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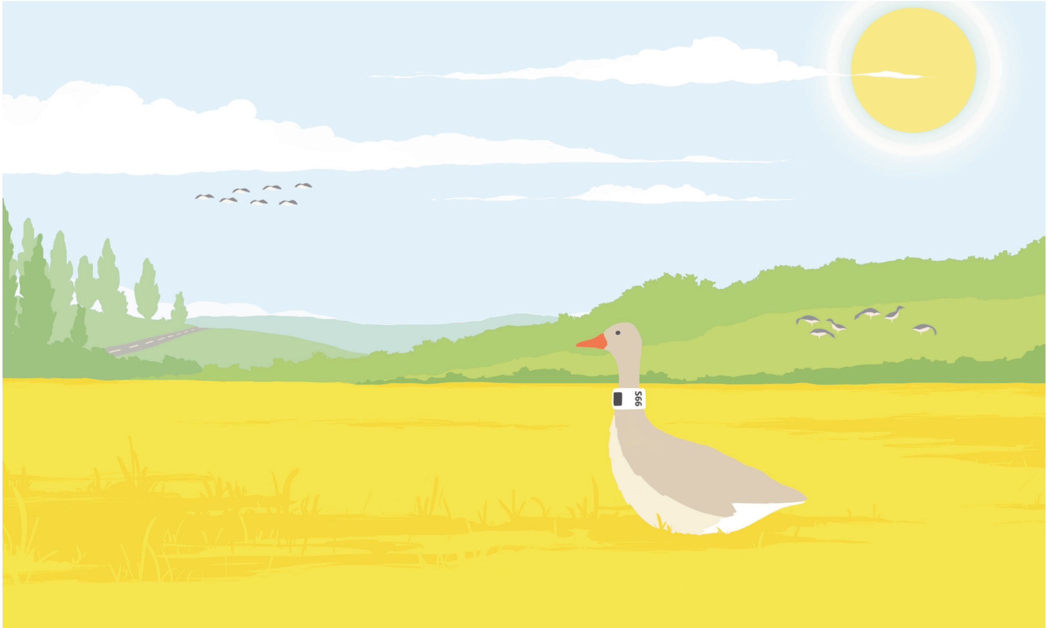
From flyway to field

Ecology and management of geese in agricultural landscapes

Camilla Olsson



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Abstract

Climate change and new agricultural practices have driven a rapid increase in numbers of most European goose populations (*Anser, Branta spp*.) and a northward expansion of their wintering range, raising growing concerns related to grazing damage to agricultural crops. To mitigate such conservation conflicts, contemporary knowledge about movement patterns and foraging site selection is needed to inform management decisions. This thesis provides ecological insights to guide management and damage prevention, from flyway to field level. Specifically, it addresses migratory patterns, foraging site selection, and local movements by geese in agricultural landscapes. My studies are based on flock surveys of multiple goose species, data derived from Greylag geese fitted with GPS devices, and data on landscape features and field characteristics. My results show that two radically different types of migration strategies occur among Greylag geese breeding in Sweden. Geese in southernmost Sweden are largely resident and remain close to their breeding sites year-round, whereas geese breeding in central Sweden still migrates. My results further show that fields located within 4 km from a roost site and situated more than 200 m from nearest forest edge or human infrastructure have a high probability to attract Greylag geese. My studies also demonstrated that selection patterns tend to vary depending on goose species, season and availability, although stubble fields in general, and barley stubble in particular, were generally selected. The combined results highlight the complexity of goose behaviour, calling for coordinated strategies and joint efforts across multiple spatial scales, from international flyway-level cooperation to collaboration among neighbouring farms and authorities, to successfully integrate the knowledge derived from my study for more accurate risk assessment and effective damage prevention.

Keywords: *Anser*, *Branta*, damage prevention, migration, resource selection

From flyway to field: Ecology and management of geese in agricultural landscapes

Abstract

Under de senaste årtiondena har många gåspopulationer ökat kraftigt i Europa. Ett mildare klimat och en ökad tillgång på vintergröna grödor har lett till att gäss tillbringar mer tid i Sverige, vilket har gjort att skador på grödor blivit allt vanligare. För att förebygga skador och förvalta gåspopulationer på ett effektivt sätt krävs bättre förståelse för vilka faktorer som styr gässens rörelsemönster i landskapet och varför de föredrar vissa fält framför andra. Denna avhandling studerar gässens migration, val av födosöksplatser samt lokala rörelser i jordbrukslandskapet. Mina studier bygger på data från flockinventeringar av flera arter av gäss samt från GPS-märkta grågäss, i kombination med fältinventeringar. Mina resultat visar att två tydligt skilda migrationsstrategier nu förekommer bland Grågäss som häckar i Sverige. De som häckar i de sydligaste delarna av landet är till stor del stationära, medan de som häckar längre norrut i Sverige är flyttfåglar. När det gäller val av födosöksplatser visar mina resultat att fält som ligger inom 4 km från gässens nattplats och mer än 200 meter från närmaste skogskant, väg eller bebyggelse har hög sannolikhet att attrahera grågäss. Mina studier visar också att gässen väljer olika grödor beroende på art, årstid och tillgång, även om stubbåkrar generellt, och kornstubb i synnerhet, ofta väljs till fördel för andra grödor. Sammantaget visar mina resultat på en betydande variation i födosöks- och rörelsebeteende mellan olika arter av gäss, årstider och platser, vilket understryker den komplexitet som präglar gässens nyttjande av jordbrukslandskapet. En effektiv förvaltning av gåspopulationer och förebyggande skador på gröda kräver därför samordnade strategier på flera rumsliga skalor från internationellt samarbete längs flyttvägen till samverkan mellan markägare och myndigheter för att kunna integrera den kunskap som genererats i mina studier i praktisk förvaltning, för en mer träffsäker riskbedömning och effektiva skadeförebyggande åtgärder.

Keywords: *Anser*, *Branta*, flyttmönster, fältval, skadeförebyggande åtgärder

Preface

In recent decades, many goose populations have increased dramatically in northwestern Europe and North America. More geese than ever now occur near humans, sometimes leading to widespread conflict between societal interests. High goose densities may inflict extensive crop damage by repeated grazing in agricultural fields, and only a fraction of this damage is reimbursed. Although the actual harvest losses by grazing geese are difficult to gauge, they may pose a serious threat to the economic sustainability of individual farmers and thus, in the long term, to the national and global food security. It is also highly relevant to address considering the European Union's increasing emphasis on resilient and sustainable food production systems. The conflict between agriculture and conservation is unlikely to subside within the near future, as most goose populations continue to grow, and today's intensively farmed landscapes offer highly favourable foraging conditions. Furthermore, current harvest levels of the abundant goose species are deemed too low to limit population growth.

Historically, goose research has largely been shaped by conservation concerns and conducted during times when agricultural practices were different. Today, the abundance and continued growth of many goose populations have become a central challenge for management, to the extent that some researchers have described these populations as "superabundant" (Fox & Madsen, 2017). Climate change and further population increases are expected to increase goose presence on farmland and further drive the northward expansion in goose distribution and related crop damage in northwestern Europe in the coming years. Addressing this conflict requires detailed knowledge of how geese utilise the landscape in the light of current conditions, including superabundant populations, climate change and agricultural practices. Such knowledge is essential for developing more effective strategies to mitigate agricultural damage and guide future management. This thesis explores movement and foraging patterns of geese in agricultural landscapes and across the flyway, with the main focus on Greylag geese (*Anser anser*) breeding in Sweden.

Dedication

Till mina barn.

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. Månsson J, Liljebäck N, Nilsson L, Olsson C, Kruckenberg H, Elmberg J (2022). Migration patterns of Swedish Greylag geese *Anser anser*: implications for flyway management in a changing world. *European Journal of Wildlife Research*, 68 (15), 1-11. https://doi.org/10.1007/s10344-022-01561-2

II. Nilsson L, Olsson C, Elmberg J, Bunnefeld N, Liljebäck N, Månsson J (2022). Leapfrog migration and residents: New migratory habits in Swedish Greylag geese. *Ecology and Evolution*. 12 (3), 1-11. https://doi.org/10.1002/ece3.8740

III. Olsson C, Nilsson L, Elmberg J, Månsson J (2025). Field selection in a guild of geese: seasonal dynamics and implications for crop damage mitigation. *Agriculture Ecosystems and Environment*. 394, 109913. https://doi.org/10.1016/j.agee.2025.109913

IV. Olsson C, Nilsson L, Elmberg J, Månsson J. Foraging site selection by Greylag geese: effects of agricultural field characteristics and landscape features. (manuscript)

V. Olsson C, Nilsson L, Elmberg J, Månsson J. From wetlands to fields: temporal variation in Greylag goose foraging distance and crop damage risk across the flyway. (manuscript)

Paper I-III are published with open access.

The contribution of Camilla Olsson to the papers included in this thesis was as follows:

- I. I contributed to conceptualisation, performed the data curation, and was involved in writing, review and editing as well as visualisation of results.
- II. I contributed to conceptualisation and performed the data curation. I contributed to analyses and visualisation of results together with L.N, and with support from N.B. I wrote parts of the original draft and was involved in editing all parts of the manuscript.
- III. I contributed to conceptualisation and designed the study together with co-authors. I performed the field surveys with contributions from co-authors and field assistants. I performed the data curation, statistical analyses, visualisation of results and writing of the original draft. I was involved in all parts of manuscript writing and editing and led the process of submission and review with support from co-authors.
- IV. I contributed to conceptualisation and designed the study together with co-authors. I performed the field surveys with contributions from co-authors and field assistants. I performed the data curation, statistical analyses, visualisation of results and writing of the original draft. I was involved in all parts of manuscript writing and editing.
- V. I contributed to the conceptualisation and designed the study together with co-authors. I performed the data curation, statistical analyses, visualisation of results and writing of the original draft. I was involved in all parts of manuscript writing and editing.

List of figures

1. Introduction

1.1 Population growth and range expansion of geese

Many populations of geese in Europe and North America have increased markedly in recent decades (Fox et al. 2010). In northwestern Europe, the total number of geese grew from approximately 3.5 million to 4.3 million between 1995 and 2008, with the Greylag goose (*Anser anser*) being one of the species showing the most notable increase (Fox et al. 2010). Since 2008, Greylag goose population in northwestern Europe has remained stable at historically high levels (AEWA 2021). However, despite these overall increases, some goose populations are declining, with current protection status in EUs Bird Directive varying among species. The population increase in Europe and Sweden is mainly attributed to changes in agricultural practices (Fox et al. 2017). The expansion of large-scale and intensified agriculture, combined with an increased cultivation of autumn-sown (winter green) crops, has unintentionally created seasonally abundant and highly attractive food resources for geese (Fox & Abraham 2017; Fox & Madsen 2017).

1.2 Factors influencing goose movement and foraging patterns

1.2.1 Migration

Knowledge about intraspecific individual variation in migration behaviour is crucial to understand patterns of phenology, changes in breeding success, resource use, and interactions with the environment. The term “flyway” is a widely used term in migration ecology, which comprise the breeding and wintering grounds, as well as the corridors used when migrating between the two. Flyways typically overlap several countries, have a north–south outline, and often comprise widely different habitats (Alerstam 1990; Boere & Stroud 2006).

Changes in migration patterns may happen as a response to short-term events (challenging weather, food shortage, etc.) that force individuals to change distance or timing of migration, or it may change because of evolutionary adaptation to long-term environmental change (e.g., land use, climate). Research accumulated over the last two decades documents significant changes in timing of migration in a wide range of avian species (Møller et al. 2010; Lehikoinen et al. 2019). This is mainly manifested by migrants arriving earlier than before to breeding grounds in spring, and in some species by a later departure in autumn (Mills 2005; Jonzén et al. 2006; Lehikoinen et al. 2019). Migration distance per se has shrunk in several species (Visser et al. 2009), and a related and widespread northward shift in wintering range in medium-and short-distance migrants in temperate areas of the northern Hemisphere has been observed in passerines, shorebirds, raptors, and waterfowl (Potvin et al. 2016; Pavón-Jordán et al. 2019).

Similar changes in migration patterns have been observed among several European goose populations (Fox et al. 2005; Podhrázský et al. 2017; Nilsson & Kampe-Persson 2018). Large-scale changes within agricultural landscapes, such as more profitable foraging and increased winter carrying capacity, have acted as important drivers not only for population growth by increased reproductive success but also for shifts in goose distribution (Fox et al. 2017). Northwestern European goose populations, including the Greylag goose, are generally expanding their winter range northwards and stay longer periods of time in the latter (Therkildsen & Madsen 2000; Clausen & Madsen 2016).

1.2.2 Food availability, quality and distance to roost in relation to central place foraging

Knowledge of how animals interact with the environment and the factors influencing resource selection are central to understanding their distribution across landscapes (Boyce & McDonald 1999; Fox et al. 2017). Geese spend a considerable amount of time on or near water, particularly during life stages when they are most susceptible to predation, such as nesting, breeding, moulting, and roosting (Cramp & Simmons 1977). The use of water bodies during these periods provides both safety from terrestrial predators, drinking water, and resting opportunities, making water and wetlands a critical component for an area to host geese (Fox et al. 2017).

Outside the breeding season, geese make repeated, daily commutes between central night roost, often located on water or in wetlands, and feeding sites located in the surrounding agricultural landscape (Chudzinska et al. 2015; Fox et al. 2017). When foraging in agricultural landscapes, geese face trade-offs among multiple environmental factors. According to the optimal foraging theory, animals are expected to select foraging sites that optimises their net energy intake while minimising energetic costs associated with movement and handling time (MacArthur & Pianka 1966). However, for large herbivorous birds such as geese, the capacity to carry out optimal foraging may be constrained by their need to repeatedly commute between feeding areas and secure roost sites (Chudzinska et al. 2015).

To account for such spatial and energetic constraints, the central place foraging theory was developed as an extension of optimal foraging theory (Orians & Pearson 1979). This theoretical framework predicts that, given that the individual goose has full knowledge of its surroundings, the probability of goose presence decreases with increasing distance from the central location (e.g., the night roost) while selectivity for high-quality feeding sites increases with distance to the central location to compensate for the energetic cost of movement (Schoener 1971; Schoener 1979; Rosenberg & McKelvey 1999).

1.2.3 Crop type and field stage

Being herbivores, geese depend on high-quality food sources, rich in protein and carbohydrates but with low fibre content (Riddington et al. 1997; Bos et al. 2005). Additionally, they are highly dynamic in their dietary selection over their annual cycle, depending on current nutritional demands and food availability in the landscape (Arzel et al. 2006).

In early spring, geese rebuild flight musculature and fat stores for the upcoming migration and breeding season, and they therefore need a high supply of food rich in protein and energy (Giroux & Patterson 1995; Sedinger 1997; Fox et al. 2017). During this time of year most geese mainly feed on managed grasslands, utilising the period of rapid plant growth, profiting from the high protein content in these plants at their onset of annual growth (Fox et al. 1994; Giroux & Patterson 1995; Sedinger 1997; Fox et al. 2017).

In autumn and early winter, when the geese have arrived in their winter quarters, they tend to select especially for foods rich in protein and fat, to repair and rebuild damaged tissues after the migration flight, and to replenish fat stores for upcoming winter demands (Giroux & Patterson 1995; Sedinger 1997; Fox et al. 2017). During this time, geese mainly feed on spilled grain left from cereal harvest in stubble fields, when available (Giroux & Patterson 1995; Sedinger 1997; Fox et al. 2017). During mid-winter, food quality and abundance is often lower, day length for foraging is shorter, and energy expenditure is higher due to increased thermoregulation. Therefore, geese typically select for foods higher in carbohydrates, such as root crops (Giroux & Patterson 1995; Sedinger 1997; Fox et al. 2017).

Geese select for food that is highly abundant, thus some of the seasonal variation in foraging behaviour reflect changes in food biomass and availability (Fox et al. 2017). Examples of seasonal changes in availability of food resources are the highly digestible and nutritious grass during the first sprouting in spring, and the short-term availability of harvest remains in autumn. In addition, certain crops become particularly attractive during specific growth or cultivation stages, i.e. “field stages”, such as pre-harvest (i.e. standing crops) and post-harvest stages (for example cereal stubble fields with spilled grain) (Fox et al. 2017). Deep snow and ground frost are shown to further affect foraging behaviour of geese, forcing them to abandon crop types such as root crops and autumn-sown cereals which they normally select in winter, and switch to foods that protrude from the snow (Fox et al. 2017). Otherwise, geese generally select for shorter vegetation, as taller crops become less nutritious and may reduce visibility and thereby increase predation risk (Fox et al. 2017; Strong et al. 2021).

1.2.4 Disturbance and predation risk

Various types of disturbances often cause geese to avoid or leave a field or an area, but also to spend more time on anti-predator behaviour such as head-raising or calling (Owens 1977; Giroux & Patterson 1995). Disturbance refers to any external factor or event that triggers a fear response, including both natural sources such as predators, as well as human activities such as traffic, active scaring measures, and hunting.

