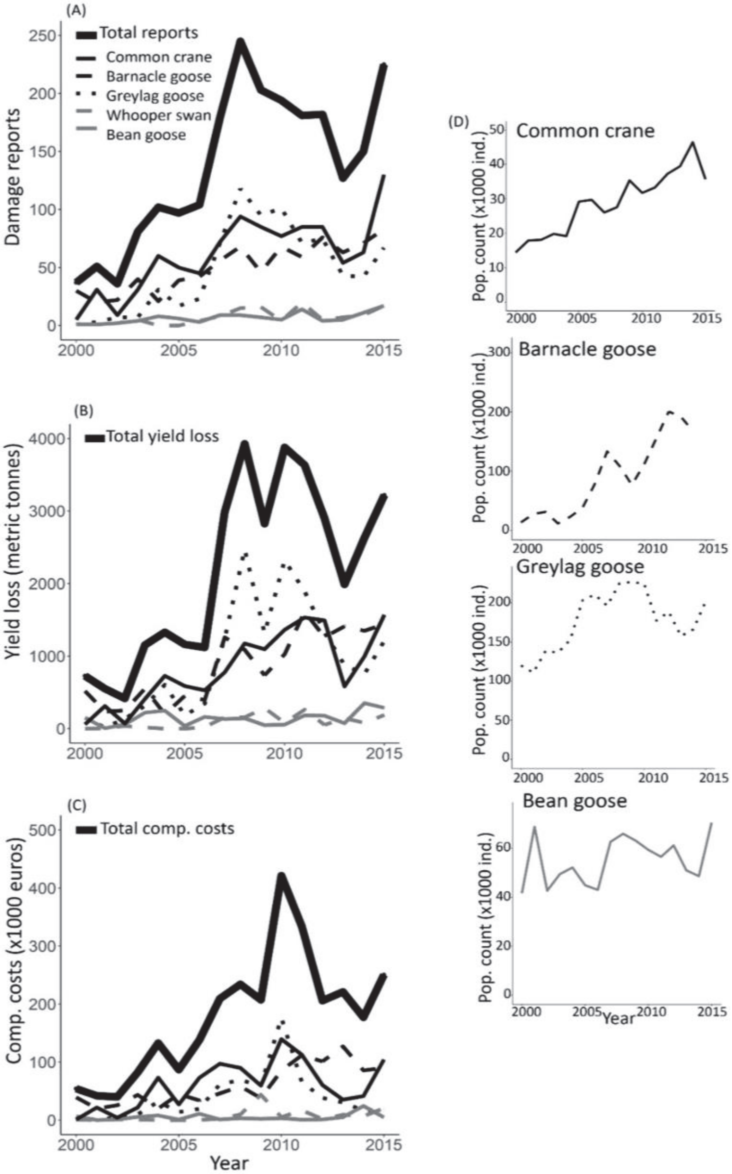
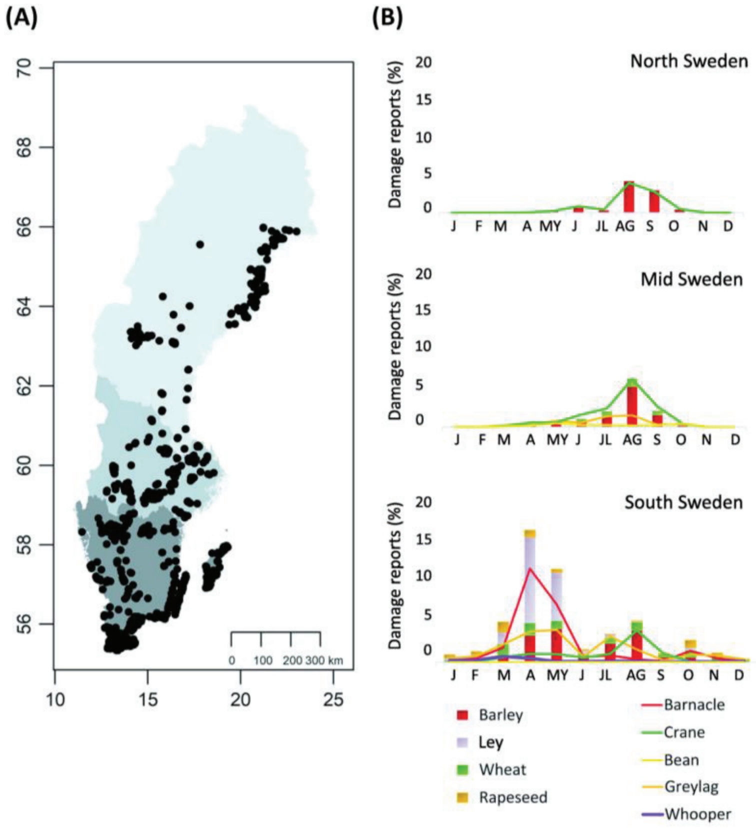


Figure 2. (A) Development of total annual damage reports, (B) yield loss (metric tonnes), (C) compensation costs (euros) and (D) Swedish national autumn counts for different species of large grazing birds in Sweden from 2000 to 2015. Note that data before year 2000 was excluded from the analysis due to small sample size and potential bias (Paper I for details). Autumn national counts for whooper swans involved poor coverage (less than 200 individuals/year) and were not included in the analyses. Source: Montràs-Janer et al. 2019.

Overall, crop damage exhibited a clustered distribution across the country, with higher damage levels involving more species and a larger variety of damaged crops in southern Sweden than in northern Sweden (Figure 3).



(C)

	Damage reports (2,198 damages)	Yield loss (34,500 metric tonnes)	Compensation costs (3.4 Million euros)
North Sweden	12.0%	4.7%	10.8%
Mid Sweden	24.8%	28.1%	23.1%
South Sweden	63.2%	67.5%	66.1%

Figure 3. (A) Spatial distribution of damage reports, (B) within year distribution of damage reports for five species of large grazing birds and the four most damaged crop types, and (C) percentage of total damage for three regions in Sweden, from 2000 to 2015. The division north, mid and south Sweden is for illustration purposes only and follows the historical division of Norrland, Svealand and Götaland respectively. Source: Montràs-Janer et al. 2019.

6.2 Temporal relationships between national abundance of birds and national damage levels (Paper I)

National levels of damage reports, yield loss and compensation costs were positively related to national bird numbers of common crane, barnacle and greylag goose. These relationships differed amongst species, were surrounded by a high level of uncertainty (i.e., model outcomes are hard to predict), and might not follow linearity (Figure 4), as commonly assumed (McKenzie & Shaw 2017; Cusack et al. 2018). Although linear relationships could not be discarded for common crane nor greylag goose, a non-linear relationship seemed to fit best for the latter. Barnacle goose on the other hand, presented a curvilinear relationship with all three damage level indicators increasing at a lower rate with increasing population numbers (Figure 4) which could be explained by a tendency for barnacle flocks to aggregate more than the other two species (Nilsson 2013). In fact, this explanation was supported by an observed increase of yield loss per reported damage at higher population indices of barnacle goose, suggesting a concentrated impact of damage at high population numbers (Paper I). Such an increase was not observed for common crane nor greylag goose, suggesting that more fields were damaged given higher numbers of common cranes and greylag geese (Paper I).