Disturbance may increase the energetic costs, as it leaves less time for feeding and alter the movement patterns of geese, which may cause temporary displacement in the distribution towards less optimal sites (Giroux & Patterson 1995; Adam et al. 2016). While the underlying causes of disturbance are diverse, their effects are often evident at the field-level, where local conditions such as vegetation structure, topography, proximity to human infrastructure and activity, directly shape spatial distribution and foraging patterns of geese. For example, environmental attributes like hedgerows, forest edges and tall crops, are all associated with perceived increased predation risk by reduced visibility and are thus generally avoided by geese (Giroux & Patterson 1995; Jensen et al. 2017).

Wetland restoration, establishment of nature reserves, and the availability of other disturbance-free refuges further influence movement patterns of geese at the landscape level. They tend to avoid areas with frequent disturbance or otherwise high, perceived predation risk, or only utilise them when other, more attractive sites, have been depleted (Si et al. 2011). As a result, the location and availability of disturbance-free refuges can shape the overall distribution of geese by displacing them from frequently disturbed areas towards protected or less disturbed sites, often leading to higher concentrations of geese in or near such refuges (Si et al. 2011; Fox et al. 2017). This may fuel conflicts between conservation and agriculture by increasing the risk of damage to surrounding fields.

1.2.5 Site fidelity

Geese exhibit site fidelity at several spatio-temporal scales, often returning to the same breeding, staging or wintering site for several years, to the same area for feeding within a season, as well as returning to the same agricultural field after being exposed to disturbance (Fox et al. 1994; Giroux & Patterson 1995; Phillips et al. 2003; Clausen & Madsen 2016; Avé et al. 2017). Returning to an area with predictable, and stable availability of resources in terms of safe foraging areas or disturbance-free roosts, is one strategy of ensuring good chances of survival and subsequent reproductive success (Fox et al. 1994; Fox et al. 2010). Thus, geese might not always select the most optimal site but instead return to a location with predictable resources of sufficient quality.

1.3 Understanding goose ecology to predict damage risk

Population growth and range expansion of geese in northwestern Europe, combined with their increased utilisation of agricultural land for foraging, have led to wide-spread crop damage and conflicts between conservation and agricultural interests. Geese cause damage to crops primarily through consumption (Flegler et al. 1987), and the risk of damage are therefore closely linked to their food and foraging site selection.

Crops that are attractive to geese and are in a growth stage particularly vulnerable to grazing, are at greater risk of damage, and especially so when located close to water or wetlands where geese tend to aggregate. Geese mainly cause damage to cereal fields and grasslands used for silage production but may also compete with livestock for food resources when foraging in pastures (Montrás-Janer et al. 2019; Jordbruksverket 2024). Because geese tend to repeatedly return to attractive and familiar foraging sites, such repeated use can cause considerable crop damage over time.

The increase in number of agricultural fields and farmers affected by goose damage has been accompanied by increasing direct costs related to yield losses and compensation schemes, and indirect costs related to damage preventive measures (Montrás-Janer et al. 2019; Frank et al. 2021; Düttmann et al. 2023). However, the total negative impact caused by geese on agricultural fields is difficult to gauge, and previous research highlights considerable variation in the extent to which grazing ultimately affects crop growth, yield and economic loss (Fox et al. 2017). Several factors may influence the extent of damage, including grazing pressure, weather, crop type, crop stage, and level of vulnerability of crop along with its ability to compensate for damage (Clausen et al. 2022). Despite this variation, grazing may have a negative impact on crops throughout the entire growing season (Montrás-Janer et al. 2020), although several studies indicate that the probability of damage increases as harvest approaches (Buitendijk & Nolet 2023; Buitendijk et al. 2023). Reported outcomes from studies of goose grazing on agricultural crops range from negligible effects to severe economic losses, with millions of euros are spent annually in the European Union alone for compensation schemes (Düttmann et al. 2023). However, the actual extent of damage is likely even higher, as some damages remain unreported or are difficult to quantify (Montrás-Janer et al. 2019; Buitendijk & Nolet 2023; Düttmann et al. 2023).

1.4 Goose management and crop damage prevention

Goose management operates at several spatial scales, from entire flyways to single fields. At the international level, the work is coordinated by AEWA (the Agreement on the Conservation of African-Eurasian Migratory Waterbirds; AEWA 1999). Within AEWA, the European Goose Management Platform (EGMP) has been formed to coordinate population monitoring across the flyways and to establish management agreements among participating countries (AEWA EGMP 2018). The management objectives of EGMP span from conservation to population control, depending on the current population status and trend of the species. At the EU level, legislation such as the EU Birds Directive also plays an important role for goose management, as it provides the legal framework for hunting and protection of the bird species, thereby regulating which goose species may be hunted and under what conditions (European Union 2009).

In Sweden, the overall responsibility for the national goose management lies with the Swedish Environmental Protection Agency (SEPA), while the County Administrative Boards (CABs) are responsible for management at the regional level with support from SEPA (Månsson et al. 2023). The CABs have several management tools at their disposal, including the authority to grant licences for derogation shooting for protected species and outside the regular hunting season, allocate subsidies for preventive measures, and economically compensate landowners for damage (Månsson et al. 2023). They are also responsible for the implementation and management of protected areas and for wetland restoration initiatives (Månsson et al. 2023). The practical responsibility for implementing preventive measures against crop damage, however, rests mainly with individual landowners and farmers, who are required to have undertaken preventive measures before applying for reimbursement for damage caused by geese (Månsson et al. 2023).

Current preventive measures can be divided into four main strategies: 1) deterring geese from vulnerable fields through scaring, 2) attracting geese to alternative, designated foraging sites where they can feed without causing damage (e.g. diversionary or set-aside fields), 3) adapting crop choice and cultivation practices to reduce risk of grazing and subsequent damage, and 4) hunting or derogation shooting (Månsson et al. 2023). Diversionary and set-aside fields are mainly used in combination with scaring, which often constitutes the primary preventive action in Sweden (Månsson et al. 2023).

For scaring to be effective, there must be alternative sites where geese are allowed to forage undisturbed, to avoid simply moving the problem to neighbouring areas (Hake et al. 2010; Simonsen et al. 2016). The implementation of changes in cultivation strategies depends on several other factors, as they must be applied in accordance with the practical and economic conditions and constraints of the agricultural system (Månsson et al. 2023). Hunting may exert both direct population-reducing effects and indirect effects by increased disturbance (Månsson 2017). However, the current hunting pressure is not considered to have a significant impact on population size for the most common goose species in Sweden (Liljebäck et al. 2021).

Successful goose management and crop damage prevention require contemporary knowledge of movements and foraging patterns in geese, as well as an understanding of their spatial and temporal variation. Such knowledge is essential for implementing preventive measures at the right time and place, and for improving their long-term effectiveness. The movement ecology and foraging behaviour of geese have been well studied. However, most of these studies were conducted under conditions that differ markedly from those of today, in terms of population sizes, distribution ranges, and the composition and management practices of agricultural landscapes (Fox et al. 2017). Given the profound changes in the ecological and agricultural conditions possibly influencing goose movements and foraging patterns over recent decades, there is a need to reassess these patterns under contemporary conditions. Additionally, although many goose populations in northwestern Europe are currently considered superabundant, some remain threatened, with low or declining numbers. Management and damage preventive strategies should therefore be designed and applied in ways that do not compromise the viability of these vulnerable populations. Even when actions are not directly targeted at such species, they may be affected indirectly (Månsson et al. 2023). Thus, understanding how species, populations, and subpopulations differ and overlap in their foraging behaviour and site selection is crucial for guiding management strategies and for reducing potential unintended effects on non-target populations.

2. Objectives

This thesis aims to improve the understanding of movement and foraging patterns by Greylag geese in agricultural landscapes across their flyway, and to link ecological insights to management and crop damage prevention. Specifically, this thesis aims to address the following objectives:

Paper I	To describe the distribution of Greylag geese across the flyway at different times of the annual cycle. I also address if these patterns differ among areas of origin in Sweden and whether they have changed over time.
Paper II	To study if Greylag geese have different migration strategies depending on area of origin in Sweden.
Paper III	To investigate if there are seasonal and interspecific differences in field selection by geese in relation to crop type and field stage (pre- or post-harvest).
Paper IV	To assess the effects of field characteristics and landscape features on foraging site selection by Greylag geese.
Paper V	To predict the foraging distance from roost sites to agricultural fields by Greylag geese and estimate the temporal and spatial variation over the annual cycle.

3. Study system

3.1 Goose ecology

Geese are large and highly selective herbivores. Outside the breeding season they generally feed during the day, mainly on agricultural crops and grasslands, and return to open waters or wetlands to roost for the night (Fox et al. 2017).

Four papers (I, II, IV, V) focus on the ecology of Greylag geese, specifically. Like most other goose species, Greylag geese are social birds that form breeding pairs which often remain together, sometimes for their entire lifespan of up to twenty years (Lorenz 1991; Nilsson & Persson 2001; Scheiber et al. 2013). Greylag geese generally form pairs already in their first or second year, and the first breeding often occurs at the age of three (Cramp & Simmons 1977; Kampp & Preuss 2005). Both parents are involved in caring for their young and the family remains together during most of the first year, with yearlings staying with their parents until the next breeding season (Cramp & Simmons 1977, Rutschke 1987; Scheiber et al. 2013). Nesting and preparation for breeding begins already in late winter and early spring when the geese return to the breeding areas from their wintering sites. During nesting, breeding, rearing of young and moulting, geese are restricted in their movements and mainly resides in wetlands, foraging in their close vicinity due to being flightless (Fox et al. 2017; Olsson et al. 2017). The incubation period lasts approximately one month (Cramp & Simmons 1977). The parents undergo moult during the rearing of the goslings and are therefore flightless but have usually completed moult by the time the goslings become fledged at around 50-60 days of age (Cramp & Simmons 1977). Greylag geese can spend up to 80% of the day foraging (Scheiber et al. 2013), during the breeding season mainly in wetlands, pastures and grasslands directly adjacent to water (Olsson et al. 2017), and later in fields in the surrounding agricultural landscape (Fox et al. 2017; Fox & Madsen 2017). During the first year, young geese follow their parents during migration, often travelling as part of a larger flock (Scheiber et al. 2013).

Outside the breeding season, geese often forage in larger, mixed-species flocks. Paper III further includes other species in addition to the Greylag goose, namely Barnacle goose (*Branta leucopsis*), Canada goose (*Branta canadensis*), Greater White-fronted goose (*Anser albifrons*), Taiga Bean goose (*Anser fabalis*), and Tundra Bean goose (*Anser serrirostris*). While established national, breeding populations exists in sizable numbers for Greylag geese, Barnacle geese and Canada geese, which occur in Sweden year-round, the other species are mainly present in larger numbers during autumn, winter and spring when they either pass through on migration or remain in the southern parts of the country throughout the winter (Haas 2025; Ottosson et al. 2025).

3.2 Population sizes and trends

Northwest/Southwest (NW/SW) European Greylag goose population has its main breeding areas in Sweden, Norway, Finland, Denmark, Germany, the Netherlands and Belgium (Nilsson et al 1999). The population includes both migratory and resident individuals, and it uses a south-westerly migration route, spanning from Northern Scandinavia across Southwest Europe to the southernmost parts of Spain (Powolny et al. 2018). There has been a northward shift in wintering area for the population during recent decades. In the early 1980s, Spain hosted the main part of the population in winter, but the proportion of greylag geese wintering in Spain has decreased since and no more than 20% of the population wintered in Spain by 2009, despite an increase in absolute numbers (Ramo et al 2015). There has also been an increase in the proportion of resident (non-migratory) individuals, that remain in the southern parts of Sweden for the winter (Powolny 2018).

The NW/SW European Greylag goose population has experienced a rapid increase in numbers in recent decades (Powolny 2018). Wetlands international (2015) estimated the total population size to 900 000—1 200 000 individuals as of 2015, and the species has remained at historically high levels since. Greylag geese breeding in Sweden has also increased, with current breeding population estimated at 50 000 pairs in 2024 (Ottosson et al. 2025). In addition to the increasing breeding population of Greylag Geese, Sweden also host Greylag geese from Finland and Norway, although the influx to Sweden from other countries is so far considered relatively low (Andersson et al. 2001; Fransson et al. 2001; Bacon et al. 2019).

However, the numbers of staging and wintering geese continue to increase, with up to 250 000 recorded in autumn and around 50 000 in mid-winter, where the wintering geese are concentrated to the southernmost parts of Sweden (Haas 2025). The EU Birds Directive permit hunting of the Greylag goose in Sweden, the open hunting season for Greylag extends from 11th of august to 31st of January. In addition, derogation shooting is permitted throughout the year on agricultural fields where the birds are causing damage.

Like the Greylag goose, the Barnacle goose has increased substantially in numbers across Europe, from an estimated 112 000 individuals in the 1980s (Madsen 1991) to a population size of approximately 1 300 000 in the 2010s (Fox & Leafloor 2018). Barnacle geese originating both from the Russia/Germany & Netherlands subpopulation (arctic breeders) and the Baltic/North Sea subpopulation (breeding in Sweden) occur in Sweden (Jensen et al. 2018). The Barnacle goose mainly breeds on islands and shorelines along the coast in Sweden and the population was recently estimated at 4 200 pairs (Ottosson et al. 2025). The highest numbers of Barnacle Geese in Sweden occur in autumn; in 2023, reported observations peaked at just under 200 000 individuals in October (Haas 2025). There is no open hunting season for the Barnacle goose as the species is protected under the EU Birds Directive, but derogation shooting is permitted in agricultural fields where the species cause damage.

Canada geese, originally native to North America, were introduced in Sweden in the 1930s (Ottoson et al. 2025). In Sweden, the species experienced a dramatic increase in numbers and range until 2000s but has since declined by approximately 20% (Ottosson et al. 2025). Breeding individuals occur throughout Sweden in lakes and along the coastline, and the breeding population is currently estimated at around 15 000 pairs (Ottosson et al. 2025). The number of autumn-staging Canada geese was estimated to 26 000–32 000 individuals in autumn 2023 (Haas 2025). In Sweden, the general hunting season for Canada goose extends from 11th of August to 31st of January, and derogation shooting is permitted throughout the year in agricultural fields where the birds are causing damage.

The breeding population of Greater White-fronted geese in Europe is estimated at 280 000-331 000 pairs, corresponding to around 560 000-662 000 adult individuals (Birdlife International 2025). The species does not breed in Sweden but passes during migration.

Roughly 1 100 individuals were observed during national counts in October of 2023 (Haas 2025). Open hunting is only permitted in the southernmost Sweden, from October 1st until January 31st.

The presence of Taiga bean geese and Tundra bean geese in Sweden consists mainly of staging and wintering individuals arriving from populations breeding in other countries. In Europe, the Tundra bean goose is considerably more abundant than the Taiga Bean goose (Fox et al. 2010). Taiga Bean goose is one of few goose species in Europe currently undergoing a population decline. Numbers in Europe have decreased from an estimated 100 000 individuals in the mid-1990s to 63 000 by 2009 (Fox & Madsen 1999, Fox et al. 2010). In Sweden, the species is a scarce breeder on mires and fens, estimated to around 1 600 pairs as of 2024, primarily found in the coniferous forests of Northern Sweden (Ottosson et al. 2025). The primary breeding range of the Tundra Bean goose spans across the tundra regions of Northern Russia, however, some 20 pairs have been observed breeding in the northern parts of Sweden in recent years (Ottosson et al. 2025). In most staging and wintering areas across Europe, Taiga bean geese occur only in small numbers among the much more numerous Tundra bean geese. In contrast, the opposite pattern is observed in Sweden (Nilsson & Månsson, 2012). In Sweden, 23 000 identified Taiga Bean geese and approximately 7,600 identified Tundra Bean geese in October of 2023 (Haas 2025). The number of unidentified Bean geese peaked at just over 44 000 individuals, also in October (Haas 2025). Taiga and Tundra bean geese are protected from hunting in Sweden, but derogation shooting is permitted in agricultural fields in southernmost Sweden between 21st of April and 20th of February.

3.3 Study areas

The study area for apers I, II and V constitutes of the main flyway used by Greylag geese breeding in Sweden, spanning across seven European countries in the southwest, from the breeding areas in Sweden to the southernmost wintering sites in Spain. Landscape characteristics vary greatly among countries and regions, but most breeding, staging and wintering sites are surrounded by intensive agricultural production or grasslands, typically situated close to wetlands or open water.

The study areas for papers III and IV are in the central and southern parts of Sweden, specifically in the counties of Örebro, Södermanland and Skåne.