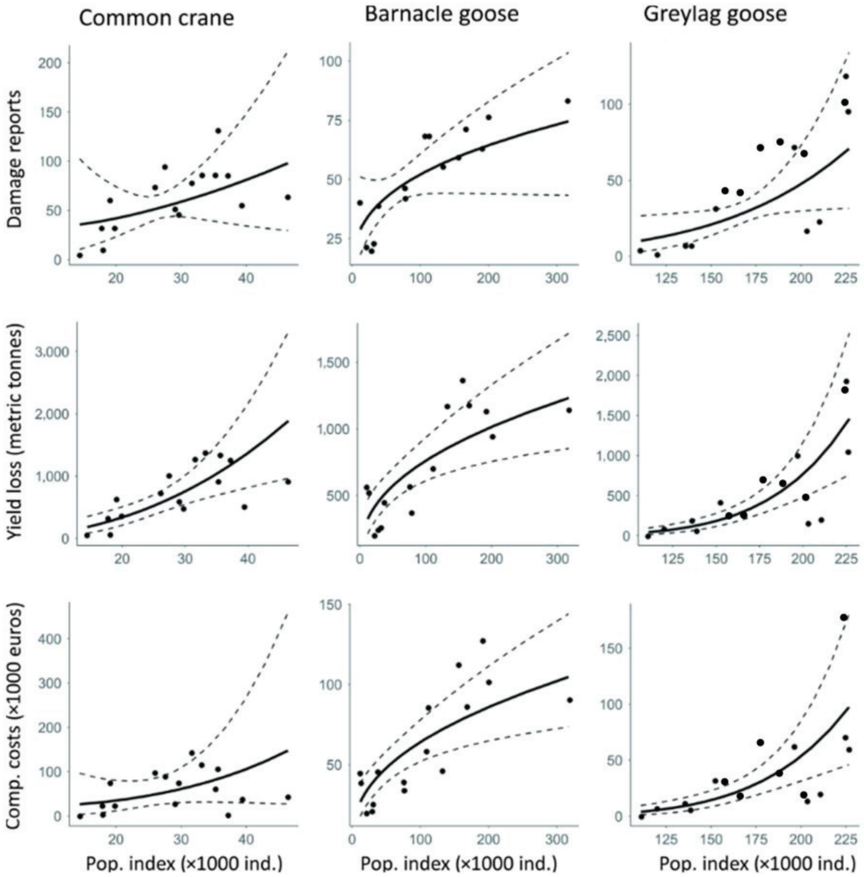


Figure 4. Relationship between damage reports, yield loss, compensation costs, and population indices for the three main species of large grazing birds causing crop damage in Sweden, from 2000 to 2015. Solid lines represent the estimated curves based on the slope coefficient for the effect of population index over the response variable. Dashed lines indicate the 95% credible interval. Black dots, the observed values. Model structure is defined in Paper I. Source: Montràs-Janer et al. 2019.

In parallel with the high levels of uncertainty, inter-annual fluctuations of population indices did not relate to inter-annual fluctuations of damage reports, yield loss nor compensation costs (Figure 5). There are different plausible explanations for such results. First, there may be a spatio-temporal mismatch between estimates of national numbers of birds and occurrence of crop damage (damage occurs year-round with certain monthly peaks, but bird counts are only available in autumn). Second, farmers may change their willingness to report damage with increasing levels of crop damage. Third, the opportunistic foraging behavior of large grazing birds (Amano et al. 2008; Chudzińska et al. 2015) may lead to sudden peaks of crop damage when local conditions change due to, e.g., weather, local farming practices or measures introduced for crop protection.

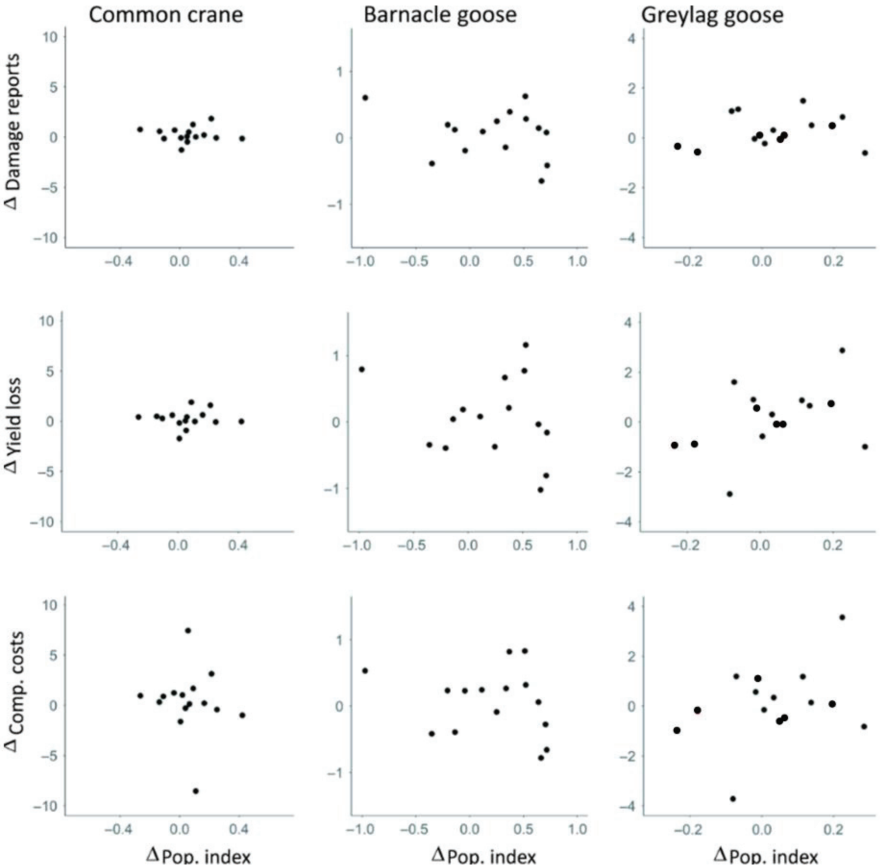


Figure 5. Scatterplots of the annual changes of damage reports, yield loss and compensation costs versus the annual changes of population index (in log scale), for the three main species of large grazing birds causing crop damage in Sweden from 2000 to 2015. Model structure is defined in Paper I. Source: Montràs-Janer et al. 2019.

6.3 Spatio-temporal patterns of crop damage (Paper II)

Crop damage was described by a seasonal (monthly) pattern consistent across the years, but differing across the country such that trans-boundary regions of similar patterns of crop damage could be identified, relating to different culprit species and damaged crop types (Figure 6). The large geographical range of Sweden, comprising different climate and vegetation zones (Ahti et al. 1968; Kottek et al. 2006) and agricultural productivity areas (Statistics Sweden 2013), together with the spatial variation of the species abundance (Madsen et al. 1999; Shah & Coulson 2018) and crop availability (Statistics Sweden 2013; Widén-Nilsson et al. 2016) would explain the spatial variation of damage patterns. The seasonal and consistent migratory patterns of large grazing birds (Madsen et al. 1999) and the regular seasonal pattern of tillage, sowing and harvesting of agricultural crops, would explain the consistency of the seasonal patterns of crop damage across the years.

Despite the variation amongst regions in species-specific relationships of crop availability and number of damage reports, broad patterns of species-wise crop selection, supported by earlier studies on crop preferences, could be identified (Paper II). For example, barley was damaged more than wheat in relation to its availability, by all species and regions (with few exceptions) especially by common crane (see also, Nilsson et al. 2016). Additionally, common crane damaged a higher proportion of potato crops than expected by availability in August and September, while whooper swan did similarly in rapeseed in March (see also, Chisholm & Spray 2002 and Nilsson et al. 2016).

Further research in Paper IV showed that species-specific seasonal patterns of crop damage and the corresponding yield loss were related to each other but not necessarily to seasonal bird abundance. This suggests that seasonal patterns of crop damage relate to the time of the year when crops are more vulnerable (i.e., when available crops suit best the nutritional needs of the species present) rather than when more birds are present (Conover 2002).

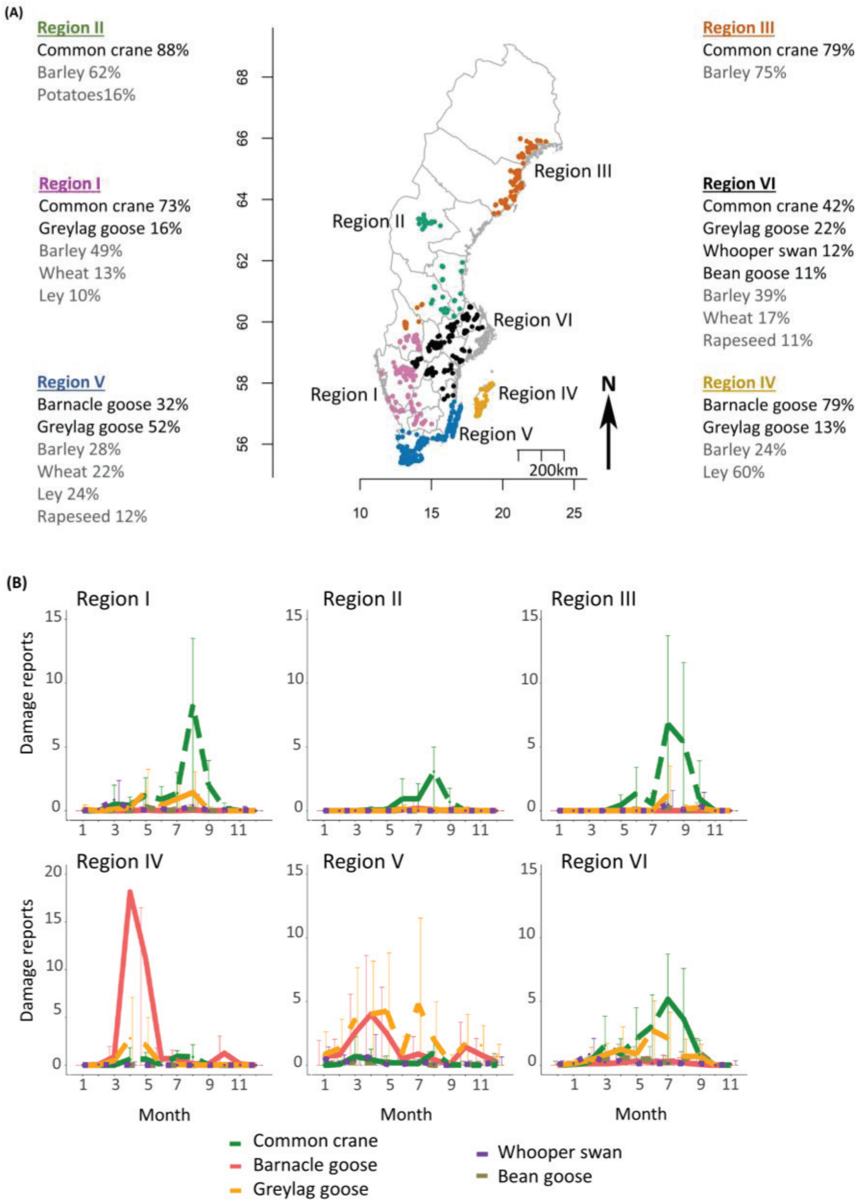
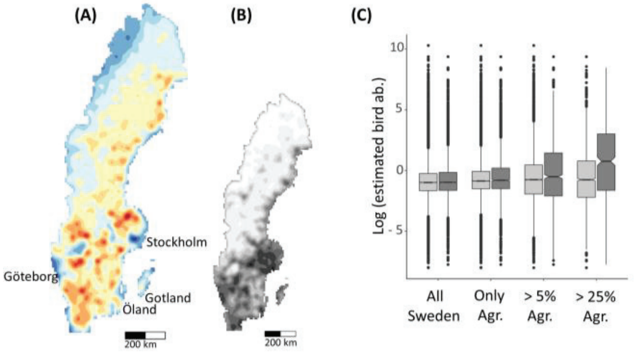


Figure 6. (A) Spatial distribution of reported crop damage caused by large grazing birds in Sweden, identifying six regions with similar seasonal patterns of crop damage, with proportion values of the species reported to cause crop damage and the affected crop type (in %, only values ≥ 10% included). (B) Seasonal patterns of crop damage per region, with number of damage reports per month (mean ± standard deviation), broken down into the five main species causing damage. Source: Montràs-Janer et al. 2020.

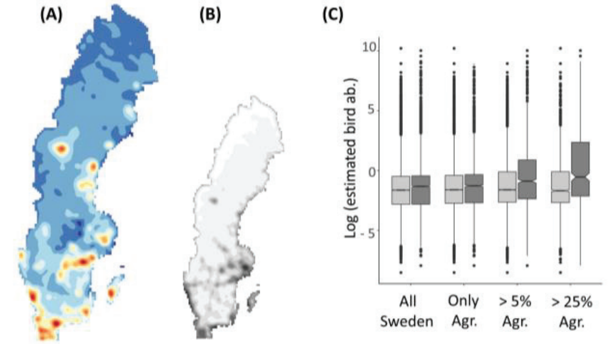
6.4 Spatial distribution of large grazing birds' abundance (Paper III)

Common crane, barnacle and greylag goose exhibited a strong spatially clustered distribution, revealing well-defined hotspots (staging sites with high concentrations of birds) with some spatial overlap between aggregations of common cranes and greylag geese (Figure 7). The Species Distribution Models (SDMs) revealed differences in the use of habitats among species, as well as within the year. For example, common cranes and greylag geese were in general more abundant in areas with higher coverage of agricultural crops, inland marshes and reed lakes; while barnacle geese were more abundant in areas with higher coverage of pastures, coastal areas and inland lakes (Paper III). Seasonal changes in the use of habitats could be explained partly by the seasonal shifts of the species' requirements throughout the year (i.e., wintering, breeding and during migration) and partly by the seasonal landscape variability (Fox et al. 2017; Forsyth et al. 2000). Further, the median of the bird abundance estimated by the SDMs was found to be higher in those areas with higher coverage of agricultural crops and to some extent also to the presence of Ramsar wetland sites (i.e., protected wetlands of international importance to guarantee conservation of habitat www.ramsar.org) (Figure 7). Previous research (e.g., Chudzińska et al. 2016 or Jensen et al. 2017) has suggested that predictability of undisturbed roosting grounds and quality of forage are key requirements for a staging site to be attractive for large grazing birds, as they ensure breeding, wintering and migratory success. Moreover, the extent of the foraging grounds surrounding the roost would ultimately determine the overall carrying capacity of the staging site (Baveco et al. 2011 or Jensen et al. 2017). Protected wetlands, like Ramsar sites, within agricultural-dominated landscapes would offer these selected staging site conditions precisely. Nevertheless, my results showed that other landscape categories (with less agricultural intensity and no protected wetlands) would also provide potentially suitable habitat for large numbers of geese and cranes (Figure 7).

COMMON CRANE



BARNACLE GOOSE



GREYLAG GOOSE

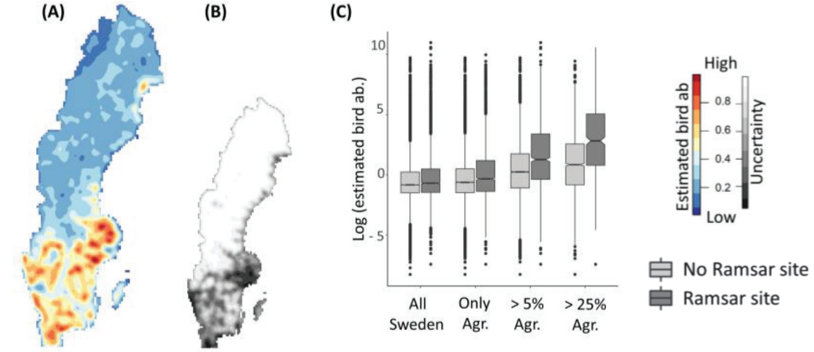


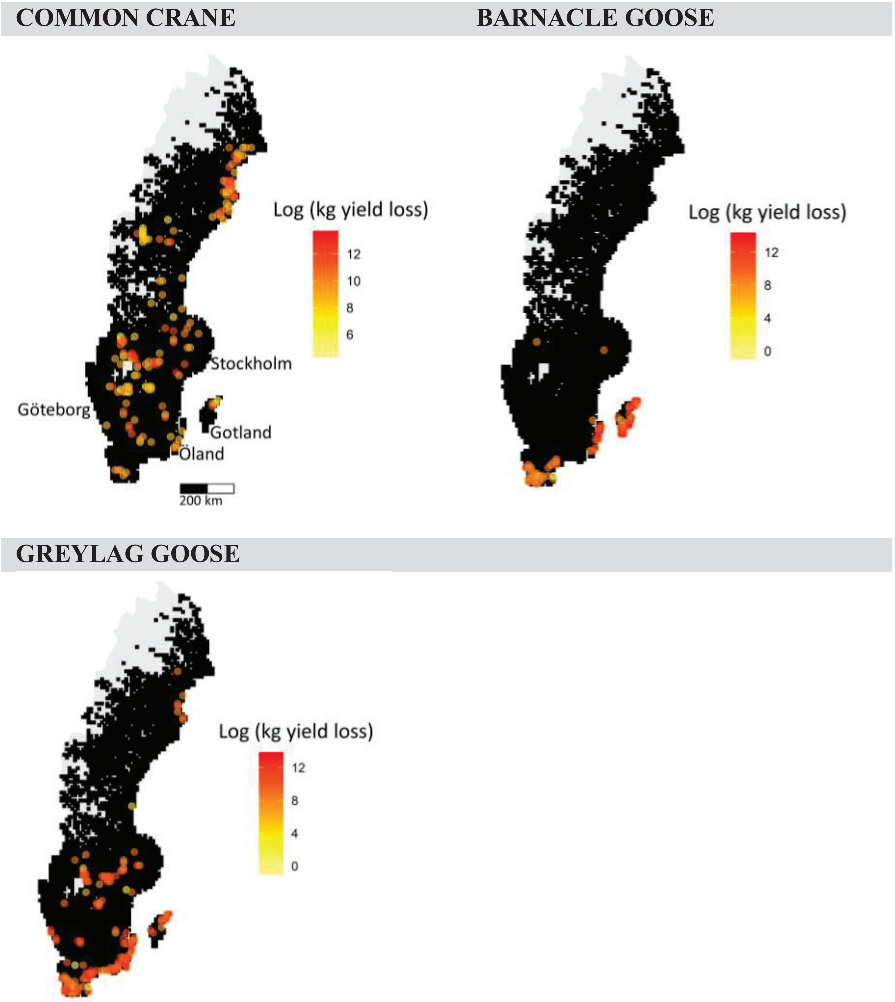
Figure 7. (A) Summary of the spatial distributions of estimated bird abundances and (B) uncertainties for three species of large grazing birds in Sweden (from March to October, 2006 - 2014). The maps are summary totals of the monthly estimated abundances and estimated abundances' standard deviations (i.e., uncertainties) computed by the SDMs (Paper III). For illustration purposes, estimated abundances and standard deviations have