Örebro county is situated farthest north, located in south-central Sweden and in the boreo-nemoral transition zone. Södermanland is located in the south-east parts of Sweden, in the boreo-nemoral zone, and the county of Skåne constitutes the southernmost part of the country, in the nemoral zone (see Hallanaro and Pylvänäinen 2002 for biotic zones). The central parts of Sweden are largely forested, but the proportion of forest decreases further south, where agricultural land increasingly dominates the landscape, as in much of Southwest-Europe. All three study areas are characterised by intensive agricultural production, but they also contain shallow lakes, wetlands, and grasslands, thus providing abundant foraging opportunities as well as suitable roost sites for all species present. These wetlands and open waters also serve as recurrent breeding sites for Greylag geese.

4. Methods

4.1 Flock surveys and individual level studies

My studies are based on two principal methodological approaches for examining spatial distribution and movement patterns of geese, each with its own advantages and limitations. Individual-level studies based on GPS location data provide highly detailed information, offering continuous tracking across the day and enabling precise reconstruction of movement paths and migration routes. Because each tagged bird is individually identifiable, these studies also provide the possibility of linking movement and foraging behaviour to known breeding origin and other individual attributes. Moreover, GPS tracking gives a much higher spatial resolution than traditional field observations, revealing exactly where a bird has been located at the within-field level. However, GPS-based approaches also have limitations. Technical issues such as device failure or data gaps may reduce the completeness of the dataset. It also remains challenging to capture and mark several species simultaneously, which complicates the inclusion of multiple species within the same study. In comparison, the precision of flock surveys is inherently limited, however, they can be conducted without specialised technology and do not require capturing or marking birds and is thus less invasive. Flock surveys further allow coverage of a larger number of individuals and the inclusion of multiple species simultaneously. However, because the birds are unmarked, no information can be obtained about individual identity, origin or life history, and observations are restricted to presence at a given time and place. The studies based on GPS location data included 76 (Papers I and II), 58 (Paper IV), and 104 (Paper V) individuals, to be compared with the study in paper III based on field surveys and flock counts, including a total of 237 105 geese of six goose species. Papers III and IV both address foraging behaviour by geese and complement each other by operating at different levels. While paper IV focuses on individual level variation, allowing a more detailed analysis of factors influencing foraging site selection by individuals, paper III provides a broader perspective by comparing patterns of field selection across multiple co-occurring species. The individual level data further enables exploration of how the same individuals adjust their movements and foraging behaviour over time and across different sites (Paper V).

4.2 Spatial and temporal scales

The studies included in my thesis cover several spatial scales from flyway level (Papers 1 and II), across breeding/staging/wintering site level (Paper V), to field level (Paper III) and foraging site level (i.e. within fields, Paper IV). Considering multiple spatial scales allows for a more holistic understanding of the movement and foraging ecology of geese, and the related management implications.

Given the pronounced seasonal variation in energetic needs as well as mobility of geese (Fox et al. 2017), variations in movement patterns and foraging behaviour is expected throughout the annual cycle. In paper III and V, the field selection and local movement patterns of the geese are studied across the full annual cycle. In papers I and II, the research questions aim specifically at the migration patterns of the Greylag geese, thus the temporal focus naturally lies when these large-scale movement patterns occur within the annual cycle, namely during spring and autumn. In paper IV, the study focused on the pre-migration period of Greylag geese, in late summer and early autumn (August–September). Late summer and early autumn coincide with a high diversity of crop types and stages, as well as with widespread availability of post-harvest cereal fields in all three study areas, providing key conditions for addressing our research questions during a period where crop damage is frequently reported.

4.3 Capture procedure

In June 2017–2019, Greylag geese were caught during breeding and moulting. A total of 161 individuals was fitted with GPS-devices. They were herded slowly by foot and/or canoe via raised net fences into corrals. There the caught geese were immediately put in gunny sacks to calm down until further handling. In addition to classical tarsal rings, geese were provided neckbands fitted with solar powered GPS tracking devices: either Ornitela (OT-N35 and OT-N44) or Made-by-Theo (Theo Gerrits). Geese were aged (juvenile or adult) based on plumage and sexed by cloacal inspection. All capturing and handling was done according to permits from the Animal Ethics Committee of Central Sweden (# 5.8.18–03584/2017).

4.4 Capture sites

Five capture sites were selected to represent a latitudinal range from central to southern Sweden, embracing the main part of the national breeding range of Greylag geese (55–61° N; Figure 1).

A) Hudiksvall (N 61° 43′, E 17° 6′) is the northernmost capture site, located by the coast of the Bothnian Sea. The site is a wetland (24.5 hectares (ha)) in an urban park area, surrounded by intensively managed grasslands including mowed lawns. The wetland holds less than five breeding pairs of Greylag geese annually, but large flocks of moulting geese.

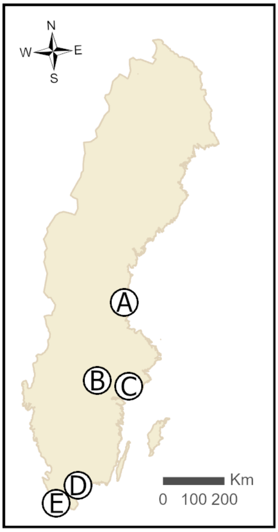

Figure 1: Map of Sweden, showing the five capture sites where Greylag geese were captured and tagged with GPS devices. A) Hudiksvall, B) Örebro, C) Nyköping, D Kristianstad, and E) Svedala.

B) The capture site in Örebro (N 59° 10′, E 15° 23′) sits within a large nature reserve (Kvismaren, 732 ha) holding vast areas of wetlands, swamp forests, and reed-beds. Management of the reserve includes cattle grazing and mowing of grassland fields to promote meadow birds. The area is surrounded by intensively managed agricultural fields and attracts significant numbers of geese for breeding, as well as for staging in spring and autumn. As large parts of the reserve are inaccessible for humans, the exact numbers of breeding and moulting Greylag geese are not known but minimum numbers of breeding pairs were estimated to 240 by the Kvismare bird observatory in 2017 and 2018.

C) In Nyköping (N 58° 58′, E 17° 9′), the geese were caught in a wetland (8.4 ha) created in 1992 to promote breeding waterfowl. It is situated in a fragmented landscape with forests interspersed by patches of agricultural fields and many lakes. Deciduous forests and extensively managed grasslands surround the wetland, which annually holds 10–20 breeding pairs, and in most years about 80–110 moulting Greylag geese.

The area (Öster Malma) was a focal site for a large-scale re-introduction program for Greylag geese in Sweden in 1970–1975 (Andersson et al. 2001).

D) The capture site in Kristianstad (N 56° 5′, E 14° 21′), is situated in two pastures on a narrow land strip between two large lakes (6200 and 1520 ha). The surrounding land comprises meadows and arable fields mixed with deciduous forests. Some 20 pairs of breeding Greylag geese and their offspring utilise the area in June, accompanied by varying numbers of moulting non-breeding birds.

E) The capture site in Svedala (N 55° 33′, E 13° 14′) consists of two artificial wetlands (2.8 and 0.8 ha respectively) situated within a golf course surrounded by beech forest and arable fields. Up to 20 families of Greylag geese utilise the area during the breeding season.

4.5 GPS-positioning (Papers I, II, IV & V)

GPS positioning rate was initially set to a default of one location per 15 min, but later came to vary, mainly due to variation in day length across the year affecting the battery charge level. Moreover, due to technical malfunction and goose mortality, GPS devices were gradually lost over time. If any birds consistently moved together (e.g., pairs or family groups) during the studies, only one individual from each group was retained in subsequent analyses.

Papers I and II: GPS locations from 76 individuals across all five capture sites were used. Individuals included were those that, between 2017 and 2021, had at least one complete annual cycle with location data from >90% of the days (i.e., GPS locations in at least 329 out of 365 days). Consequently, up to three complete annual cycles were obtained for some individuals. All data available, independent of positioning rate, was used to create migration paths routes for each individual, but when calculating mean coordinates and the proportion of locations in different countries, the data were standardised to only include one location per 24 hours.

Paper IV: GPS locations (one location every 30 minutes) from 58 individuals across three capture sites (see 4.4.B-D) during August-September of 2018 and 2019 were used. GPS location data were complemented with field surveys of crop stages and food availability, see description below.

Paper V: GPS locations from 104 individuals across four capture sites (see 4.4.B-E) during 2017-2025 were included in paper V. One, daytime location situated in an agricultural field, were randomly selected for each goose individual and date to estimate the distance to the roost location the preceding night (on water or in wetlands).

4.6 Survey of GPS locations within agricultural fields (Paper IV)

Paper IV was based on a combination of GPS location data and field surveys. We surveyed locations used by GPS tagged individuals and randomly distributed locations (i.e. representing the availability of foraging sites), in agricultural fields situated within the daily foraging range of a specific individual. One GPS location per goose, located on arable land and not in flight, was randomly selected for a survey, from the data derived from the previous day. A buffer was created around the night roost location with the radius based on the maximum, daily flight distance of the goose, and a second location to be surveyed was randomly assigned to agricultural land within this buffer. The buffer was based on individual, maximum distance between the last GPS location at the night roost and each of the daily goose locations situated within arable fields that day. During the surveys, we noted crop type and field stage (pre- or post-harvest).

In total, 262 goose locations and 262 related, randomly distributed locations were surveyed across three study sites (B, C and D, Figure 1), allocated from the 58 individuals included in the study. For surveyed foraging sites (used and randomly distributed) situated in harvested cereal fields, biomass of spilled grain was also estimated. To assess the influence of cereal type and abundance of spilled grain on field selection when geese used harvested cereal, such sites were treated separately during field surveys as well as later in the analyses. In total, we surveyed 100 used locations and 100 randomly distributed locations, derived from 52 unique individuals located specifically on harvested cereals.

4.7 Flock surveys of geese on agricultural fields (Paper III)

Paper III was based on monthly surveys of goose flocks present on agricultural fields, including six different goose species in total. Field surveys were carried out monthly in the area of Örebro (see Figure 1, site B) from April 2018 to March 2021 (in total 27 months; no counts in December—February when geese were not present), and in the area of Kristianstad (Figure 1, site D) from October 2017 to September 2021 (48 consecutive months). In each study area surveys of geese and crops were done along two routes: one inner (nearer) and one outer (more distant) encircling major waterbodies used by geese as roost sites (Figure 2). The inner routes were 29 km and 30 km, and the outer routes 70 km and 75 km in North and South, respectively.

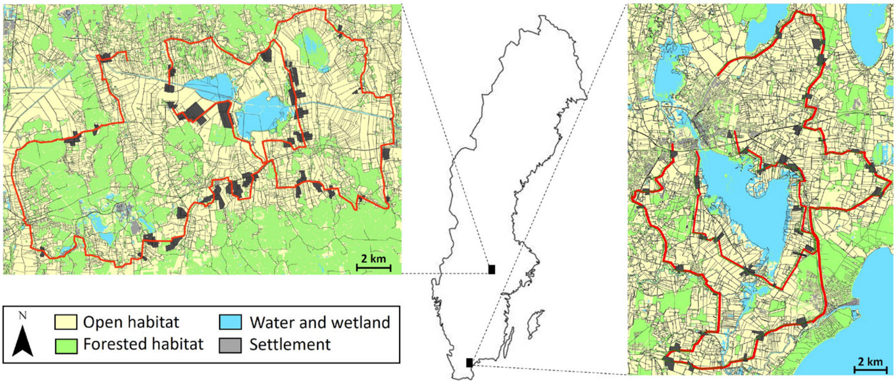

Figure 2: Location of the study areas in Sweden included in Paper III (left map = ‘Örebro’; right map = ‘Kristianstad’). The describes the main habitat types. Red lines show the routes of monthly surveys conducted. Along these routes, all geese present on agricultural fields and identifiable to species were counted, and crop type and field stage were recorded. To assess field availability, data on crop type and field stage were also collected from randomly distributed reference fields (dark grey), which were surveyed on every occasion, regardless of goose presence.

All geese observed on agricultural land (i.e., cropland and pastures) along a survey route were counted and identified to species. Crop type and field stage (pre- or post-harvest) in fields used by geese were noted.

In addition to these observation fields, where goose presence differed among survey occasions (i.e. goose use of fields), 36 permanent survey points were distributed along the routes in each study area. These points were randomly distributed along the routes with a minimum distance of 1000m between them and they served as fixed locations for selecting permanent reference fields. Each point was adjacent to one or several agricultural fields (i.e. ’reference fields’), whose individual crop types and field stages were recorded on each survey occasion, regardless of goose presence, to quantify availability of different field types to geese. The total number of such reference fields along the survey routes was 134 in the northern study area and 93 in the southern study area (Figure 2).

4.8 Additional data and data processing

4.8.1 Crop type and distance to landscape features (Papers III & IV)

As some crops were only available in a few fields, some combinations of crop type and field stage (i.e. pre- or post-harvest) were subsequently pooled into new categories to ensure statistically manageable analyses (see papers III & IV). However, different field stages were always treated separately, as knowing whether the crop was still growing or had been harvested was deemed especially relevant for risk assessment of potential crop damage. The field surveys served as the primary source for crop type classification, while supplemental information on field level crop type (e.g. for hybrid varieties or recently sprouted crops, such as cereals in early growth stages) was obtained from the SAM14 administrative database provided by the Swedish Board of Agriculture (Jordbruksverket).

In paper IV, spatial information from cartographic sources was incorporated to characterise key landscape features. Specifically, distance from night roost, distance to nearest forest edge and human infrastructure (e.g. roads or buildings) were obtained using a combination of cartographic sources and administrative records. Data on land cover were retrieved from the Swedish Land Cover Map provided by the Swedish Environmental Protection Agency (Naturvårdsverket 2018) and later used to calculate the distance to nearest forest edge. Spatial information from national authorities (Swedish national topographic map, Lantmäteriet 2023) was used when calculating distance to human infrastructure, i.e. roads and buildings.

Distance to the latest night roost location the preceding night, to each goose location or available location was also measured. All distances (i.e. from night roost locations, and to forest edge and human infrastructure) were calculated in ArcGIS Pro ver. 3.4.0 (Esri 2025).

4.8.2 Foraging distances, day of the year and habitat classification (Paper V)

In paper V, “day of the year” and latitude were to estimate potential temporal and spatial variation in foraging distances over the annual cycle. “Day of the year” (i.e. 1-365) was transformed into two circular components using sine and cosine functions, thus ensuring that 1st of January and 31st of December are treated as adjacent days. To estimate the foraging distance from night roosts to agricultural fields, the geodetic distance in metres between each daytime location and its related nighttime location was calculated.

Furthermore, effects of availability of agricultural land on foraging distance as well as differences in foraging distance among night roost sites were included in paper V. The availability of agricultural land in the landscape for individual geese was estimated by calculating the proportion of agricultural land within a narrow buffer of 2m along the flight trajectories (1m on each side). Land cover classification was based on the CORINE Land Cover dataset provided by the European Environment Agency. Paper V focused on the foraging distance between night roost sites located on water or wetlands, and foraging sites in agricultural fields. Accordingly, we only included locations on water and wetlands for nighttime locations and in agricultural fields for daytime locations.

4.9 Statistical analyses

4.9.1 The Net Squared Displacement (NSD) modelling framework (Paper II)

In paper II, the scale-independent net squared displacement modelling framework, developed by Bunnefeld et al. (2011), was used to quantify distance, timing, and duration of autumn and spring migration for Greylag geese from each capture site. The analysis is based on data on spatiotemporal displacement (i.e., net squared displacement, “NSD”) of individual geese during the annual movement cycle.

The NSD value is calculated using the squared distance (km2) based on a straight line from the starting location (July 1 each year) to all consecutive daily locations for each individual and annual cycle (July 1 year t to June 30 year t + 1). Specifically, we used a non-linear mixed model (package nlme) based on the following equation (derived from Bunnefeld et al. 2011):

$$\mathrm{NSD} = \frac{\delta_a}{1 + \exp\left(\frac{\theta_a - t}{\varphi_a}\right)} + \frac{\delta_s}{1 + \exp\left(\frac{\theta_s - t}{\varphi_s}\right)}$$

The terms δa and δs represent the asymptotic height of the annual movement cycle (i.e., movement distance during autumn and spring), θa the date of reaching half of the asymptotic distance during autumn migration, θs the date of reaching half of the spring migration distance to the sites of origin (i.e., timing), and φa and φs the number of days lapsed to cover a quarter of the distance moved (from ½ to 3/4 of the asymptotic migration distance) in autumn and spring (i.e., duration), respectively. The equation is divided into two sub-equations to allow for variation in movements in autumn versus spring (e.g., differences in timing and duration due to potential alteration of staging sites or migration triggers) (Bunnefeld et al. 2011). NSD values (km2) were used as response variable, capture site (Figure 1) as a fixed-effect variable of distance, duration and timing of autumn and spring movement, and goose ID as a random effect on migration distance.

To test if Greylag geese breeding in Sweden differ in their migration pattern depending on origin, model predictions were used to identify the month when geese from each capture site (Figure 1) reached their asymptotic distance and calculated mean coordinates for geese from each capture site at that time. To obtain mean coordinates, we first calculated the mean value for each individual having data from multiple annual cycles and then estimated the grand mean for all individuals from each capture site.