been smoothed with a kernel of bandwidth 45,000 and standardized; from deep blue (and black) = lower estimated bird abundance (and lower uncertainty); to deep red (and white) = higher estimated bird abundance (and higher uncertainty). (C) Notched boxplot contrasting estimated bird abundances of three species of large grazing bird predicted by the SDMs in grids (100km^2) with and without Ramsar sites, and four different scenarios: 1) comparing grids over all Sweden, 2) only comparing grids with agricultural crops, 3) only grids with > 5% of agricultural crops, 4) only grids with > 25% of agricultural crops.

One possible explanation to the relatively weak effect of Ramsar areas on the expected abundance of geese and cranes could be that the SDMs have over-estimated abundances in some non-protected areas, with good habitat suitability but currently, not so many birds (i.e., with currently less birds than indicated by the model estimates). Another explanation could be that the models have under-estimated abundance in some protected areas with large abundance of birds, or that birders are not eager to count and report these common birds where other species may be more attractive to be reported. In any case, the SDMs suggested some potential hotspots where currently, birds were less abundant. Perhaps these areas are of the highest importance as they can identify where potential future conservation conflicts may arise.

6.5 Relating spatial variation of crop damage to spatial variation of bird abundance and crop availability (Paper IV)

Spatial distributions of crop damage caused by common crane, barnacle and greylag goose were clustered across the agricultural landscape and revealed an extensive area of crops and pastures with no damages yet observed (Figure 8). For all three species, probability of crop damage to occur and agricultural yield loss were positively associated to bird abundance and, depending on the species, differently to crop type (Figure 9). Nonetheless, spatial probability of crop damage was mostly associated with bird abundance for all three species, rather than crop availability (Paper IV). Also, although linearity could not be discarded between yield loss and bird abundance, yield loss increased on average at a lower rate at higher bird abundance, which could be partly due to other factors related to accessibility of foraging resource (e.g., local farming strategies, weather or measures for crop protection) affecting these relationships. Crop-wise, high uncertainties surrounded the parameter estimates (Figure 9) which could be explained, at least in part, by local farming practices or measures for crop protection constraining selection of crop type (see Box 2) and masking potential spatial patterns between damage levels and crop availability.

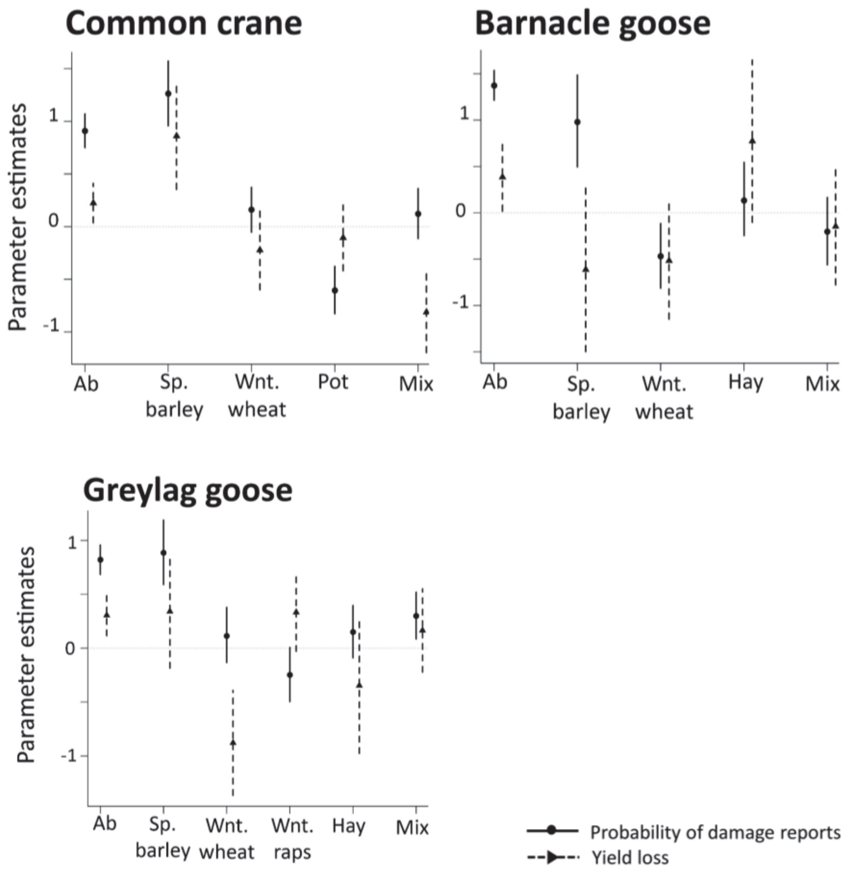


COMMON CRANE

BARNACLE GOOSE

GREYLAG GOOSE

Figure 8. Spatial distribution of yield loss (in natural logarithm) caused by three species of large grazing birds in Sweden, from 2006 to 2014, across the agricultural land (crops and pastures, in black) and within the periods when crops are more vulnerable, i.e., July to September for common crane, March to May for barnacle goose, March to August for greylag goose. Each dot represents the total yield loss registered per period across the years.



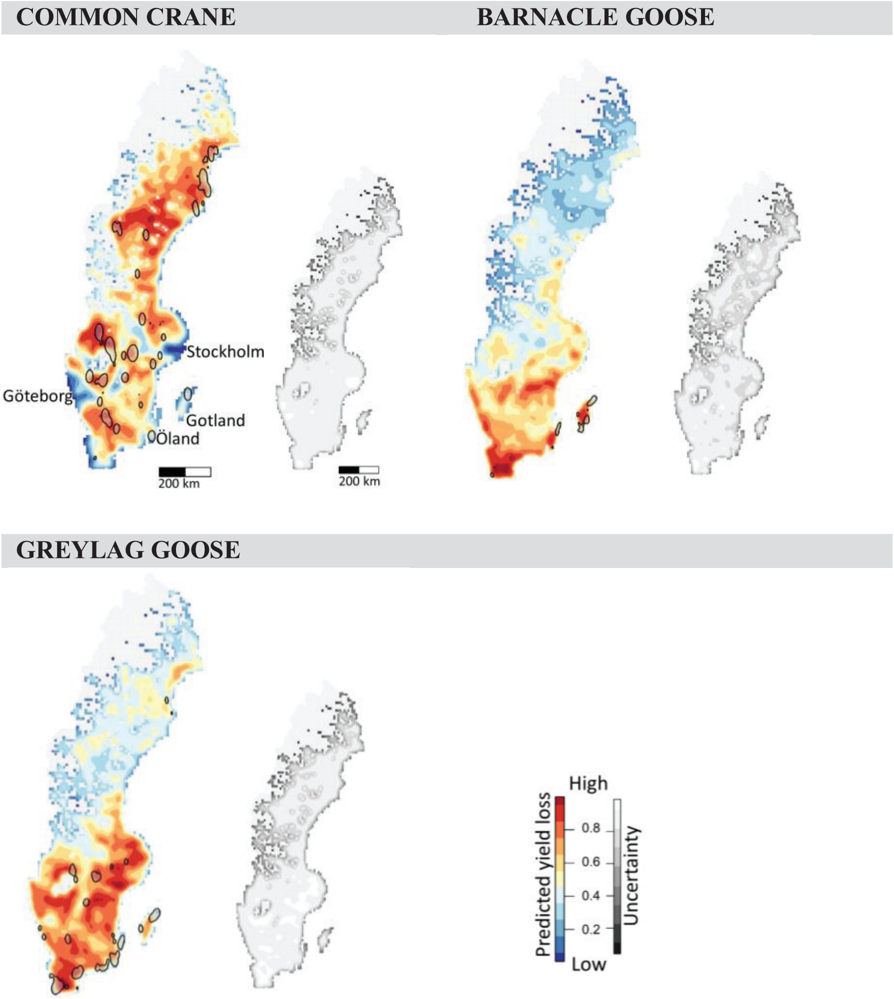
Common crane

Barnacle goose

Greylag goose

Figure 9. Posterior mean and 95% credible intervals for the fixed parameter of the covariates affecting probability of crop damage (logistic regression model, Paper IV) and yield loss (log-normal mixed linear model, Paper IV), caused by three species of large grazing birds in Sweden, from 2006 to 2014 (within the periods when crops are more vulnerable, i.e., July to September for common crane, March to May for barnacle goose, March to August for greylag goose). All covariates are log transformed (with natural logarithm). Abbreviations for covariates: Ab = bird abundance, Sp. barley = spring barley, Wnt. wheat = winter wheat, Pot. = potatoes, Mix = mixed crops, Wnt. raps = winter rapeseed.

When predicting yield loss across the agricultural landscape in relation to bird abundance and crop availability, results suggested that as far as there are birds and crops, crop damage could occur and lead to similar yield loss despite the abundance of birds (Paper IV). However, the *probability* for crop damages to occur was found to be mainly driven by bird abundance. Therefore, areas of higher intensity of yield loss were mainly revealed when spatial predictions of yield loss were weighted by the probability of damage to occur due to bird abundance (i.e., Probability of crop damage due to bird abundance * predicted yield loss) (Figure 10). Yet, model predictions were surrounded by large uncertainties (Figure 10) for which there may be various explanations. Firstly, for all three species, crop damage was observed in a relatively small part of the total area of agricultural land in Sweden (Figure 8) implying a vast amount of space with missing data which would be inferred with high uncertainties. Secondly, farmers may perceive higher risks of crop damages when bird abundance is higher (Simonsen et al. 2016) and be more prone to report damage. Hence, there could be a threshold of bird abundances (not included in the presented modelling) constraining occurrence (or report) of crop damage, above which probability of damage could increase at a higher rate for the same increase of bird abundance below the threshold. Thirdly, the opportunistic foraging behaviour of large grazing birds and their clustered distributions (Jankowiak et al. 2015; Paper III), can also lead to sudden peaks of crop damage when local conditions change, e.g., due to weather, farming practices or measures for crop protection (Béchet et al. 2003; Tombre et al. 2008; Clausen & Madsen 2015). Accordingly, the data showed annual peaks of yield loss, occurring at different localities, diverging among species, and not clearly relating to either bird abundance or resource availability (Paper IV).


COMMON CRANE

BARNACLE GOOSE

GREYLAG GOOSE

Figure 10. Predicted yield loss (left map) and related uncertainty in standard deviation (right map) caused by the three main species of large grazing birds causing crop damage in Sweden, from 2006 to 2014. For illustration purposes, predicted yield loss and standard deviation have been smoothed with a kernel of bandwidth 45,000 and standardized. Deep blue (and black) means lower predicted yield loss (and lower uncertainty). Deep red (and white) means higher yield loss (and higher uncertainty). In large maps, solid black lines represent the smallest area containing 75% of all reports of crop damage for the species.

7. Management implications

My thesis provides answers relating to the management of the agricultural landscape/large grazing bird systems to prevent crop damage, from a local to national level and across temporal scales. The relevance of implementing such multiscale approaches in ecology to reveal and explain spatial patterns and ecological processes for conservation and management decision-making, has been increasingly recognized (Zhang et al. 2018). Below, I provide management recommendations related to my findings at three different spatial levels.

7.1 National level. Annual relationships between damage levels and bird numbers

Adaptive goose flyway management plans are currently developed in Europe suggesting population control to reduce crop damage and mitigate conservation conflicts (e.g., Madsen & Williams 2012 for pink-footed goose or Jensen et al. 2018 for greylag goose). My research suggests that population control could be a potential tool to reduce crop damage, especially when populations increase and damage levels are positively related to bird numbers (Paper I). However, interpretation and guidance should be made with caution because model predictions are surrounded by high uncertainty, and the slope of the relationship may change along the population trajectory and differs amongst species (Paper I). Consequently, given a particular population size, damage levels cannot be predicted from one year to another based on this information alone as other factors like weather, farming practices or measures for crop protection may also vary and affect resource accessibility and ultimately, damage levels (Paper I).

7.2 Regional level. Seasonal patterns and the management across spatial scales

My findings reveal that strategies for crop damage prevention can be tailored for specific regions, targeting different species and protecting different crops at specific times of the year, i.e., when crops are more vulnerable (Paper II). Because these regions do not follow administrative borders, my results call for a coordination of preventive actions and sharing of experiences between the administrative bodies. Coordination over large areas can also decrease the risk of conflict displacement, i.e., to avoid moving the birds between their staging sites and creating damage and conflicts in other regions, such as in the case of the greater snow goose in North America (Béchet et al. 2003). Additionally, as culprit populations are now identified across the country, flyway management plans could be adapted to target the actual agents causing crop damage. Some of these practices are already included in the European flyway management processes (e.g., Madsen et al. 2017), but there will be a need for improved knowledge and communication across management units, within each participating country, to be able to link management at different spatial levels. Although legislation systems for large grazing birds and the administrative management borders are well defined in Sweden, the above recommendations may still be valuable as communication and cooperation processes to facilitate the management practice.

7.3 Local level. Cluster distributions of birds and damage

The importance of local measures to reduce crop damage has been highlighted throughout my thesis. Due to the clustered distribution of large grazing birds across space (Paper III), equating to a clustered distribution of crop damage (Paper IV), measures to reduce crop damage can be targeted at specific locations. These locations are the staging sites, especially those with higher concentrations of birds (hotspots) where risk of crop damage and yield loss are higher (Paper IV). Nonetheless, peaks of yield loss may occur if local foraging conditions change (Paper I and IV), even where bird abundances are not particularly high (Paper IV). Therefore, there is a need to be prepared at any staging site (i.e., both traditionally used and newly established areas) for changes affecting the accessibility of resources that may attract large grazing birds such as weather conditions, wetland restorations and farming practices. Because some of these changes may occur suddenly, local strategies for crop protection should be ready for rapid implementation. A high abundance of large grazing birds is mainly associated with wetlands within a predominantly agricultural landscape (Paper III). Hence, it is important to consider crop damage risk at an early stage when planning for wetland restorations to mitigate future conservation conflicts. For example, including areas within the reserve where large grazing birds are provided with high quality food and where they can forage undisturbed (Madsen 1998). Also, to include support for farmers i.e., scaring birds from fields with sensitive crops (Paper II), accommodation fields (Simonsen et al. 2016), financial compensations (Hake et al. 2010; Eythórsson et al. 2017) and to have a plan for implementation of lethal scaring and derogation (Månsson 2017). Such support is especially needed in close vicinity to the wetlands and should be adapted to meet any local conditions and take into account the behavior of the birds. For example, Nilsson et al. (2016) suggested extra awareness and support to farmers in an area corresponding to a radius of 10km around the roosting site for common cranes.

8. Future perspectives

In the previous section, I have described how the results of my thesis can be applied to management of crop damage and conservation conflicts, assessing practices and steps forward at different spatio-temporal scales. Yet, there is scope for improvement. Below, I summarize some future perspectives to improve the knowledge about the system and management of large grazing birds and wetland conservation to prevent crop damage.

8.1 Reduce the uncertainty around the model predictions

The uncertainty around model predictions makes model predictions difficult to quantify and therefore, needs to be reduced. There are several factors that may affect the degree of the uncertainty e.g., the spatio-temporal resolution of the available data, its high spatial and temporal variation (concerning bird abundances, foraging resources and crop damage), missing data or missing variables.