To test for individual consistency in migration strategy over consecutive annual cycles, data were extracted from individuals that had NSD covering at least two consecutive annual cycles (n = 43) and estimated the Pearson correlation coefficient between the NSD values for individuals at each given point in time (days since July 1) during an annual cycle (i.e., 2017/2018 vs. 2018/2019 and 2018/2019 vs. 2019/2020) and the following. All statistical modelling was carried out in R (version 3.6.3; R Core Team 2020).

4.9.2 Binomial mixed models & resource selection functions (Papers III & IV)

Field (Paper III) and foraging site (Paper IV) selection were analysed by comparing use in relation to availability in the landscape (i.e. relative probability of goose presence in fields or foraging sites, Lele & Keim 2006). All models in papers III and IV used a binomial error structure and logit link function and they were conducted using the "glmer" and "glm" functions in the R package "lme4" (Bates et al. 2023). Variables that did not meet the criteria for normality was log-transformed prior to analysis.

Paper III: Study area (n=2, figure 2), season (spring, summer, autumn, winter), and goose species (Barnacle goose, Canada goose, Greater White-fronted goose, Greylag goose, Taiga bean goose, and Tundra bean goose) were treated separately to avoid overfitting of models. Consequently, 17 separate global models were assessed, each comprising a unique combination of study area, season, and goose species. All 17 global models had the same setup, with goose presence (binomial) as the response variable, and field type and size (km2) as explanatory variables. Field size was included as a fixed effect in the models to account for larger fields having higher probability of goose presence just by chance, due to their larger area.

Paper IV: Two separate models were fitted to assess factors influencing foraging site selection by Greylag geese. Model 1 was based on the total sample (58 individuals), to assess the influence of the following explanatory variables on foraging site selection: field category, distance from night roost, distance to forest edge and to human infrastructure. Model 2 was restricted to harvested fields and a subsample (52 individuals), assessing the influence of cereal type and abundance of spilled grain on selection when geese forage on harvested cereal. Thus, cereal type and abundance of spilled grain were added to the explanatory variables, which were otherwise the same as in the Model 1. Furthermore, Model 2 only included two of the three study areas (Kristianstad and Örebro, see "capture sites" in Figure 1) as the total sample size of stubble fields was too low in Nyköping. To account for potential behavioural differences among them, "study area" was included as a random effect in the Model 1, as previous research has shown that Greylag geese may behave differently depending on origin (Papers I-III). In Model 2, however, the variance explained by "study area" was non-significant, with zero variance contribution, and the term was therefore omitted to improve model stability.

In both papers (III & IV) model assumptions, including checks for multicollinearity, were assessed following the protocol outlined in Zuur et al. (2010). Furthermore, model selection was carried out using the “dredge” function from the MuMIn package in R (Barton 2025), to generate and compare all possible subsets of fixed effects. The model with the lowest AIC was considered the best-supported, for each of the global models (Burnham & Anderson 2002).

4.9.3 Generalised additive models (Paper V)

In paper V, two generalised additive mixed models (GAMMs) were fitted using the “bam” function in the R package “mgcv” (Wood 2017), to estimate foraging distance of Greylag geese and assess the temporal and spatial variation over the annual cycle. Model 1 used “Day of year” as the temporal explanatory variable, and Model 2 used “Latitude” as the spatial explanatory variable. In both models, the response variable was the log-transformed foraging distance, and the proportion of agricultural land was included as an additional fixed effect. The variables for proportion agricultural land and latitude (Model 2) were standardised (mean-centred and scaled by one standard deviation) prior to analysis to improve model fit and to facilitate comparability of effect sizes.

In model 1, “day of year” was included as a cyclic, smoothed function to capture temporal patters in foraging distance across the annual cycle. To allow for deviations from the general, temporal trend depending on the origin of individual geese, i.e. where they were initially tagged, an additional smoothed function varying by “Origin” (Örebro, Nyköping, Kristianstad, Svedala) was included. In model 2, the scaled variable “latitude” was modelled depending on the origin of individual geese.

Individual (“Goose ID”, n = 104), night roost site (“Night roost ID”, n = 510), and year (“Year”, n = 9) were included as random intercepts in both models, to account for potential individual variation, variation among night roost sites, and yearly differences. Both models were fitted with a Gaussian error distribution, using the fast restricted maximum likelihood method (fREML; Wood et al. 2015), which provides efficient and stable smoothness estimation for large datasets. Visual inspection of QQ-plots, histograms, and residuals versus fitted values were performed to assess normality and homogeneity of variance as outlined in Zuur et al. (2010).

5. Results and discussion

5.1 Migration patterns of Greylag geese (Paper I-II)

The Greylag geese breeding in Sweden show a cohesive south-westerly autumn migration corridor and a north-easterly return direction in spring, with very few individuals deviating from this pattern (Figure 3). The combined paths and thus the flyway outline suggested by the locations in the entire sample ranges from the coastal areas of the Bothnian Sea in the northeast, to southern Spain in the southwest.

GPS locations were obtained from eight countries in total; the majority were within Sweden (on average 74% for all individuals), followed by lower proportions in the Netherlands (9%), Denmark (8%), and Germany (8%), the three countries where most of the migrating individuals spent the winter. Less than 5% of the locations were found in Belgium or France, and only one individual migrated to Spain and two individuals to France, thus representing <0.05% of the locations, respectively.

Geese tagged at the southernmost capture site Svedala showed very limited movements overall, some birds appearing to be more or less resident and only making local movements (82% of the locations within Sweden). The individuals from Svedala that left Sweden migrated no farther than across Öresund to nearby Denmark. Birds from the second site in southernmost Sweden (Kristianstad) were also mainly resident and non-migratory (96% of the locations within Sweden). Despite a large share of resident birds at both these southern sites, the general axis of movement was SW-NE, conforming to the general flyway outline. In contrast, geese tagged at the three northerly sites left Sweden for the winter (62–66% of the locations per individual within Sweden, except for one goose that remained in the southeast of the country.

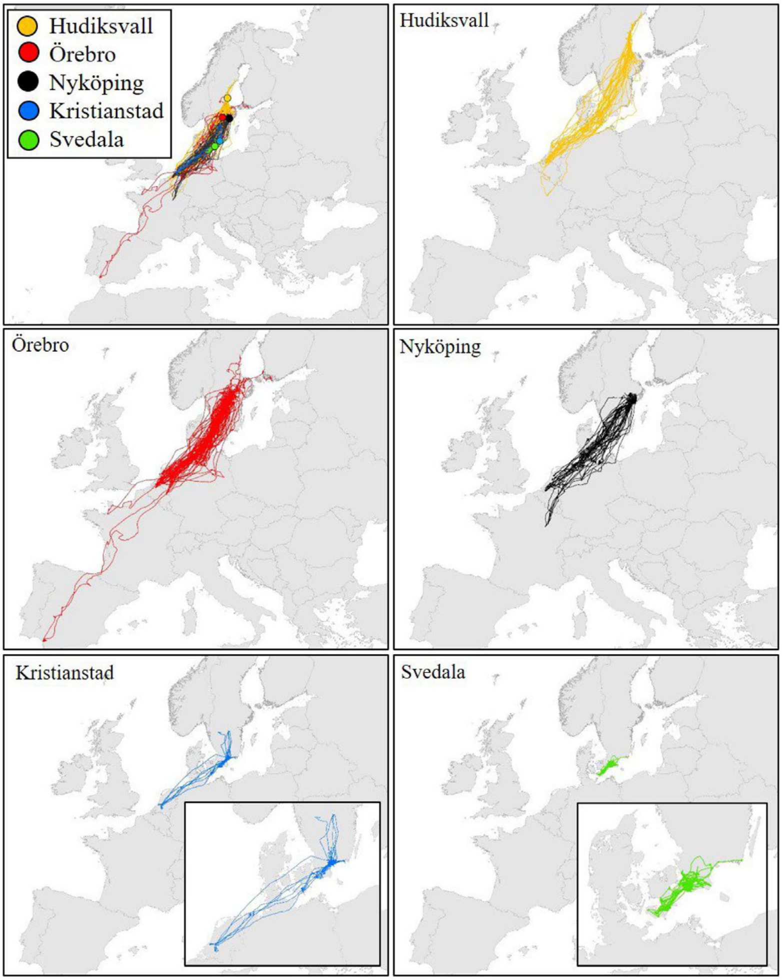

Figure 3: Migration paths by GPS tracks for 76 Greylag geese originating from five different capture sites in Sweden (from Paper I).

The findings in paper I indicated that Greylag geese breeding in Sweden may have switched migration strategy from a “chain migration” where all individuals migrate similar distances, to a “leapfrog” pattern in which northern breeders overshoot southern breeders in autumn and winter, thus with migration distance increasing with breeding latitude (c.f., Salomonsen 1955, Alerstam & Hedenström 1998; Newton 2008). This pattern was confirmed in paper II, showing that geese from the northernmost site on average migrated farther south and about 15 times as far as the short-moving or resident geese from the two southernmost sites (Figure 4 & 5).

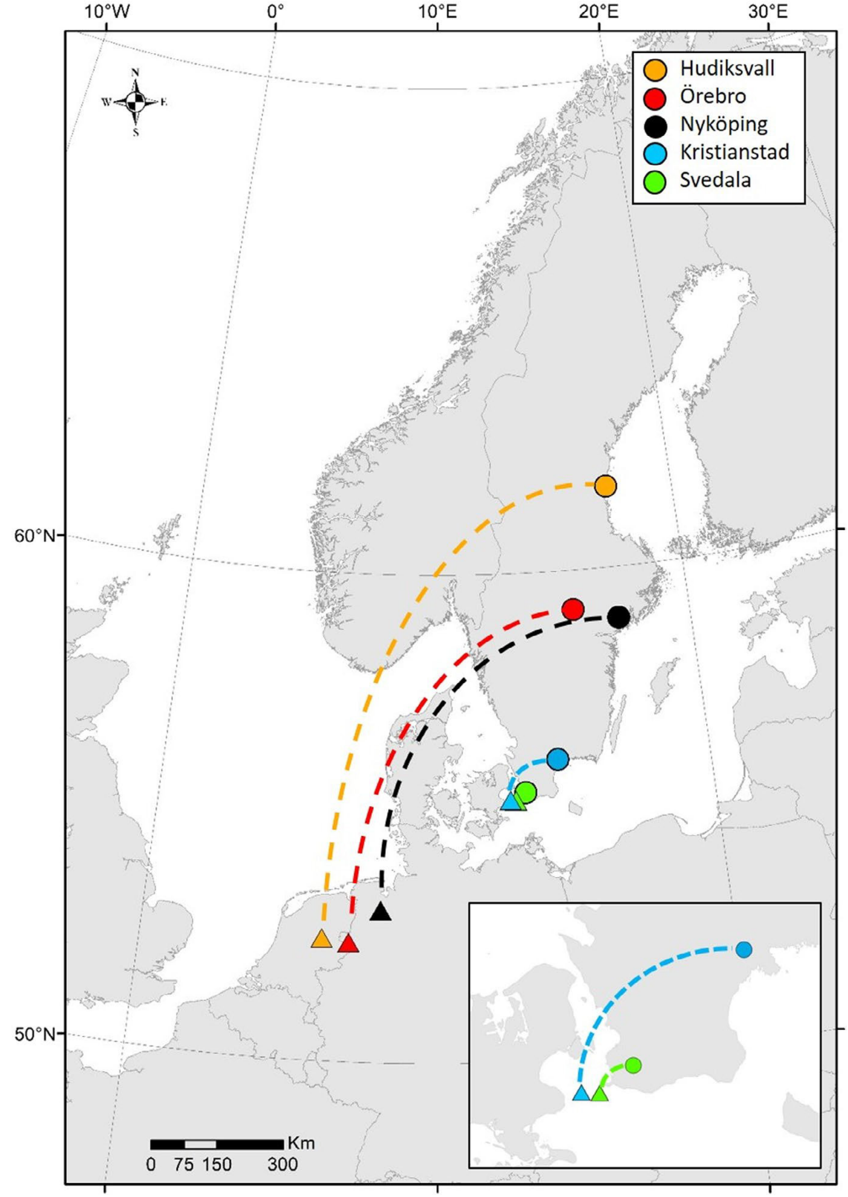

Figure 4: Capture sites (circles) and coordinates (triangles) for mean GPS locations at the predicted mean date when individuals from each capture site have reached the asymptotic migration distance (i.e., farthest distance from the capture sites). Dashed lines do not represent actual migration routes (from Paper II).

Geese from Örebro reached half their migration distance in autumn by the beginning of October, followed by those from Nyköping a week later, Hudiksvall by the end of October and the few geese migrating from Kristianstad reaching half their migration distance by the end of November. During spring migration geese had covered half of their migration distance back to Örebro by the second week of February, followed by geese from Kristianstad and Nyköping roughly a week later, and geese from Hudiksvall by early March. Duration of autumn migration ranged between 1-8 days across all capture sites, with geese that migrated the farthest (Hudiksvall) also migrating the fastest. Spring migration was slower than autumn migration in geese from the three northernmost capture sites, with an average duration ranging between 10-16 days.

A more detailed picture of the migration patterns of Greylag geese breeding in Sweden has been provided by the results in papers I and II, with similarities as well as dissimilarities compared with previous studies. Although the general flyway outline has not changed, thus corresponding well to patterns described earlier (Andersson et al. 2001; Fransson & Pettersson 2001), a much smaller fraction of geese nowadays continues southwest to historical wintering areas in France and southern Spain. The main wintering area has shifted far to the northeast, to the Netherlands and Denmark. A sizeable proportion now winter in Sweden, where wintering Greylag geese were unknown 30–40 years ago (Andersson et al. 2001). The results from papers I and II imply that the change in migration patterns has continued and that it has been more pronounced in the southernmost part of the country (Figure 3 & 4). Thus, papers I and II demonstrate that Greylag geese originating from different regions show not only different migration strategies but also a different degree of change.

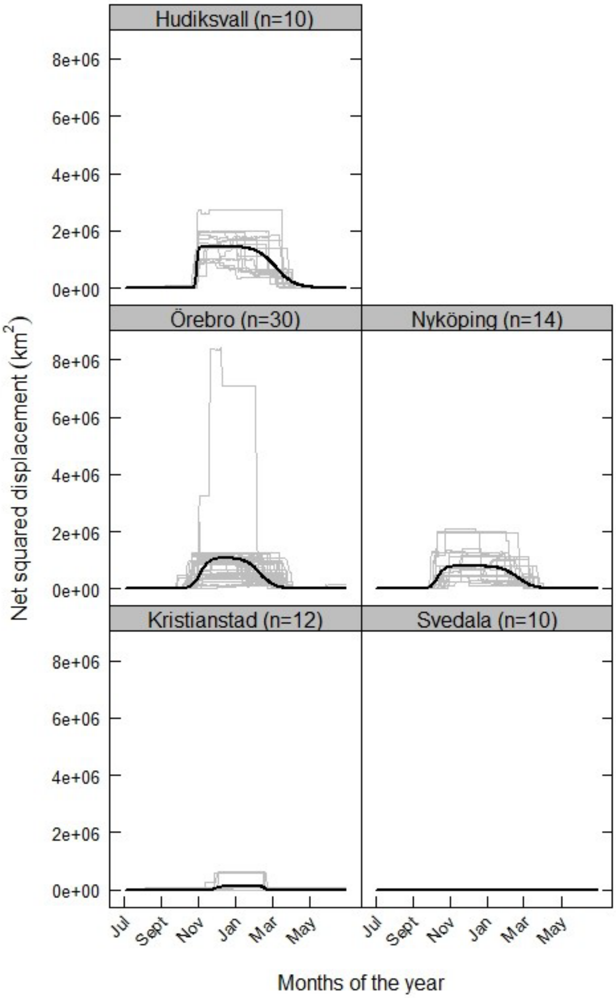

Figure 5: Net squared displacement, from paper II, based on GPS data over the annual cycles (July 1 to June 30, 2017–2020) for individual Greylag geese (grey lines) originating at five capture sites in Sweden; Hudiksvall (n = 10), Nyköping (n = 14), Örebro (n = 30), Kristianstad (n = 12), and Svedala (n = 10). Model predictions (black lines) show the mean movement strategy for geese from each capture site and are based on a non-linear mixed model with the net squared displacement distance (km2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effects on the asymptotic migration distance. The Y-axis is kept constant for comparison.

5.2 Field selection by co-occurring goose species in the agricultural landscape (Paper III)

Several overarching trends were found in field selection and use of growing crops across species and study areas but also considerable variability, particularly among seasons. In total, 237 105 geese were counted across study areas, years, and seasons. Slightly more than one third (37%) was found in post-harvest fields, 32% in fields used for livestock feed production (growing ley and pasture), and 31% in fields with other types of pre-harvest crops. Fields used for livestock feed production, such as pastures and ley fields, were typically the most selected in spring and summer, as were postharvest fields when and where available in summer. In autumn and winter geese mainly selected post-harvest fields. Selection for growing cereal crops was generally higher in winter and spring. This is in line with previous research demonstrating such patterns, which are often related to shifts in nutritional needs between seasons (Fox et al. 2017). Geese tend to select fields with food that are locally highly abundant, thus some of the seasonal variations in distribution and field selection of geese might be due to spatial and temporal variation in food biomass and availability in the landscape (Fox et al. 2017). Furthermore, some indications of variation across species were found, and especially so during winter in the southernmost study area where multiple species co-occurred. Three species stood out as deviating more in their selection in winter; Canada geese appear to be selecting winter- green autumn-sown cereals, Greater White-fronted geese have the strongest selection for ‘lawn-like’ grasslands (i.e., ley), as do also Taiga and Tundra bean geese in spring (i.e., ley and pasture). These potential, interspecific differences in field selection may reflect variation in migratory strategy, breeding status, or general habitat preference among species (Fox et al. 2017).

5.3 Foraging site selection in relation to landscape- and field level features (Paper IV)

The results show that foraging site selection by Greylag geese is not only influenced by available crops but also a combination of factors in the surrounding landscape, such as distance from roost site and distance to forest edge and human infrastructure (Figure 6). In line with previous studies, the probability of Greylag goose presence increased with increasing distance to forest edge and human infrastructure, with a negative effect most pronounced within ~200 m. Factors associated with increased disturbance risk have been linked to elevated energetic costs due to increased vigilance, more frequent flight take-offs, and re-distribution to less favourable sites (Owens 1977; Adam et al. 2016; Jensen et al. 2017). The relationship between foraging site selection and distance from human infrastructure may not only reflect a response to increased predation risk and reduced visibility near tall structures, as it may also be influenced by more frequent presence and disturbance from humans. It is also likely that active scaring occurs more frequently in areas where people keep a closer watch on agricultural fields near residential housing and roads. Since the configuration and intensity of human infrastructure relative to agricultural land vary considerably among regions (e.g. road type and density, building clustering), absolute distance thresholds should be regarded as context-dependent and applied with caution. Greylag geese were also found to be more likely to select fields close to the roost sites (Figure 6). The majority of individuals use fields located within only a few kilometres from the night roost, the mean distance between night roost and used fields was 3 km, the median was slightly below 2 km.

The influence of distance from roost on field selection is often attributed to reducing the energetic cost of movement and is evident in most herbivorous waterfowl and for geese in particular (Baveco et al. 2011; Johnson et al. 2014; Fox et al. 2017). However, the average and maximum distances at which geese make foraging travels from the roost tend to vary greatly among species, populations, seasons, and study sites in previous studies (Johnson et al. 2014; Fox et al. 2017).

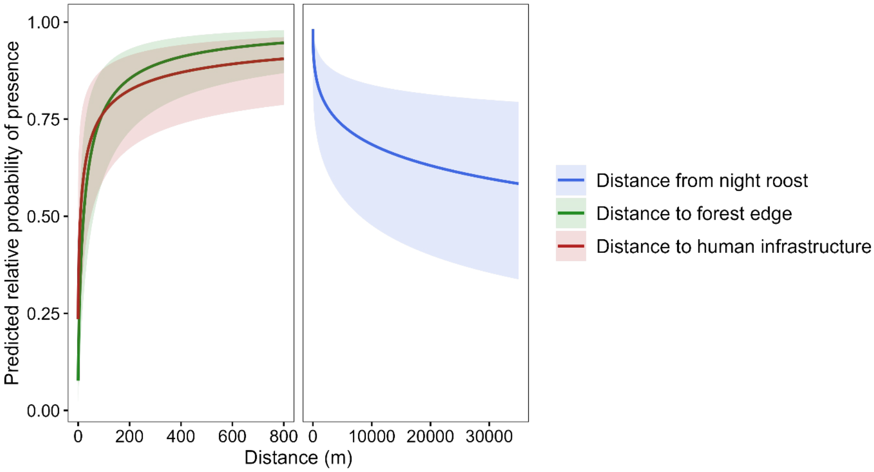

Figure 6: Goose presence and distance to roost, forest edge and human infrastructure (Paper IV). Effect of distance to closest forest edge, human infrastructure (left panel), and from the last location at the night roost site used the preceding night (right panel) on the relative predicted probability of presence of Greylag geese on cereal stubble, derived from Model 1 in paper IV (binomial GLMM with logit link; "site" as a random intercept). Each continuous variable was predicted separately, with the other variables held constant at their respective predicted median values within the field category "cereal stubble". Curves show marginal predictions (fixed effects; averaged among sites) with 95% confidence intervals computed on the link scale and back-transformed to metres. Note the different x-axis scales (0–800 m in the left panel; up to 35 km in the right panel). "Cereal stubble" was used as a reference field category.

Consistent with what was found in paper III, probability of presence of Greylag geese was approximately twice as high in fields with cereal stubble and pasture, relative to other available crops, during late summer and early autumn (Figure 7). However, even though Greylag geese tended to select pastures and harvested cereal fields, there was a notable relative probability of presence also on growing crops. No effect of field level abundance of spilled grain was detected when Greylag geese foraged on harvested cereal; however, barley was selected in favour of other cereals.

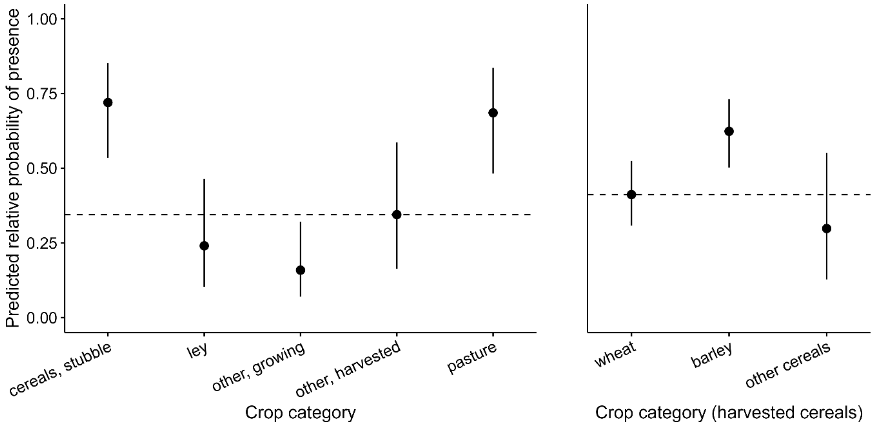

Figure 7: Predicted relative probability of Greylag goose presence by field category (Paper IV). Panel A (Paper IV, Model 1; binomial GLMM with logit link and "site" as random intercept) shows the effect of the crop categories "cereals, stubble", "ley", "other, growing", "other, harvested", and "pasture". Panel B (Paper IV, Model 2; binomial GLM with logit link) shows the effect of harvested cereal types: "wheat", "barley", and "other cereals". In both models, predictions are based on other continuous variables held at their median values and averaged across sites for Model 1. Points represent marginal predictions with 95 % confidence intervals; the dashed line indicates the model-specific median predicted relative, probability.

5.4 Temporal and spatial variation in Greylag goose foraging distances

The study in paper V revealed that variation in foraging distance was quite low, the vast majority (90%) of locations in agricultural fields were situated within 4 km from the night roost sites, independent of season and site. Occasional foraging distances of Greylag geese exceeding 50 km from night roost to agricultural fields were observed, but most foraging distances were considerably shorter.

Temporal variation emerged as the most influential variable. The general trend showed that foraging distances were shorter in spring and summer and longer in autumn and winter (Figure 8), but no significant latitudinal variation was found. Predicted, foraging distances peaked in early September at 2.9 km (95% CI 2.48–3.28), remained longer during autumn and winter, and decreased in spring (Figure 8). Foraging distances remained generally short during spring and summer, with a minimum distance from night roost predicted at 700m in April (95% CI 600–800).

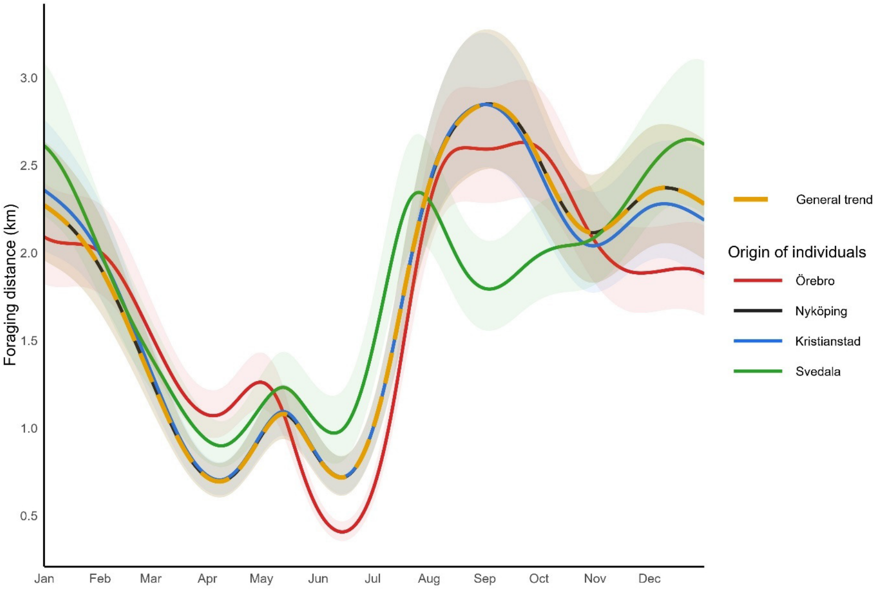

Figure 8: Foraging distances over the annual cycle (Paper V). Predicted foraging distances (i.e. distance moved from night roost site to agricultural fields) in km, of Greylag geese breeding in Sweden, modelled as a cyclic, smoothed function over the annual cycle (dashed line) and with separate, smoothed functions depending on the origin of individuals included in the study (Örebro, Nyköping, Kristianstad, Svedala; coloured, solid lines). Distance was measured as the geodetic distance between a daytime location in an agricultural field and roost location the preceding night. The predictions were derived from a Generalised Additive Mixed Model (Model 1), with "Goose ID", "Night roost ID", "Year" included in the model as smoothed, random intercepts). The covariate "Proportion agricultural land" was set to its scaled, centred mean (0) and random intercepts were excluded from the predictions. Each curve was predicted separately, with the other functions by origin or general annual function, held at their respective median values. Predictions and 95% confidence intervals were computed on the link scale and back-transformed to kilometres for visualisation. Major grid lines and x-axis labels mark the first day of each month.

Still, the annual, non-linear pattern aligns well with our predictions, as geese were expected to undertake shorter foraging movements during the nesting, breeding, and moulting periods, when mobility is limited and the nutritional demands differ (Fox et al. 2017). Some variation depending on origin was found in the relationship between foraging distance and time of year, compared to the general, temporal trend (Figure 8).

Geese originating from Örebro exhibited shorter foraging distances during autumn, winter and summer and the individuals originating from Svedala, had relatively shorter foraging distances during autumn, but longer during winter and spring (Figure 8). However, the deviations from the general trend exhibited by geese from Örebro and Svedala corresponded to 1 km or less (Figure 8). Although this represents a proportionally large difference given the generally short foraging distances, the impact of the increased energetic costs on the energy budget of individual geese is likely minor if increased movements by 1 km greatly improves the availability of high-quality foraging sites. Furthermore, it does not substantially alter the management implications derived from our results. In addition to the temporal variation, the potential variation in foraging distance in relation to latitude was also examined, but no relationship could be found.

This study presents a broad-scale perspective on some temporal and spatial drivers affecting foraging distances of Greylag geese. Despite occasional long, daily flights, the vast majority of locations (90%) of geese foraging on agricultural fields were found within 4 km of their night roosts. This distance can therefore be considered a general "risk zone" within which foraging geese is most likely to occur. Given the negative relationship observed between number of goose locations and foraging distance, one can still expect damage mitigation measures such as diversionary fields to be increasingly efficient with decreasing distance to roosts within these 4 km. Conversely, highly attractive, vulnerable, or economically valuable crops should preferably be located more than 4 km from major roosts to minimise the risk of damage caused by foraging geese. When planning wetland restoration or the establishment of reserves, it is therefore crucial to ensure that alternative undisturbed foraging sites are available within a few kilometres, to avoid foraging and subsequent damage by geese on surrounding agricultural land. The spatial extent of crop-damage risk around wetlands frequently used for roosting by Greylag geese appears relatively consistent across years and within the migratory range for Greylag geese breeding in Sweden, suggesting that management recommendations may be broadly applied across the flyway.

6. Management implications and future perspectives

Population size, trends and distribution are mainly addressed at the flyway level, for example through coordinated population surveys as well as joint harvest and conservation strategies, while measures preventing damage are often implemented at regional and local levels. For example, the establishment of diversionary fields or reserves are made within the scale of staging sites, while measures such as scaring or derogation shooting are performed at the field level, often initiated and implemented by individual farmers or landowners. To achieve a more effective management of geese, a range of spatial and temporal scales need consideration, from the flyway to field level, and across the annual cycle.

6.1 Flyway and national level management

The results from papers I and II implies that Greylag geese breeding in Sweden have progressively abandoned former wintering sites in the southwest (Spain, France) and that individual birds may change migration strategy during their lifetime. My results further shows that two radically different types of migration strategy now occur among Greylag geese breeding in Sweden, depending on where in Sweden the breeding area is located. Today, Greylag geese originating from the three northerly capture sites in our study constitute a common management concern for all countries within the flyway, i.e., from Sweden to Spain. Even so, and although the flyway still embraces the southernmost countries such as Spain and France, Greylag geese originating in these three northern capture sites still spend much of their annual cycle within Sweden, and almost all of it in Sweden, Denmark, the Netherlands, and Germany combined. In addition, Greylag geese tagged at the two southernmost sites spent 97 and 100% of their time in Sweden and Denmark only. Consequently, the appropriate delineation of management units may vary from a regional to an international scale depending on the origin of geese and the migratory habits in specific breeding areas.

The spatiotemporal patterns demonstrated in papers I and II further reveal that Greylag geese seem to stay close to their respective capture site from April to September. From this perspective, this period would be best suited for monitoring Greylag geese, if the aim is to estimate the national breeding population size of Sweden. However, this assumption presumes that a possible influx of staging geese from Norway and/or Finland and moulting geese from other countries is either negligible or possible to control for.

In terms of managing population size, current harvest levels are not deemed sufficient for effective population control or reduction (Liljebäck et al. 2021). However, knowledge about when different subpopulations is present in certain areas, and when different subpopulations are more prone to mix, are important if a need arises to target or to avoid harvest of certain subpopulations. Regardless if the goal is an even harvest of the Swedish population or targeting specific problem areas, hunting should preferably take place before migration starts in late September, i.e. when geese still reside near their breeding area, to maintain some degree of control over which part of the population is being reduced. On the same note, if management incentives are to target the southernmost part of the Swedish population, hunting during September and October is likely less effective, as local subpopulations are more prone to mix with staging flocks of geese from other breeding populations passing through the area on their southward migration.

6.2 Regional and local level management

On a regional level, targeting damage mitigation efforts within 4 km of frequently used roost sites are recommended to effectively reduce damage. This distance can therefore be considered a general “risk zone” within which foraging geese is most likely to occur. Given the negative relationship observed between number of goose locations and foraging distance, one can still expect damage mitigation measures such as diversionary fields to be increasingly efficient with decreasing distance to roosts within these 4 km. When planning wetland restoration or establishment of reserves, it is also crucial to ensure that alternative undisturbed foraging sites are included in the plan to minimise the risk of conflicts between conservation and agriculture.

In such planning, distance to wetlands should be taken into account as well as distance to nearest forest edge or human infrastructure, crop type and field stage. For example, post-harvest crops (particularly barley stubble) yielded a high predicted probability of use, and foraging sites located more than 200m from nearest forest edge or human infrastructure were attractive to geese. The spatial extent of crop-damage risk around wetlands frequently used by roosting Greylag geese appears relatively consistent across years and along the flyway. This suggests that management recommendations may be broadly applied across the flyway.

Delayed ploughing or harrowing of cereal stubble and post-harvest root crops can further help maintaining alternative foraging opportunities and thereby reduce damage risk to nearby growing crops. This is especially true throughout winter in areas when geese occur all year, i.e. when mitigation of damage risk to autumn-sown crops may be required (Gill et al. 1996; Kubasiewicz et al. 2015, Montrás-Janer et al. 2020). This supposes such practices do not conflict with regulations for farming, for subsidies, or other important aspects of agricultural management, such as crop rotation or practical constraints related to soil and weather conditions. On the same note, the overall high selection for grasses and cereals in late autumn, winter, and early spring makes the time of sowing a crucial aspect. Since too intense goose grazing can become a serious and costly problem any time during this period (Montrás-Janer et al. 2019; 2020), sowing cereals in spring may eliminate or reduce grazing problems during the months goose numbers in some areas peaks. Furthermore, by postponing the time of sowing the total amount of time the crop is potentially subjected to grazing, and possibly damaged, is reduced. The same argument can be applied to oilseed rape. However, changes in sowing time must be assessed in the context of local feasibility, as crop-specific growth requirements, soil conditions, and potential impact on economic returns may limit the extent to which sowing time can be adjusted.