To reduce the uncertainty around the predictions for the damage models (Papers I and IV), I suggest there is a need to:

a. design standardized national bird surveys for each targeted species of LGBs, at those times of the year and within the spatial ranges where damage occurs, to avoid mismatch around the national relationships between annual bird counts and annual levels of damage
b. investigate the willingness from farmers to report damage and integrate this information in the models to predict crop damage. For example, what makes farmers to report crop damage and has this changed over the years? Why are some areas within the agricultural landscape not registering crop damages (i.e., no damage or damage

not reported)? Is there a threshold of large grazing bird abundance above which crop damage is more likely to occur or be reported? Additionally, encourage farmers to report all damages to enlarge the dataset. Increasing cooperation with farmers would also build trust, benefit understanding of attitudes, favor the effectiveness for managing conservation conflicts and aid the success of implementation of new knowledge (Tuvendal & Elmberg 2015; Redpath et al. 2016; Young et al. 2016; Mishra et al. 2017; Josefsson et al. 2018)

c. incorporate the annual component in the models to predict levels of damage, i.e., to include 1) environmental variables that can affect accessibility of foraging resources and prompt the observed annual peaks of damage, such as temperature or precipitation, and 2) actions for crop protection (although these may be harder to measure)

The uncertainty of the SDMs (Paper III) could be partly reduced by decreasing the amount of missing data, inaccurate counts, species reported but not counted and species absence not reported. However, a complete dataset including all these factors may be unrealistic, unless survey programs are designed and successfully established (i.e., with enough participation from volunteer ornithologists committed to following standardized protocols). Some approaches have improved inference and SDMs performance by 1) using stringent data filtering from the citizen science itself (e.g., Steen et al. 2019), 2) using information about observers' identification skills and reporting consistency to add inferred absences (e.g., Bradter et al. 2018), or 3) developing Integrated SDMs, where data from targeted surveys (e.g., standardized surveys at specific staging sites, hunting bags or observations of marked individuals) is integrated in the SDMs (e.g., Fletcher et al. 2019). Another way to improve the model predictions could be adding factors into the SDMs that may be constraining the choice of staging site. For example, patterns of tradition in terms of site fidelity to staging sites (constraining probability of the species' occupancy across the space) (Box 1) or quality of roosting and foraging grounds (constraining the choice of staging sites) (Box 2).

8.2 Facilitate the management across the spatial scale

Collaboration between administrative bodies has been suggested in this thesis to ameliorate damage management. To facilitate such collaboration, I suggest to:

a. improve the understanding of the connectivity among staging sites, to be able to predict the effects that wetland restorations, creations of new wetlands and measures for crop protection such as scaring, may have on the distribution (and re-distribution) of large grazing bird species' abundances and the associated levels of damage
b. coordinate and standardize over administrative borders, the assessment of management practices. For example, a comparison of experimental trials of measures for crop protection at different staging sites can offer the possibility to evaluate the performance of different management strategies. Likewise, a comparison between staging sites with different bird abundances (hotspots versus less populated sites) can improve our understanding of the ecological mechanisms behind spatial distributions of bird abundances and reveal potential constraints
c. improve the knowledge of current bird abundances at the areas identified as potential hotspots for large grazing birds (in Paper III), especially where high bird abundances were *predicted* but low bird abundances were *observed*. The design of standardized surveys via engagement with local bird organisations, could be a way to monitor species abundance at certain staging sites, providing tailored knowledge relevant for the administrative bodies. Alternatively, this data could be acquired via already available citizen science datasets or by developing programs via citizen science platforms where absences of the species and counts of individuals should be encouraged to report.

8.3 Forecasting spatial patterns of birds and damage

Forecasting spatial patterns of birds and damage is especially important in a world in constant change (e.g., warming climate, new crops are introduced and populations of large grazing birds increase and expand over new areas; Tombre et al. 2008; Nilsson, 2013; Teitelbaum et al. 2016; Fox & Madsen 2017). As spatial patterns of damage and species abundances change in the future, adaptive management strategies for conservation and damage prevention will be required.

8.4 Improve crop damage data collection to enhance local management. Recommendations for the County Administrative Boards

My study covered several spatial scales from local (staging sites) to national level but did not cover the finest level on which measures for crop protection are performed i.e., within the staging site, at the field level. When designing local measures for crop protection, characteristics of fields, landscape structure and species-specific foraging strategies within the staging site need to be taken into account as they all play an important role driving spatio-temporal patterns of damage within the staging site (see Box 2). Hence, knowledge of 1) mechanisms behind distribution and prediction of risk of crop damage within the staging site; 2) risk of a particular field to be repeatedly damaged due to its location within the staging area; or 3) size effect of the flock of foraging birds on the total yield loss registered on a field, is required. To achieve such knowledge, damage data at the field level is needed. Although some of this data is available on the protocols of the inspectors of the County Administrative Boards, this information is not available in the crop damage dataset. To improve the effectiveness of the crop damage dataset, facilitate the analysis of the collected data and ultimately improve management at the local level, the final point of this section is a recommendation for the Swedish County Administrative Boards to:

a. divide the reports of crop damage into single species and crops. When farmers contact the County Administrative Board, the large grazing birds may have affected several fields within the farm. Currently, the crop damage data has been collected so that one report of damage may include several species and crop types. Consequently, when the report of damage involves more than one species and crop, the data cannot always be used to disentangle species-crop type specific information
b. register georeference for each inspected field (i.e., GPS location). Such information will provide opportunities to perform studies within the staging sites and increase knowledge for management

c. combine the reports of crop damage with the information referring to yield loss. At present, data referring to yield loss is found in a separate dataset. Because the information concerning yield loss is broken down into different varieties of crops (i.e., different varieties may have different market prices), joining the two datasets for further analysis is, in some cases, not possible when damage reports contain more than one species and crop type.

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Popular science summary

Populations of geese, swans and cranes (large grazing birds) have dramatically increased in Europe and North America since the 70s due to a combination of factors: increase in conservation efforts e.g., wetland restoration and decreased hunting; agricultural intensification providing high quality of food all year-round; and warmer climate.

Large grazing birds are social and migratory species, moving across vast ranges, often staging in huge numbers (tens and hundreds of thousands of individuals) in wetlands where they roost, foraging in the surrounding agricultural land, causing yield loss for farmers, and fueling conflicts of interest between conservation and farming groups. To mitigate the conflicts arising from these human-wildlife interactions and achieve a successful management for crop damage prevention, it is crucial to know where and when damage occurs and how the relationship between damage levels and population numbers behaves. Unfortunately, few studies have tackled the question about *when* and *where* crop damage can be expected and *how* the relationships between damage levels and bird numbers interact. These knowledge gaps are even more pronounced at large spatial scales such as national and flyway levels, where political decisions about re-imbursement for crop damage, conservation and management actions are agreed. Difficulties and costs in quantifying crop damage caused by large grazing birds, especially across large spatial ranges (e.g., over all of Sweden) is the main reason for this lack of data. In Sweden however, the government launched a system in 1995 where farmers can report crop damage to the County Administrative Boards and receive economic compensation. Once the farmers have contacted the County Administrative Boards, an authorized inspector visits the field(s) to certify the damage, estimate the yield loss and identify the culprit species. In this thesis, I have investigated the unique data collected during the inspections and used data from large scale monitoring of birds and other data sources possibly affecting levels of damage (crop availability, land cover and vegetation) in four different studies to: (1) reveal temporal relationships between national bird abundance and national damage levels (across the years and from one year to another); (2) explore seasonal (monthly) patterns of crop damage across Sweden and reveal which species of large grazing birds causes what, when and where; (3) identify optimal staging areas for large grazing birds across the country (i.e., where they can gather in large numbers as their populations increase and expand) and (4) predict probability of crop damage and yield loss across Sweden if populations would expand and stablish in the predicted areas (in point 3), by relating spatial variation of crop damage to spatial variation of bird abundance and crop availability. The results of my thesis can be used to improve strategies for crop damage reduction, ultimately conservation-farming conflicts, and are as follows,

1) Over the years, the total national reports of crop damage, yield loss and costs for compensation would increase as populations of large grazing birds increase. However, these relationships are species-specific, hard to predict and from one year to another, non-existent. Why? Because there are other factors rather than just bird numbers influencing crop damage. For example, sudden heavy rains may change sudden accessibility to certain crops - which these very opportunistic species will take advantage of, leading to sudden peaks of crop damage. Also farming practices (e.g., time of harvest or distribution of crops on the landscape) can induce changes on the accessibility of resources at a certain time and prompt crop damage.

2) Within the year, crop damage occurrence and yield loss are described by seasonal (monthly) patterns, consistent across the years but differing across the country, in a way that regions with similar seasonal patterns relating to specific species and crops can be identified. These regions do not follow administrative borders. Moreover, these seasonal patterns do not necessarily correspond to when more birds are present but to periods of the year when crops are more vulnerable. Vulnerability of crops occurs when the available crops satisfy the nutritional requirements of the species that are present at that time.

3) Species' nutritional requirements change during their annual cycle: wintering, migration, breeding and moulting periods and so does their distributions. My results show that large grazing birds are not homogenously

distributed across the country, but rather display clustered distributions, concentrated in higher numbers in their main staging sites (also called hotspots) and in general, with slightly higher frequency of birds on protected wetlands, especially within dominated agricultural areas. Overall, common crane and greylag goose are more abundant in areas with higher coverage of agricultural crops, inland marshes and reed lakes, while barnacle goose is more abundant in areas with higher abundance of pastures, open lakes and coastal areas. Moreover, my results also suggest some potential hotspots where currently, birds are less abundant. This is highly relevant as these areas may identify where potential future conservation conflicts might arise.

4) The clustered distribution of birds appears to lead into a clustered distribution of crop damage. Overall, the probability of crop damage and amount of yield loss are higher at larger bird abundances. However, there could be (hypothetically) a threshold of bird abundance, above which either crop damage occurs more or simply where farmers are more likely to report it (e.g., being more aware of the risk when more birds are around). Nonetheless, this idea would need to be investigated further. My results also show that it is difficult to predict spatial amount of yield loss due to foraging birds. There are several reasons for such difficulties. One reason is that crop damage is only registered in a small area in relation to the wider, available, agricultural landscape. This means that, when we try to predict yield loss in areas where crop damage has not yet been registered, we do not really know how likely it is for crop damage to occur there in the first place i.e., is crop damage not reported because it does not occur or because farmers do not report it? Another reason is, once more, the opportunistic foraging behaviour of large grazing birds and their clustered distributions, leading to sudden peaks of crop damage when local conditions changes. Regardless, it seems that the probability for crop damage to occur across the Swedish agricultural landscape depends more on bird abundance rather than on the spatial availability of crops.

How do the findings in my thesis assists management in preventing populations of large grazing birds to damage crops? Firstly, it emphasizes that something should be done if we do not want crop damage to increase as population numbers continue increasing (as it seems it may for most species). Nowadays, adaptive goose flyway management plans (across the whole spatial range that these species occupy) are developed in Europe promoting the use of population control measures to reduce crop damage and help mitigate conservation conflicts. My research suggests that such large-scale population control strategies could be a potential tool to reduce crop damage in the long-term. However, this tool should be used with caution because the outcomes (a) are difficult to predict and may change along the population temporal tendencies, (b) differ between species and (c) are not possible to predict from one year to another. Secondly, strategies for crop damage can potentially be tailored to specific regions, targeting different species and protecting different crops at specific times of the year. Because these regions are trans-boundary, my results call for collaboration between administrative bodies (responsible for management interventions). For example, exchanging experiences of newly implemented protective measures or coordinating measures such as scaring and accommodation fields. Moreover, such collaboration could also avoid moving the conflict across the country by avoiding moving birds around as a result of scaring measures (as happened in 1999-2000, with the greater snow goose in North America). Thirdly, measures to reduce crop damage can be targeted at specific locations e.g., the main staging sites (hotspots), where larger numbers of birds concentrate. In this scenario, the probability for crop damage to occur is higher and the expected yield loss likely to be larger. Nevertheless, high yield loss can also occur with lower bird abundance. Therefore, attention needs to be paid at (a) any time large grazing birds are present; (b) newly established staging sites and (c) conditions that contribute to sudden changes in food accessibility, especially during these times of the year when crops are more vulnerable. Because these sudden local changes may lead to peaks in crop damage, local strategies to protect crops need to be ready to adapt and implement quickly.

Most of the Swedish large grazing birds' hotspots are already known. However, in a changing world with a warming climate and where new crops are introduced, populations of large grazing birds are not only increasing but also expanding geographically. Hence, there is a need to identify potential future species' hotspots to help managers target such areas to avoid conservation conflicts. My results have shown that choice of staging sites differs between species and may vary during the year, resulting in seasonal changes on the distribution of species' abundance. Regardless, high estimated abundances of large grazing birds relate to the proximity of protected wetlands within the most intensely managed agricultural areas (with more crops), amplifying the magnitude of conflicts. Large, protected wetlands assure undisturbed roosting grounds. Where these coincide with extensive areas of available crops providing birds with high quality suitable food, conflicts can arise. As large grazing birds tend to repeatedly use staging sites that guarantee and satisfy their roosting and foraging needs, agricultural land in the vicinity of protected wetlands are constantly under risk of crop damage, year after year. This may result in negative attitudes towards large grazing birds and wetland conservation projects within agricultural land being aggravated further, hence the need for conflict mitigation measures to be introduced.

Populärvetenskaplig sammanfattning

Populationerna Populationerna av gäss, svanar och tranor (härefter stora betande fåglar) har ökat dramatiskt i Europa och Nordamerika sedan 1970-talet. Populationsökningarna beror på en rad olika faktorer så som bevarandeåtgärder i form av minskad jakt och våtmarksrestaureringar , men också intensifierat jordbruk som innebär tillgång på bra föda för fåglarna året runt och ett varmare klimat som gör att fåglarna inte behöver flytta lika långt. Stora betande fåglar är flocklevande och flyttar mellan sommar och vinterområden. De rör sig således över stora områden och rastar ofta i stora antal under flytten (tio- till hundratusentals individer). De rastar ofta i områden med våtmarker där de kan söka skydd och övernatta men födosöker gärna på omkringliggande jordbruksmark. När de födosöker på växande grödor kan de orsaka skördeförluster för lantbrukare, vilket i sin tur orsakar intressekonflikter mellan naturvård (t.ex. bevarande av våtmarker dit de stora betande fåglarna lockas) och jordbruket. För att kunna hantera sådana konflikter och arbeta effektivt med skadeförebyggande åtgärder är det viktigt att ha kunskap om var och när skador på gröda uppstår och hur sambandet mellan skadenivåer och antal fåglar ser ut. Kunskapen om de här frågeställningarna är dock knapp, speciellt på större skalor som nationell och flyttvägsnivå, det vill säga på den geografiska nivå där många politiska beslut fattas kring förvaltningen av dessa arter och miljömål.

Det är generellt svårt och kostsamt att samla in bra och omfattande data på skador på gröda, speciellt över stora geografiska områden, därför saknas ofta data för att kunna lära sig mer kring sambanden mellan fåglarna och skadorna. I Sverige infördes ett system för rapportering av skador på gröda 1995. Lantbrukare kan därför rapportera upptäckta skador på gröda som tros ha orsakats av stora betande fåglar till länsstyrelserna och få ekonomisk ersättning. Länsstyrelsen skickar ut en utbildad besiktningsman som undersöker fältet och bedömer vilken art som orsakat skadan, skadans omfattning och skördeförlusten.

I den här avhandlingen har jag använt data från besiktningarna av grödoskador, samt data från storskaliga fågelinventeringar och rapporter av stora betande fåglar i Artportalen. Dessa data har kombinerats med data satellitbilder och grödor på fälten, för att i fyra olika delstudier studera: (1) relationen mellan förekomst av stora betande fåglar och skador på gröda på nationell nivå, över tid, (2) säsongsmässiga mönster av skador på gröda i Sverige från de olika arterna, (3) varför vissa rastlokaler är mer attraktiva än andra för stora betande fåglar och (4) hur sannolikheten för skador på gröda hänger ihop med fåglarnas val av rastlokalerna. Resultaten från mina fyra studier kan användas för att utveckla mer kostnadseffektiva strategier för skadeförebyggande arbete och kan i förlängningen bidra till att minska konflikter mellan jordbruks- och naturvårdsintressen.