My findings not only demonstrate where in the agricultural landscape Greylag geese are most likely to feed, but also where potential damage to crops is most likely to arise. Conversely, highly attractive, vulnerable, or economically valuable crops should preferably be located more than 4 km from major roosts to minimise the risk of damage caused by foraging geese. Such crops may include autumn-sown cereals and newly established ley-fields that are highly selected by geese at certain growth stages, but also especially valuable and sensitive crops like vegetables in which the economic loss even under low foraging pressures can be severe. When this is not possible, it is advisable to be prepared to implement other means of management such as scaring practices and/or derogation shooting, preferably in combination with diversionary fields (Simonsen et al. 2016; Teräväinen et al. 2022; Jager et al. 2023).

6.3 Management implementation

Even though my studies have resulted in specific management recommendations for how to improve the accuracy of risk assessment and how to increase the effectiveness of damage preventive measures, they also demonstrate considerable variation that needs to be accounted for. Such variation is evident at both temporal and spatial scales, such as differences in migration patterns among Greylag geese breeding in Sweden, as well as variation in foraging site selection among goose species, seasons, and regions. Thus, the combined results from my studies highlight the complexity of goose foraging- and movement behaviour within the agricultural landscape, and consequently, the challenges associated with implementing effective crop-damage prevention strategies. Effective management of goose populations and damage mitigation therefore requires coordinated strategies and joint efforts across multiple spatial scales, from flyway-level collaboration to regional and field-level cooperation among neighbouring farms and regional authorities, to successfully integrate the knowledge generated from my studies into practical management planning.

Moreover, all management efforts must operate within the legal framework, provided primarily by the EU Birds Directive regulating, for example, hunting and derogation shooting at the national and regional levels. In addition to legal constraints, other limiting factors include the availability and structure of economic compensation schemes, which are typically devised and decided at the regional and national levels. Furthermore, the ability of farmers and landowners to implement damage-preventive measures locally is often restricted by what is temporally, economically, and practically feasible within the context of prevailing farming practices and conditions.

6.4 Future research needs

6.4.1 Continuous knowledge update of goose migration strategies

With expected continued changes in climate combined with the proven long-term change and plasticity in migration by Greylag geese observed in papers I and II, there is a need for continuously updated knowledge. Future monitoring of movements and migration strategies of European Greylag geese is therefore needed for designing appropriate management schemes. Such considerations are likely to apply not only to Greylag geese, but to other goose species as well

6.4.2 Further understanding of interspecific and seasonal variation in goose foraging behaviour

The influence of landscape features and field characteristics studied in paper IV is limited to a single species and season, and it remains uncertain whether similar patterns would be observed also during other parts of the annual cycle and for other species. Seasonal differences in availability, abundance, and quality of crops and other resources, as well as potential shifts in nutritional demands and habitat requirements of geese, are likely to influence their behaviour and thus the selection process across the year. Considering the vast differences in population size and management needs of different goose species, often co-occurring across the flyway, such information is vital for effective and sustainable management of goose populations.

The unexpected positive effect of proportion agricultural land on foraging distance in paper V, remains intriguing and warrants further investigation. Agricultural landscapes are inherently dynamic systems, often changing rapidly even from day to day, due to ongoing agricultural activities. In combination with the structural heterogeneity in the landscape, this creates a fine-scale mosaic of foraging sites that vary greatly in attractiveness to geese. Such temporal and spatial variability may obscure or dilute broader landscape-level relationships, highlighting the need for future studies to incorporate more fine-grained landscape- and field level features. Knowledge about potential relationships between proportion agricultural land and movement patterns of geese can provide valuable insights for anticipating how they may respond to future changes in land use and landscape composition, and for evaluating the generality of such patterns under changing conditions.

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Popular science summary

Over recent decades, many goose populations across northwestern Europe have increased substantially. A warmer climate and increased availability of winter green crops have further contributed to geese spending more time in Sweden, with some remaining year-round in the southern parts of the country. Geese often gather in large numbers at wetlands, lakes, and rivers to nest, moult, and rest overnight, and forage in the surrounding agricultural landscape. This may result in extensive crop damage, leading to economic losses for farmers. To prevent such damage and to manage goose populations effectively, we need a better understanding of the environmental factors that shape goose movements and their distribution in the landscape, and why they choose to feed in certain fields over others. Changes in climate and agricultural practices have unintentionally created more favourable conditions for geese, altering both their population size and distribution. As a result, new knowledge of goose movement and foraging behaviour in today's agricultural landscapes is essential. By studying these patterns, we can improve our understanding of goose behaviour and develop more accurate risk assessments and increase the efficiency of damage mitigation measures, thus reducing economic losses and ease potential conservation conflicts.

Like many bird species, most geese in Europe are migratory. This means they spend spring and summer in one area to breed and raise their young, and winter in another area farther south. Sweden hosts breeding geese, migratory geese passing through during spring and autumn, and overwintering geese. The timing, duration and destination of their migration varies among individuals and goose species, but many travel long distances and often cross several national borders along their migratory routes. Geese are herbivores and feed exclusively on plants. Their foraging behaviour changes throughout the year depending on nutritional needs and what is available in the landscape, such as different crops in various stages of growth. Their behaviour is further influenced by other factors, particularly landscape features that limit visibility or increase perceived predation risk. These may be natural, such as the presence of predators, or human-related, such as hunting, scaring, or other disturbances associated with human presence such as proximity to roads and buildings.

Local conditions, including vegetation height and structure, shrub cover, forest edges, hedgerows, and topography may also affect the behaviour and distribution of geese. Certain crops are particularly attractive to geese and highly vulnerable to grazing, especially when located near wetlands or water where geese roost. Geese commonly cause damage to cereals as well as grasslands and pastures used for hay production or grazing grounds for livestock. Because geese often return repeatedly to attractive fields, grazing can lead to substantial damage to crops. In recent years, the number of affected fields and farmers has increased, as have the direct and indirect costs associated with crop damage and measures to prevent such. The overall negative impact of goose grazing is, however, difficult to estimate, as studies show large variation in how grazing ultimately affects the growth and yield of crops and economic loss. The level of damage depends on several factors, such as the number of grazing geese, weather conditions, soil type, crop types, and the plant's ability to recover from grazing. Despite this variation, goose grazing can affect crops throughout the growing season, with the risk of damage increasing closer to harvest. Reported economic losses amount to several million Euros annually within the EU, and the true economic loss is likely even greater, as some damage goes unreported or is difficult to measure.

Goose management is challenging because several species often occur together and some have different management needs. While many populations have increased, some are declining. Management is further complicated by the fact that most geese are migratory and cross multiple national borders, requiring coordinated efforts across countries. Management operates at multiple levels. Internationally, cooperation among member states of EU includes shared management plans and coordinated monitoring, and the EU Birds Directive provides the legal framework for which species may be hunted. In Sweden, the Swedish Environmental Protection Agency (Naturvårdsverket) coordinates the national management of geese, while county administrative boards are responsible for the implementation of regional measures such as granting permits for derogation shooting, providing financial support for preventive measures, and economically compensating farmers for damage. Farmers themselves carry much of the practical responsibility for preventing damage and must implement appropriate preventive measures before economic compensation can be granted.

Preventive measures generally fall into four main categories: (1) scaring geese from vulnerable fields, (2) directing them to alternative foraging areas where they can feed undisturbed and without causing damage to crop (for example diversionary fields or reserves), (3) adjust choice of crop types and farming practices to avoid damage, and (4) hunting as well as derogation shooting. Effective management requires up-to-date knowledge about goose movement and foraging behaviour, as these patterns change with shifts in climate, populations, and agricultural practices. At the same time, management needs to take into account that some goose populations are declining, so it is important to avoid actions that could harm vulnerable or unintended groups of geese. Understanding behavioural differences and similarities between goose species and populations is therefore crucial.

My studies on Greylag goose migration covers eight European countries, from Sweden in the north to Spain in the south, encompassing breeding, staging, and wintering areas throughout the flyway. Studies focusing on foraging behaviour and local movements (Papers III and IV) were carried out in central and southern Sweden (Örebro, Södermanland, and Skåne), all within the core breeding range of Swedish Greylag geese. These landscapes are dominated by intensive agriculture but also include shallow lakes, wetlands, and grasslands that provide feeding and resting opportunities. My work combines data from flock counts (Paper III) covering several goose species, and GPS-tracked Greylag geese (Papers I, II, IV, and V). These data were complemented with field surveys of crop type, crop stage (growing or post-harvest), food availability, and landscape features such as distance to roosts, roads, houses, and forest edges.

Papers I and II examined the large-scale movements of Greylag geese breeding in Sweden. Clear differences in migration strategies could be observed depending on where the birds were captured and tagged. Geese from the southernmost sites (Svedala and Kristianstad) showed limited movements year-round and appeared largely resident near their respective breeding areas, with individuals rarely leaving Sweden. In contrast, almost all geese from Nyköping, Örebro, and Hudiksvall migrated south during the winter period. The results further showed that the migrating geese had a very consistent migration pattern, with a south-westerly autumn migration and a north-easterly spring return, with only a few exceptions. Across all GPS positions, the full migratory corridor stretched from the Bothnian Sea coast in northeastern Sweden to southern Spain.

Of all recorded positions, most occurred in Sweden (74%), followed by the Netherlands (9%), Denmark (8%), and Germany (8%). Less than 5% were in Belgium or France, and only one individual reached Spain.

The level of crop damage depends strongly on which crops geese select and whether these are grazed before or after harvest. In Paper III, over 237,000 geese were counted. Of these, 37% were found on cereal stubble (post-harvest), 32% on grasslands and pastures, and 31% on growing crops. During spring and summer, geese mainly selected grasslands, while in autumn and winter they selected stubble fields and harvest residues from crops such as carrots, potatoes, and sugar beets. Growing winter cereals were selected primarily during winter and early spring. These patterns match previous findings that goose foraging shifts seasonally with nutritional needs of geese as well as crop availability. Species-specific differences were also observed, for example Canada geese mainly selected winter-sown cereals, while White-fronted geese grazed almost exclusively on grasslands.

To predict where geese are likely to forage, we need to understand what factors they consider when they select fields. Paper IV showed that crop type alone does not explain why some fields are selected in favour of others. Instead, a combination of factors, including distance to roosts, forest edges, and human infrastructures such as roads and buildings, also plays an important role. Geese were more likely to use fields farther from forest edges and human infrastructure, especially within 200 metres. They also selected fields near their night roost site, with 90% of all goose positions occurring within 4 km of the night roost. This well-known behaviour reduces energy expenditure by minimising travel costs. By keeping flights short, this behaviour helps geese save energy and allocate more time for feeding. Consistent with Paper III, Greylag geese mainly selected cereal stubble and grasslands, with these fields being twice as likely to attract geese compared to other crops. Although they mostly used harvested crops, they also used growing crops to a large extent, highlighting the importance of preventive measures.

Because geese roost on water and forage in surrounding fields, understanding how far they typically travel to forage is essential for assessing how far from the roost sites there is a risk of crop damage. Paper V showed that Greylag geese generally travel short distances from their roosts: 90% of their daily travels were shorter than 4 km, although occasional flights exceeded 50 km.

Foraging distances were shorter in spring and summer and longer in autumn and winter, likely influenced by breeding and moulting constraints when the geese are unable to fly. No major variation was found across years or along their flyway, suggesting that management recommendations can be broadly applied.

Effective goose management must operate across multiple spatial and temporal scales. While population trends and migration patterns are handled at the flyway level, preventive measures, such as establishment of diversionary fields, scaring, or derogation shooting, take place regionally or locally. Legal frameworks (e.g., the EU Birds Directive), limitations of economic compensation systems, and practical farming constrains the implementation of preventive measures.

Greylag geese breeding in Sweden have largely abandoned their former wintering grounds in southwestern Europe and now wintering farther north. Different migratory strategies exist depending on where in Sweden they breed. Northern-breeding geese require international coordination across the flyway from Sweden to Spain, while southern-breeding geese spend nearly the entire year in Sweden and Denmark. Therefore, different management strategies may be required depending on breeding area. The period April–September is well suited for monitoring Swedish breeding populations, as most birds remain near their breeding sites. Understanding when different subpopulations mix or remain separate is important, if the management stratgeis aim to target or avoid certain groups of geese. Hunting early in the open hunting season is preferred, when birds remain near their breeding sites, to be to be able to control which part of the population is harvested. If the goal is to target Greylag geese that breed in southernmost Sweden, hunting in September and October is likely less effective. During this period, local birds tend to mix with geese from populations breeding in other Nordic countries, which pass through the area during their autumn migration.

Based on my findings, damage preventive measures should be concentrated within 4 km of wetlands frequently used by geese. When planning wetland restoration or new reserves, it is essential to ensure nearby alternative feeding areas exist within this range, otherwise geese may feed on surrounding crops and potentially cause damage. At the field scale, the highest likelihood of having geese on a field occurred within 4 km of a roost, in open landscapes, and with a distance more than 200 m from nearest building or road.

Diversionary fields should therefore be placed in high-risk areas that match these conditions. Leaving stubble fields unploughed longer can also provide attractive alternative feeding sites, reducing pressure on vulnerable crops, especially during late autumn and winter when autumn-sown cereals are most exposed to grazing. Sowing cereals in spring rather than autumn can further reduce the risk of damage in areas where geese are numerous in winter, because the crop is then exposed to grazing for a much shorter period. Similar reasoning applies to autumn-sown oilseed rape, although sowing timing must always be balanced with crop requirements and other practical constraints for agricultural production.

My results not only demonstrate where Greylag geese typically forage but also where crop-damage risk is highest. Growing crops at high risk of damage should ideally be located more than 4 km from wetlands or waters used as roost sites by geese. This includes, for example, autumn-sown cereals and newly established grasslands, which are particularly sensitive and attractive at certain growth stages. It also applies to high-value and vulnerable crops such as vegetables, where even low grazing pressure can lead to substantial economic losses. When these adjustments are not feasible, it is important to be prepared to implement alternative management measures to prevent damage.

Populärvetenskaplig sammanfattning

Under de senaste årtiondena har många gåspopulationer ökat kraftigt i Sverige, liksom i nordvästra Europa och Nordamerika. Det varmare klimatet och den ökade tillgången på vintergröna grödor har lett till att de också tillbringar mer tid i Sverige. I de södra delarna av landet finns det numera gäss året runt. Gäss samlas ofta i stora antal i våtmarker, sjöar och mindre vattendrag, för att häcka och rugga samt för att spendera natten, där de betar på omkringliggande jordbruksmark. Detta kan leda till omfattande skador på grödor, vilket i sin tur innebär ekonomiska förluster för lantbrukare. För att kunna förebygga skador på gröda och förvalta gåspopulationerna på ett effektivt sätt krävs bättre förståelse för vilka faktorer som styr gässens rörelsemönster i landskapet och varför de föredrar vissa fält framför andra. De förändringar vi har sett under de senaste årtiondena vad gäller klimat samt ett förändrat och alltmer intensifierat jordbruk, har skapat gynnsammare förutsättningar i landskapet för gässen vilket har lett till förändringar i gåspopulationers storlek och utbredning. Därför behövs ny kunskap om gässens rörelsemönster och födosöksbeteende i dagens jordbrukslandskap. Genom att studera gässens födosöks- och rörelsemönster kan vi bättre förstå deras uppträdande i jordbrukslandskapet, vilket i sin tur kan bidra till mer träffsäkra riskbedömningar och effektivare skadeförebyggande åtgärder. På så sätt kan de ekonomiska förlusterna minska och målkonflikterna mellan bevarande av gäss och hållbart jordbruk dämpas.

Precis som många andra fågelarter är majoriteten av gäss i Europa flyttfåglar. Detta innebär att de under vår och sommar befinner sig i ett område för att häcka (dvs. ruva och ta hand om sina ungar) och tillbringar vintern i ett annat område, ofta längre söderut. I Sverige har vi både häckande gäss, gäss som passerar under vår- och höst flytt som stannar och rastar, samt övervintrande gäss. Var de häckar, rastar och övervintrar varierar både inom och mellan arter, men gemensamt för många gäss är att de kan flytta långa sträckor och ofta korsar flera landsgränser under sin flytt. Gäss är herbivorer, och lever uteslutande av växter och växtdelar. Deras födosöksbeteende förändras mycket över året beroende på både näringsbehov och vad som finns tillgängligt i landskapet som till exempel grödor i olika växtstadier. Gässens födosöksbeteende påverkas också av andra faktorer, framför allt av landskapselement som begränsar deras sikt eller på annat sätt upplevs som en ökad risk för att bli utsatta av rovdjursattacker, och därför undviks.