Jag fann följande i min avhandling:

1) Över en längre tidsperiod kan man förvänta sig att skador på grödor och kostnaderna kommer att öka med ökande populationer av stora betande fåglar. Men de här sambanden ser lite olika ut för de olika arterna och det är mycket svårt förutspå hur stora skadorna kommer att bli från ett år till ett annat även om man vet hur många fåglarna är. Varför är det så? Anledningen är att inte bara antalet fåglar utan även andra faktorer påverkar hur omfattande skadorna blir, t.ex. kan kraftiga regn orsaka liggsäd där fåglarna lätt kan landa och beta i grödorna. Även åtgärder inom jordbruket kan påverka skaderisken, så som tid för skörd eller var man väljer att odla olika grödor i landskapet kan påverka hur tillgängliga grödorna är för fåglarna och därmed också risken för skador.

2) Inom åren varierar skadorna på gröda mellan månaderna. Sådana säsongsbetonade mönster skiljer sig mellan olika områden i Sverige, men för en given plats ser mönstren likadana ut från år till år. Dessa mönster gör att det går att identifiera områden i Sverige med liknande skademönster. De identifierade områdena följde dock inte de administrativa länsgränserna som normalt gäller för det skadeförebyggande arbetet. Resultaten visade även att skadorna inte nödvändigtvis uppstår när det är som flest stora betande fåglar i ett område, utan främst när grödorna är som mest känsliga för skador (t.ex. vid sådd eller strax innan skörd). Störst risk för skador på en gröda uppstår när grödan är tillgänglig och uppfyller näringsbehovet för de stora betande fåglarna som finns i området vid en given tidpunkt.

3) De stora betande fåglarnas behov förändras under året, och därmed förändras även fördelningen av fåglarna i landskapet. Stora betande fåglar är inte homogent fördelade i Sverige, utan samlas i stora antal på rastlokaler (s.k. ”hot spots”). Rastlokalerna blir extra populära om det finns både lämpliga våtmarker för skydd och övernattning och produktiv jordbruksmark där fåglarna kan söka föda. Tranor och grågäss är särskilt kopplade till jordbruksmark, inlandsvåtmarker och grunda vassjöar, medan vitkindade gäss är mer kopplade till betesmarker, öppna sjöar och kustområden.

4) Den ojämna geografiska fördelningen av stora betande fåglar innebär också att fördelningen av skador på gröda blir ojämnt fördelad över landet. Generellt innebär det större risk för skador i områden där det förekommer ett större antal stora betande fåglar i, men resultaten indikerar också att det skulle kunna finnas ett tröskelvärde som avgör hur många fåglar som krävs för att det ska uppstå skador eller då lantbrukare blir mer angelägna att rapportera skador. Det är komplext att förutspå var och när skador på gröda på grund av stora betande fåglar kan uppstå. En anledning är att skador på gröda rapporteras på fältnivå, vilket endast är en liten del av vad som är tillgängligt i jordbrukslandskapet i stort. Detta innebär att när man försöker förutspå grödoskador i områden där ännu inga grödoskador rapporteras kan man inte veta om det beror på att det ännu inte uppstått skador eller om lantbrukarna valt att inte rapportera. En annan anledning som gör det svårt att förutspå skador är att stora betande fåglar är anpassningsbara vilket kan innebära plötsliga förändringar om de lokala förhållandena förändras t.ex. häftiga slagregn som skapar liggsäd eller kyla som gör att övernattningsplatserna fryser. Oavsett så visar mina resultat att sannolikheten för skador på grödor i jordbrukslandskapet i Sverige påverkas mer av antalet stora betande fåglar än tillgängligheten av olika typer av grödor.

Hur kan nu resultaten från min avhandling användas i förvaltningen av stora betande fåglar och för att förebygga skador på gröda?

Först och främst, om målet är att minska skadenivån i Sverige, så visar mina resultat att mer behöver göras i förvaltningen eftersom populationerna av stora betande fåglar och skadorna kan förväntas fortsätta att öka. Nu för tiden finns adaptiva förvaltningsplaner för flera av gåsarterna som syftar till reglera populationer och därmed minska skadorna på gröda längs med fåglarnas flyttvägar. Mina resultat visar att sådana storskaliga strategier kan fungera för att minska skadorna på gröda på lång sikt. Men man ska ha i åtanke att effekterna av åtgärden (a) är svåra att förutspå och kan förändras beroende på hur stor populationen är, (b) varierar mellan arterna och (c) inte är möjliga att förutspå från ett år till ett annat.

Mina resultat visar också att strategier för skadeförebyggande åtgärder bör skräddarsys efter regionala förhållanden då olika arter och grödor skapar olika förutsättningar för att det förebyggande arbetet och att även årstid kan spela roll för hur förvaltningen bör agera. Eftersom det finns likheter mellan olika län och för att fåglarna rör sig över administrativa gränser innebär det att länsstyrelserna med fördel bör samarbeta över länsgränserna. Det kan gälla utbyte av kunskap kring skadeförebyggande åtgärder och dess effekter på olika arter men även koordinering av skrämsel och avledningsåkrar så man inte bara flyttar fåglarna och problemen sinsemellan, något som man sett hända med snögäss i Nordamerika. Mina studier visar också att skadeförebyggande åtgärder med fördel främst bör användas vid specifika rastlokaler där stora antal stora betande fåglar ansamlas. Vid rastlokalerna föreligger en större risk för skador på grödor, även om skador kan uppstå även vid mindre antal stora betande fåglar. Det innebär att man i förvaltningen behöver vara extra uppmärksam på risken för skador på gröda när (a) ett stort antal stora betande fåglar är närvarande, (b) vid nyligen uppkomna rastlokaler och (c) förhållanden som kan bidra till att födotillgången plötsligt förändras, speciellt under tidpunkter på året då grödor är extra känsliga för skador. Eftersom lokala förhållanden kan förändras relativt snabbt och att omfattande skador då fort kan uppstå, så är det viktigt att det finns lokala strategier för skadeförebyggande åtgärder som snabbt kan anpassas och sättas i bruk.

De flesta rastlokalerna för stora betande fåglar är redan kända i Sverige. Men i en föränderlig värld med ett allt varmare klimat, nya grödor som introduceras och våtmarksrestaureringar så kan man förvänta nya problemområden kan uppstå. Därmed finns det ett behov att identifiera de olika arternas potentiella rastlokaler (”hot spots”) för att informera förvaltarna om var intressekonflikter kan komma att uppstå. Rastlokalerna varierar mellan arter och år, vilket resulterar i säsongsbetonade förändringar i arternas utbredning. Oavsett, så innebär stora antal av stora betande fåglar i produktiv jordbruksmark i närheten av skyddade våtmarker en större risk för intressekonflikter. Ostörda våtmarker omgivna av produktiv jordbruksmark innebär att fåglarna med stor sannolik återkommer och innebär därmed en stor skaderisk för lantbruket år efter år. Sådana upprepade erfarenheter med skador från de stora betande fåglarna kan bidra till negativa attityder och motstånd mot våtmarksrestaureringar i jordbrukslandskapet bland markägare. Det är därför viktigt att ta fram tydliga mål och strategier för skadeförebyggande åtgärder och konflikthantering för att inte naturvården av våtmarksmiljöer och de arter som är beroende av dessa ska ta skada på grund av de grödoskador de stora betande fåglarna orsakar.

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Appendix

Appendix 1. Bayesian vs. Frequentist approach

On the frequentist approach, all parameters are fixed and the uncertainty (e.g., standard errors) refers to the variability of all possible outcomes after a long sequence of repetitions of the same experiment. Frequentists do not ask about the probability of the parameters themselves, but the probability of the data given certain values of the parameters. On the Bayesian approach, parameters, inferences, predictions follow their own probability distribution, which, at the same time is a measure of uncertainty (Kéry & Schaub 2012). Bayesians ask about the probability of a parameter to take a certain value (or an event to occur) given the data we have observed. Hence, it is a conditional probability, based on the Bayes' theorem (Bayes 1763) which has the form,

$$\underset{\text{Posterior distribution}}{P(\theta|\, data)} = \frac{\overset{\text{Likelihood}}{P(data|\theta)} * \overset{\text{Prior}}{P(\theta)}}{P(data)}$$

Ɵ is the parameter or the hypothesis of interest; **P(Ɵ│data)** 'posterior distribution', refers to the probability of the parameter given the data; **P(data│Ɵ)** 'likelihood', probability of the data given the parameter. This is the function that the frequentist approach tries to maximize; **P(Ɵ)** 'prior' is the probability distribution of the parameter and will need to be defined during the model process; **P(data)** is the probability distribution of the data.

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