Sådana faktorer kan vara naturliga, som risken för faktisk närvaro av rovdjur, eller mänsklig i form av ökad närvaro och störningar. Exempel på mänskliga störningar kan vara jakt, skrämselåtgärder, samt infrastruktur såsom vägar och bebyggelse. Lokala förhållanden som växtlighetens höjd och struktur, förekomst av buskage, skogspartier eller häckar, samt terrängens topografi är andra faktorer som kan påverka gässens födosöks- och rörelsemönster.

Grödor som är särskilt attraktiva för gäss och extra känsliga för bete löper större risk att skadas, särskilt om de ligger nära vatten eller våtmarker där gäss ofta samlas. Gässen orsakar framför allt skador på spannmålsfält och på gräsmarker som används till foderproduktion, och de kan också konkurrera med tamdjur om födan på betesmarker. Eftersom gäss ofta återvänder till attraktiva platser, kan ett upprepat bete på samma fält leda till omfattande skador på grödan. Antalet fält och lantbrukare som påverkas av gässkador har ökat kraftigt under de senaste åren, liksom de direkta och indirekta kostnaderna kopplade till skördeförluster och skadeförebyggande åtgärder. Men, den totala negativa påverkan från gäss på jordbruksmark är dock svår att uppskatta och tidigare forskning visar att effekterna varierar mycket när det gäller hur betet påverkar grödornas tillväxt, skörd och de ekonomiska förlusterna. Flera faktorer kan påverka hur stora skadorna blir, till exempel antal gäss som betar på fältet väderförhållanden, jordmån, typ av gröda samt grödans förmåga att återhämta sig efter bete. Trots denna variation har bete av gäss visat sig kunna påverka grödor under hela växtsäsongen, även om risken för skador verkar öka ju närmare skördetid man kommer. Resultat från studier visar att skador på grund av gåsbete kan variera från obetydliga till mycket allvarliga, med ekonomiska förluster på flera miljoner euro varje år enbart inom EU. Det verkliga skadeläget är troligen ännu större, eftersom en del skador inte rapporteras eller är svåra att mäta.

Förvaltning av gäss är särskilt utmanande eftersom flera arter ofta förekommer tillsammans och kan ha olika förvaltningsbehov. Många gåspopulationer har ökat i storlek, men det finns också några arter som det går sämre för. Dessutom är förvaltningen av gäss en internationell utmaning, eftersom många arter är flyttfåglar som korsar flera landgränser under året. Det innebär att ett framgångsrikt arbete kräver kunskap och samarbete mellan aktörer, från fält till flyttväg.

Gåsförvaltning sker på flera nivåer. Internationellt sker det ett samarbete inom EU med gemensamma förvaltningsplaner och koordinerad övervakning av gåspopulationer.

EU:s fågeldirektiv utgör den juridiska ramen och reglerar vilka arter som får jagas. I Sverige ansvarar Naturvårdsverket för den nationella samordningen, medan länsstyrelserna genomför förvaltningsåtgärder regionalt. De kan bland annat bevilja skyddsjakt, ge bidrag till skadeförebyggande åtgärder och ersätta lantbrukare för skador. Det praktiska arbetet med förebyggandet ligger till största del på enskilda markägare och lantbrukare, som också är ålagda att vidta egna skadeförebyggande åtgärder innan de kan ansöka om ersättning för skador på gröda. Skadeförebyggande åtgärder kan delas in i fyra huvudstrategier: 1) att skrämma bort gäss från känsliga eller särskilt utsatta fält, 2) att styra dem till alternativa födosöksplatser där de inte orsakar skada, 3) att anpassa grödoval och odlingsmetoder, samt 4) att tillämpa jakt eller skyddsjakt. Effektiv förvaltning kräver aktuell kunskap om gässens rörelsemönster och födosöksbeteende, eftersom dessa mönster har förändrats i takt med förändringar i klimat, gåspopulationer och odlingssystem. Samtidigt måste förvaltningen ta hänsyn till att vissa populationer är hotade och att åtgärder inte får påverka sårbara arter negativt. Därför är det viktigt att förstå hur olika arter och delpopulationer skiljer sig åt, eller överlappar, i sitt beteende.

Mitt studieområde sträcker sig över åtta europeiska länder, från Sverige i norr till Spanien i söder, vilket täcker in såväl häckningsområden, rastlokaler och övervintringsområden för de grågäss som häckar i Sverige. De studier som rör gässens födosöksbeteende och lokala rörelsemönster (studie III och IV) är koncentrerade till de centrala och södra delarna av Sverige, närmare bestämt Örebro, Södermanland och Skåne län, vilka alla ligger i det huvudsakliga häckningsområdet för grågässen i Sverige. Samtliga studieområden kännetecknas av intensivt jordbruk, men rymmer även grunda sjöar, våtmarker och gräsmarker, vilket erbjuder goda födosöksmöjligheter samt lämpliga rast- och viloplatser för de gåsarter som förekommer där. Mina studier innefattar data från både flockinventeringar (studie III) av flera arter av gäss, och från GPS-märkta grågäss (studie I, II, IV och V). Dessa data har kombinerats med inventeringar i fält som innefattar gröda, grödostadie (växande eller skördad) och födotillgång, samt kartmaterial för att uppskatta bland annat avstånd till övernattningsplats, vägar, hus och skogskant.

Syftet med studie I och II var att undersöka och beskriva de storskaliga rörelsemönstren hos grågäss som häckar i Sverige. Resultaten visade ett konsekvent flyttningsmönster med en sydvästlig flyttkorridor under hösten och en nordostlig återflyttning på våren, där endast ett fåtal individer avvek från detta mönster. Den sammantagna flyttvägen, baserad på alla GPS-positioner, sträckte sig från Sveriges kusttrakter vid Bottenhavet i nordost till södra Spanien i syd. Av de åtta länder som besöktes av de GPS-märkta grågässen, registrerades den största andelen positioner i Sverige (74 %), följt av Nederländerna (9 %), Danmark (8 %) och Tyskland (8 %). Färre än 5 % av positionerna fanns i Belgien eller Frankrike, och endast en individ nådde Spanien, motsvarande mindre än 0,05 % av alla positioner. Resultaten visade också tydliga skillnader i flyttmönster beroende på var i Sverige individen märktes. Gässen som märktes vid de två sydligaste fångstlokalerna, Svedala och Kristianstad, visade mycket begränsade rörelser över årscykeln och verkade till stor del vara stationära. De individer som trots allt lämnade Sverige flög inte längre än över Öresund till Danmark. De genomförde alltså inte någon flyttning i klassisk bemärkelse. I kontrast till detta lämnade alla gäss, undantaget en individ, från fångstplatserna i Nyköping, Örebro och Hudiksvall, Sverige under hösten. Det betyder att flyttningsavståndet till vinterområdet ökar ju längre norrut fågeln häckar, vilket innebär att de nordliga häckarna flyttar förbi de sydliga och tillbringar vintern betydligt längre söderut. Utöver skillnaderna i rörelsemönster mellan de olika fångstplatserna visade resultaten också att enskilda gäss kan ändra sitt flyttningsmönster mellan olika år.

Hur stor risken för skada är till följd av gåsbete, påverkas i hög grad av vilka grödor som gässen föredrar att födosöka på, och om grödan utnyttjas före eller efter skörd. I studie III räknades mer än 237 000 gäss i de två studieområdena under de år och årstider som studien pågick. Mer än en tredjedel (37 %) av gässen observerades på spannmålsstubb (efter skörd), 32 % på vall- och betesmarker, och 31 % på övrig åkermark med växande grödor. Under vår och sommar föredrog gässen i hög grad betesmarker och vall, medan de valde stubbåkrar och skördespill från till exempel morot, potatis och sockerbetor under höst och vinter. Växande, höstsådd spannmål valdes framförallt under vinter och vår. Dessa mönster stämmer väl överens med tidigare forskning som visar att gässens födosök förändras under året med deras växlande näringsbehov, och med vad som finns tillgängligt i odlingslandskapet.

Mina resultat indikerade även vissa skillnader mellan arter, särskilt under vintern i det sydligaste studieområdet där flera arter uppehöll sig samtidigt. Arter som utmärkte sig särskilt i sina val var till exempel Kanadagås som nästan uteslutande valde vintergrön, höstsådd spannmål, och Bläsgås som föredrog vall framför andra grödor.

För att kunna förutsäga gässens fördelning i jordbrukslandskapet krävs kunskap om på vilka grunder de väljer vilket fält att födosöka på. Studie IV visade att det inte bara är grödan som spelar roll, utan en kombination av faktorer som inkluderar avstånd från övernattningsplatsen samt närhet till skogskanter, vägar och byggnader. Sannolikheten att ha grågäss på ett fält ökade med dess avstånd till skogskant och mänsklig infrastruktur. Denna effekt var som tydligast inom cirka 200 meter. Detta beror sannolikt på att områden nära människor innebär en större risk för störning vilket gör att gässen undviker eller lämnar område. Grågässen visade också en tydlig tendens att välja fält som låg nära deras övernattningsplatser. Majoriteten använde fält som låg bara några få kilometer bort, där 90 % av gåsobservationerna återfanns inom 4 km från deras nattplats (på vatten eller i våtmark). Att hålla sig nära övernattningsplatserna är ett välkänt mönster hos gäss, eftersom det minskar energikostnaden för att förflytta sig mellan nattplats och födosöksområde. I likhet med resultaten från studie III fann jag att gässen föredrog spannmålsstubb och betesmarker framför andra grödor. Sannolikheten att grågäss skulle befinna sig på ett fält var dubbelt så hög för dessa grödor jämfört med andra grödor. Jag fann också att kornstubb föredrogs framför andra skördade spannmålstyper. Även om grågässen främst föredrog skördade grödor under den tid då studien genomfördes (Augusti-September), så ska det noteras att den relativa sannolikheten att ha gäss på fält med växande gröda var ganska hög, vilket understryker vikten av skadeförebyggande åtgärder.

Eftersom gäss samlas vid våtmarker, sjöar och vattendrag för natten, och födosöker dagtid i det omgivande jordbrukslandskapet, är det viktigt för förvaltningen att veta hur långt de vanligtvis rör sig från sina nattplatser när de födosöker och hur konsekventa de är i sitt rörelsemönster över året och längs flyttvägen. Sådan information är helt avgörande för att kunna göra riskbedömningar för betesskador samt rikta skadeförebyggande åtgärder där de gör mest nytta. I studie V fann jag att grågässen rör sig förhållandevis korta sträckor från sin nattplats; majoriteten av positionerna (90 %) från de GPS-märka individerna låg inom 4 km från övernattningsplatsen.

Enstaka avstånd över 50 km uppmättes, men de allra flesta avstånd mellan nattplats och födosöksområde var betydligt kortare än så. Jag fann också att födosöksavståndet var kortare under vår och sommar medan de längsta avstånden uppmättes under höst och vinter. Detta beror troligen på att gässen är begränsade i hur långt de kan röra sig från nattplats under den tid på året då de häckar och ruggar, eftersom de inte kan flyga då. Jag kunde inte finna någon betydande variation i födosöksavstånd längs med flyttvägen eller mellan år, vilket tyder på att råden för förvaltningen bör kunna tillämpas generellt längs flyttvägen.

Effektiv förvaltning av gäss kräver att man tar hänsyn till flera rumsliga och tidsmässiga skalor, från flyttvägen ner till enskilda fält och över hela årscykeln. Populationsutveckling och arters geografiska utbredning hanteras främst på flyttvägsnivå, medan skadeförebyggande åtgärder som till exempel anläggning av avledningsåkrar eller reservat, skrämsel och skyddsjakt i regel sker på regional eller lokal nivå. Samtidigt måste all förvaltning ske inom ramen för gällande lagstiftning, som till exempel EU:s fågeldirektiv, vilket reglerar exempelvis jakt och skyddsjakt. Utöver juridiska begränsningar påverkas förvaltningsarbetet även av hur ekonomiska ersättningssystem är utformade, vilka vanligtvis fastställs nationellt eller regionalt. På lokal nivå begränsas dessutom lantbrukarnas möjligheter att vidta skadeförebyggande åtgärder av vad som är tidsmässigt, ekonomiskt och praktiskt möjligt inom den aktuella jordbruksverksamheten. Mina studier visar på en del skillnader i gässens födosöks- och rörelsemönster mellan arter, årstider och områden. Detta understryker hur komplext gässens utnyttjande av jordbruksmark är, och att skadeförebyggande insatser behöver vara flexibla och anpassas efter specifika arter, regioner och tidpunkter på året.

Mina studier visar att grågäss som häckar i Sverige i stor utsträckning har övergett sina forna vinterområden i sydvästra Europa till fördel för övervintring längre norrut. Vidare visar resultaten att olika migrationsstrategier förekommer, beroende på var i Sverige som grågässen häckar. Grågäss från de tre nordligaste fångstplatserna utgör idag ett gemensamt förvaltningsansvar för samtliga länder längs flyttvägen från Sverige till Spanien. Samtidigt visar mina studier att dessa gäss tillbringar en stor del av året i Sverige, och nästan hela årscykeln i Sverige, Danmark, Nederländerna och Tyskland. För de två sydligaste fångstplatserna var mönstret ännu tydligare: där tillbringade gässen 97 respektive 100 procent av sin tid enbart i Sverige och Danmark.

Detta innebär att en lämplig indelning av förvaltningsenheter kan variera från regional till internationell nivå, beroende på gässens ursprung och flyttningsstrategi. Vidare visar mina studier att grågässen tenderar att hålla sig nära platsen där de fångades under perioden april–september. Denna period är därför bäst lämpad för att övervaka storleken på den svenska häckningspopulationen, förutsatt att eventuella inflöden från populationer som häckar i andra länder är små eller hanterbara.

När det gäller förvaltning av populationens storlek bedöms dagens jaktuttag inte vara tillräckligt för att kontrollera eller minska den del av grågåspopulationen som häckar i Sverige). Kunskap om när olika delpopulationer är mest stationära respektive när de blandas är därför viktig om det skulle bli nödvändigt att rikta åtgärder mot, eller undvika, särskilda grupper av gäss. Oavsett om målet är att uppnå ett jämnt jaktuttag över hela populationen eller att hantera problem lokalt, bör jakten helst ske tidigt under jaktsäsongen medan gässen fortfarande befinner sig nära sina häckningsområden, för att kunna ha kontroll över vilken del av populationen som faktiskt beskattas. Om målet är att rikta insatser mot grågäss som häckar i sydligaste Sverige är jakt under september och oktober sannolikt mindre effektiv. Under denna period tenderar de lokala fåglarna att blandas med gäss från populationer som häckar i andra nordiska länder, vilka passerar området under sin höstflyttning.

Baserat på mina studier rekommenderas att regionala åtgärder som avledningsåkrar och riktade skrämselinsatser bör koncentreras inom 4 kilometer från våtmarker och vatten som nyttjas av gäss. Vid planering av våtmarksrestaurering eller etablering av reservat är det därför viktigt att det finns alternativa födosöksområden inom detta avstånd, annars riskerar gässen att i stället födosöka på kringliggande åkrar där de kan orsaka skada.

På lokal nivå hade fält som låg inom 4 km från en våtmark eller annat vatten som användes som nattplats, samt som omgavs av öppet landskap och med minst 200 meter från bebyggelse och infrastruktur en hög sannolikhet att användas av gäss. Detta innebär att avledningsåkrar bör placeras med detta i åtanke, i områden som är särskilt utsatta för gåsskador, för att effektivt styra bort gässen från särskilt känsliga eller värdefulla grödor. Att låta stubbåkrar och fält med skördespill ligga obearbetade längre genom att senarelägga plöjning och harvning, kan också bidra till att bibehålla attraktiva alternativa födosöksplatser och därmed minska risken för skador på närliggande, växande grödor.

Detta är särskilt viktigt under senhöst och vinter i områden där gäss förekommer året runt, eftersom höstsådda grödor ofta är särskilt utsatta under just denna period. Sådana åtgärder måste dock vara förenliga med regler för jordbruksstöd, växtföljd samt lokala förhållanden såsom jordart och väderförhållanden. Eftersom gäss ofta väljer att födosöka på vall och spannmål under sen höst, vinter och tidig vår blir tidpunkten för sådd en viktig aspekt. Återkommande betning av gäss kan orsaka stora skador på sådana fält. Genom att så spannmål på våren istället kan man minska skaderisken betydligt i områden där gässen är som talrikast under vinterhalvåret. En senare sådd minskar även den tids period som grödan potentiellt är utsatt för betning. Samma resonemang gäller för höstraps, även om förändringar i tidpunkt för sådd alltid måste vägas mot grödans odlingskrav samt jordbrukets praktiska och ekonomiska förutsättningar.

Mina resultat visar inte bara var grågäss oftast födosöker i jordbrukslandskapet, utan också var risken för betesskador är som störst. Särskilt attraktiva, känsliga eller ekonomiskt värdefulla grödor bör därför, om möjligt, placeras minst 4 km från våtmarker och vatten som används ofta av gäss. Detta innefattar till exempel höstsådd spannmål och nyanlagda vallfält, vilka är särskilt känsliga och attraktiva i vissa växtstadier, men det innefattar också särskilt värdefulla och känsliga grödor som grönsaker där även lågt betestryck kan innebära stora ekonomiska förluster. När sådana anpassningar inte är möjliga bör man vara beredd att tillämpa andra förvaltningsmetoder för att förebygga skada.

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ORIGINAL ARTICLE

Migration patterns of Swedish Greylag geese *Anser anser*—implications for flyway management in a changing world

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Abstract

Significant population growth of some European goose populations has led to initiatives to implement management at the flyway level. Understanding migration routes and spatiotemporal distribution is crucial for the successful and coordinated management of migratory species such as geese. In this study, we describe movements across the entire annual cycle in 76 Greylag geese (*Anser anser*) fitted with GPS tracking devices at five catch sites in Sweden. We show that Greylag geese breeding in Sweden still use a NE-SW migration path. However, the wintering range has undergone a northward shift during the last decades. Compared to previous studies, our data suggest a continued reduction in migration distance, being most pronounced in birds in southernmost Sweden. Greylag geese tagged in southernmost Sweden spent almost the entire annual cycle in Sweden and Denmark (97 and 100% of all GPS locations). In contrast, the flyway of Greylag geese from the northern catch sites still covers countries from Sweden to Spain, but presently, only a small fraction of the population migrates to Spain. Instead, most of the annual cycle is spent in Sweden, Denmark, the Netherlands, or Germany. The contrasting spatiotemporal distribution in geese of different geographical origin indicates that management initiatives for the NW/SW European Greylag Goose population need to consider that different migration strategies occur within previously defined management units. As a consequence, coordination of management actions (e.g. monitoring, harvest quotas, reserves) may need to consider different spatial scales, i.e. from the regional to the international scale depending on the origin of the Greylag geese.

Keywords Anatidae · Birds · GPS tracking · Movement patterns · Waterfowl

Introduction

Waterfowl management has a history dating back to the early 1900s and it is seen by many as one of the success stories in wildlife management (Nichols et al. 2007; Anderson and Padding 2015). Individual marking of birds and the possibility to study movements of individuals have been crucial for coordinated management actions over larger areas. The latter has also rested on an early recognition of the 'flyway' concept, i.e. that management needs to embrace the entire geographical area used by a species or a population during its annual cycle (Lincoln 1935; Crissey 1955; Boere and Stroud 2006). Accordingly, flyways comprise breeding and wintering grounds, as well as the corridors used when migrating between the two. Flyways typically overlap several countries, have a north–south outline, and comprise widely different habitats, often in more than one biome (Alerstam 1990; Boere and Stroud 2006).

Management of North American ducks and geese is a long-standing example of concerted efforts in conservation, hunting regulation, and monitoring at the flyway level (Hawkins et al. 1984; Anderson and Padding 2015; Lefebvre et al. 2017). In Europe, though, flyway level management has become adopted for geese only during the last few decades, in order to handle rapidly increasing as well as declining populations (Madsen et al. 2017). For centuries, European goose populations faced over-harvest and habitat loss, but this 'historical debt' has largely been reversed during the last 70 years (Fox and Madsen 2017). Present numbers of some goose species in Europe are higher than ever, due to increasing survival and reproductive success (Fox and Madsen

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2017). The increase in numbers and spatial expansion has not gone unnoticed when it comes to conflicts between human interests (Buij et al. 2017; Fox and Madsen 2017). Damage to agricultural crops, compromised airport safety, and negative impact on natural ecosystems are examples of impacts (Bradbeer et al. 2017; Bakker et al. 2018; Montràs-Janer et al. 2019) that often lead to stakeholder conflicts and subsequent calls for population reduction (Buij et al. 2017). However, not all goose populations are thriving. The Lesser White-fronted Goose and the Red-breasted Goose are two examples of populations in Europe in urgent need of reduced hunting mortality and increased conservation efforts (Jones et al. 2008; Simeonov et al. 2014).

It is thus a true challenge for European goose management to devise conservation policies for the rare and declining species, and at the same time, when other effective mitigating measures are not available, reduce the populations causing conflicts due to their high abundance. Common to both categories is, however, the need to provide decision makers with knowledge so that management and conservation actions can be applied at the appropriate spatiotemporal scale (Nichols et al. 2007; Madsen et al. 2017). To facilitate action planning, there may be a need to delineate management units within a flyway, for example, when the latter hosts migratory as well as resident birds (Madsen et al. 2017; Bacon et al. 2019).

In Europe, the first flyway management plan for geese was implemented in 2012 for the Svalbard-breeding population of Pink-footed geese (Madsen et al. 2017). A European goose management platform has been launched, with the purpose to facilitate similar plans for other goose species (Mediated by AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds); Marjakangas et al. 2015; Jensen et al. 2018; Powolny et al. 2018). The Greylag goose is one of the focal species in this endeavor, as the European population has gone from rarity to being widespread and numerous in just five decades (Fox and Madsen 2017). Due to its present high abundance, wide geographical range, and continued population growth, the European Greylag goose population has become subject of management and conservation conflicts in terms of negative impact on human livelihoods and putative negative effects on natural ecosystems (Bakker et al. 2018; Montràs-Janer et al. 2019; Heldbjerg et al. 2021). As a result, the flyway management plan for this species will likely include measures to control population size and growth at the flyway scale (Powolny et al. 2018).

In the ongoing AEWA-based effort to instate a flyway management plan for European Greylag geese, re-sighting data of neck-banded individuals have been used to suggest delineation of the population into three management units (MUs) based on migration patterns and connectivity (Bacon et al. 2019). Two different units, separating the migrating (Nordic breeders, MU1) and the sedentary (Central European breeders, MU2), were later adopted in the management plan (Powolny et al. 2018). However, such analyses of movements of neck-banded individuals commonly include biases caused by uneven spatiotemporal distribution of ringing and observer effort (Korner-Nievergelt et al. 2010). Consequently, the recent emergence of GPS tracking devices suited for geese is a source of movement data of entirely different resolution and reduced bias (Bacon et al. 2019). To remotely GPS track individual birds continuously makes it possible to efficiently study variation in movement behaviour among individuals in a population, as well as between populations breeding in different areas of a management unit or flyway. Such differences, should they exist, are crucial for management to consider. For example, location data derived from GPS tracking devices can help managers to better understand the origin and likely imminent movements of geese occurring in a certain area at a given time. GPS location data may also allow for comparison with older data based on leg band recoveries and neck collar readings. Several previous studies, based on these older techniques, indicate that Greylag geese in Europe have changed their migratory behaviour significantly in recent decades, including bird breeding in southernmost Sweden (Andersson et al. 2001; Ramo et al. 2015; Podhrázský et al. 2017; Nilsson and Kampe-Persson 2018). If so, flyway delineation may change altogether, or for specific management units.

The Greylag goose breeds over most of Sweden, a country covering a long latitudinal gradient and a wide range of climatic conditions. Swedish Greylag geese are thus well suited for a study of present migratory patterns, including possible variation among individuals within a management unit. Further reasons for this claim are the availability of historical ringing data for comparison (Andersson et al. 2001; Fransson and Pettersson 2001; Nilsson and Kampe-Persson 2018), and a well-documented long-term increase in Greylag goose numbers in Sweden in all seasons, e.g. ~ 170.000–250.000 individuals staging in September in recent years (Haas and Nilsson 2019; Liljebäck et al. 2021).

In this paper, we describe movements over the entire annual cycle for 76 Greylag geese fitted with GPS tracking devices at five catch sites within the species' main breeding range in Sweden. The explicit aims were to answer four questions of imminent relevance for management of this species in Europe:

1) What is the present geographical extent of the flyway of Swedish Greylag geese?
2) Where are Swedish Greylag geese at different times of annual cycle?
3) Which countries are used by Swedish Greylag geese during the annual cycle?

4) Do the patterns (1–3 above) differ among areas of origin in Sweden?

Methods

Catching procedures

In June 2017–2019, breeding and moulting Greylag geese were caught when foraging in fields, pastures, or lawns near water. They were herded slowly by foot and canoe via raised nets into corrals. Caught geese were immediately put in gunny sacks to let them calm down until further handling. In addition to classical tarsal rings, geese were provided neckbands fitted with solar powered GPS tracking devices: Ornitela (OT-N35 and OT-N44) and Made-by-Theo (Theo Gerrits). Geese were aged (juvenile or adult) based on plumage and sexed by cloacal inspection. All catching and handling were done according to permits from the Animal Ethics Committee of Central Sweden (# 5.8.18–03584/2017). In total, 83 individuals from five different catch sites in Sweden (Fig. 1; Table 1) were tracked for at least one annual cycle.

Catch sites

Five catch sites were selected to represent a latitudinal range from central to southern Sweden, embracing the main part of the national breeding range of Greylag geese (55–61° N; Fig. 1).

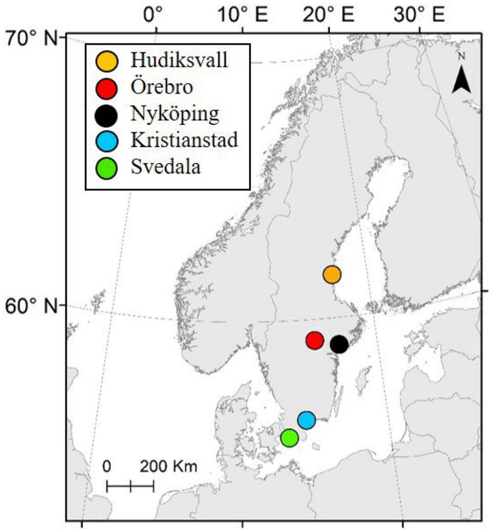

Fig. 1 Sites in Sweden where Greylag geese were caught and equipped with GPS tracking devices

Table 1 Number of studied individuals (females within brackets) and subsequently recorded annual cycles for Greylag geese provided with a GPS tracking device at five catch sites in Sweden in 2017–2019

Site	Individuals	Annual cycles
Svedala	10 (5)	17
Kristianstad	12 (7)	20
Nyköping	14 (14)	22
Örebro	30 (12)	50
Hudiksvall	10 (10)	17

Hudiksvall (N 61° 43′, E 17° 6′), by the coast of the Bothnian Sea in the southern boreal biotic zone (see Hallanaro and Pylvänäinen 2002 for classification of biotic zones in the Nordic countries). The site is a wetland (24.5 hectares (ha)) in an urban park area, surrounded by intensively managed grasslands including mowed lawns. The wetland holds less than five breeding pairs of Greylag geese annually, but numerous moulting flocks.

Örebro (N 59° 10′, E 15° 23′), just south of the border between the southern boreal and the boreo-nemoral biotic zones. The catch site sits within a large nature reserve (Kvismaren, 732 ha) holding vast areas of wetlands, swamp forests, and reed-beds. Management of the reserve includes cattle grazing and mowing of fields to promote meadow birds. As large parts of the reserve are inaccessible for humans, the exact numbers of breeding and moulting Greylag geese are not known but minimum numbers of breeding pairs were estimated to 240 by the Kvismare bird observatory in 2017 and 2018.

Nyköping (N 58° 58′, E 17° 9′), in the boreo-nemoral biotic zone. The site (Öster Malma) is a wetland (8.4 ha) constructed in 1992 to promote breeding waterfowl. It is situated in a fragmented landscape with forests interspersed by patches of agricultural fields and many lakes. Deciduous forests and extensively managed grasslands surround the wetland, which annually holds 10–20 breeding pairs, and in most years about 80–110 moulting Greylag geese. Öster Malma was a focal site for a large-scale re-introduction program for Greylag geese in Sweden in 1970–1975 (Andersson et al. 2001).

Kristianstad (N 56° 5′, E 14° 21′), in the nemoral biotic zone. The catch site (Bäckaskog) is situated in two pastures on a narrow land strip between two large lakes (6200 and 1520 ha). The surrounding land comprises meadows and arable fields mixed with deciduous forests. Up to 20 pairs of breeding Greylag geese and their offspring utilize the area in June, accompanied by varying numbers of moulting non-breeding birds.

Svedala (N 55° 33′, E 13° 14′), in the nemoral biotic zone. The catch site consists of two artificial wetlands (2.8 and 0.8 ha respectively) situated within a golf course surrounded by beech forest and arable fields. Up to 20 families of Greylag geese utilize the area during the breeding season.

Data treatment

Movement data from 83 individuals carrying GPS tracking devices were manually inspected for possible inter-dependence bias, i.e., if any bird was consistently moving together with other GPS tagged individuals. When this was the case, only one individual from pairs or family groups was retained in the study. Accordingly, 7 individuals were removed from the data set, leaving 76 individual geese in which the number of complete annual cycles ranged from one to three (Table 1; Supplemental Information 1). We only included an annual cycle if data could be retrieved from > 90% of the days within it (i.e., GPS locations in at least 329 out of 365 days). July 1st was set as the start of the annual cycle, as this is a time when all birds were positively at the breeding or moulting site (i.e., being flightless for 3–4 weeks). As geese migrate in pairs and family groups (Black et al. 2014; Kölzsch et al. 2020), we did not separate between the sexes when compiling the data.

The GPS positioning rate was first set to a default of one location per 15 min, but later came to vary over the annual cycle, mainly due to solar panel recharging problems in mid-winter (less frequent positioning) and some periods of individual behavioural studies (more frequent positioning). We used all data available independent of positioning rate for all complete annual cycles to create migration paths for each individual (Fig. 2). Consequently, up to three complete annual cycles were obtained for some individuals.

When calculating mean coordinates and the proportion of locations in different countries within the flyway, we standardized data to only include one location per 24 h, and we used the location closest in time to 12:00 AM UTC (Coordinated Universal Time; i.e. noon) to avoid possible bias due to different positioning rates along the migration path. Before calculating mean coordinates by catch site, we calculated a mean value for individuals with more than one annual cycle, and then the grand mean for all individuals. Maps were created in ArcMap (version 10.7).

Results

The studied Swedish Greylag geese show a cohesive southwesterly autumn migration corridor and a northeasterly return direction in spring, with very few individuals deviating from this pattern (Fig. 2). The combined paths and thus the flyway outline suggested by the locations in the entire sample ranges from the coastal areas of the Bothnian Sea in the northeast, to southern Spain in the southwest (Fig. 2). However, only one individual migrated to Spain and two individuals to France. One of the latter paths passed the southeast corner of Great Britain, deviating slightly to the west from the general migration corridor. Another individual showed a somewhat deviating path by passing the southeast corner of Norway during one spring migration. To the east, only one individual crossed the Baltic Sea, to reach the archipelagoes of SW Finland in summer.

For the standardized data set (one location per 24 h), we obtained locations from eight countries in total; the majority were within Sweden (on average 74% for all individuals), followed by lower proportions in the Netherlands (9%), Denmark (8%), and Germany (8%) (Fig. 3). The migration paths passing Norway and Great Britain were not covered by the standardized data (i.e. one location per 24 h) as the time spent within these countries was too short and did not coincide with the noon locations.

Geese tagged at the southernmost site Svedala showed very limited movements overall, some birds appearing to be more or less resident and only making local movements (82% of the locations within Sweden; Figs. 2 and 3). The individuals from Svedala that left Sweden migrated no farther than across Öresund to nearby Denmark. Birds from the second site in southernmost Sweden (Kristianstad) were also mainly resident and non-migratory (96% of the locations within Sweden), although two out of twelve individuals migrated to the Netherlands and three other individuals made a summer flight to moulting sites ~ 250 km to the north (Figs. 2 and 3). Note though that despite a large share of resident birds at both these southern sites, the general axis of movement was SW-NE, conforming to the general flyway outline. In contrast, geese tagged at the three northerly sites left Sweden for the winter (62–66% of the locations per individual within Sweden) (Figs. 2 and 3), except for one goose that remained in the southeast of the country. Only a few individuals from the two northernmost catch sites reached as far as France and Spain (Fig. 2). In addition to the variation found among catch sites, it is evident that individuals may change migration pattern between years, e.g. one goose migrated to France in one year but spent the winter in the Netherlands the other two years.

Monthly mean coordinates show that geese were in or near their respective catch site from March to September (Fig. 4). In October, geese from the three northerly catch sites started to migrate (Fig. 2), a month when also birds from the largely resident two southernmost catch sites displayed a minor SW shift of the mean coordinates (Fig. 4). Geese from four of the catch sites have their southernmost mean coordinates in November–December (Fig. 4), whereas geese tagged at Kristianstad reached the farthest SW later, in December–January (Fig. 4). Mean coordinates for the three northerly populations started shifting NE already in January, indicating a start of the return migration.

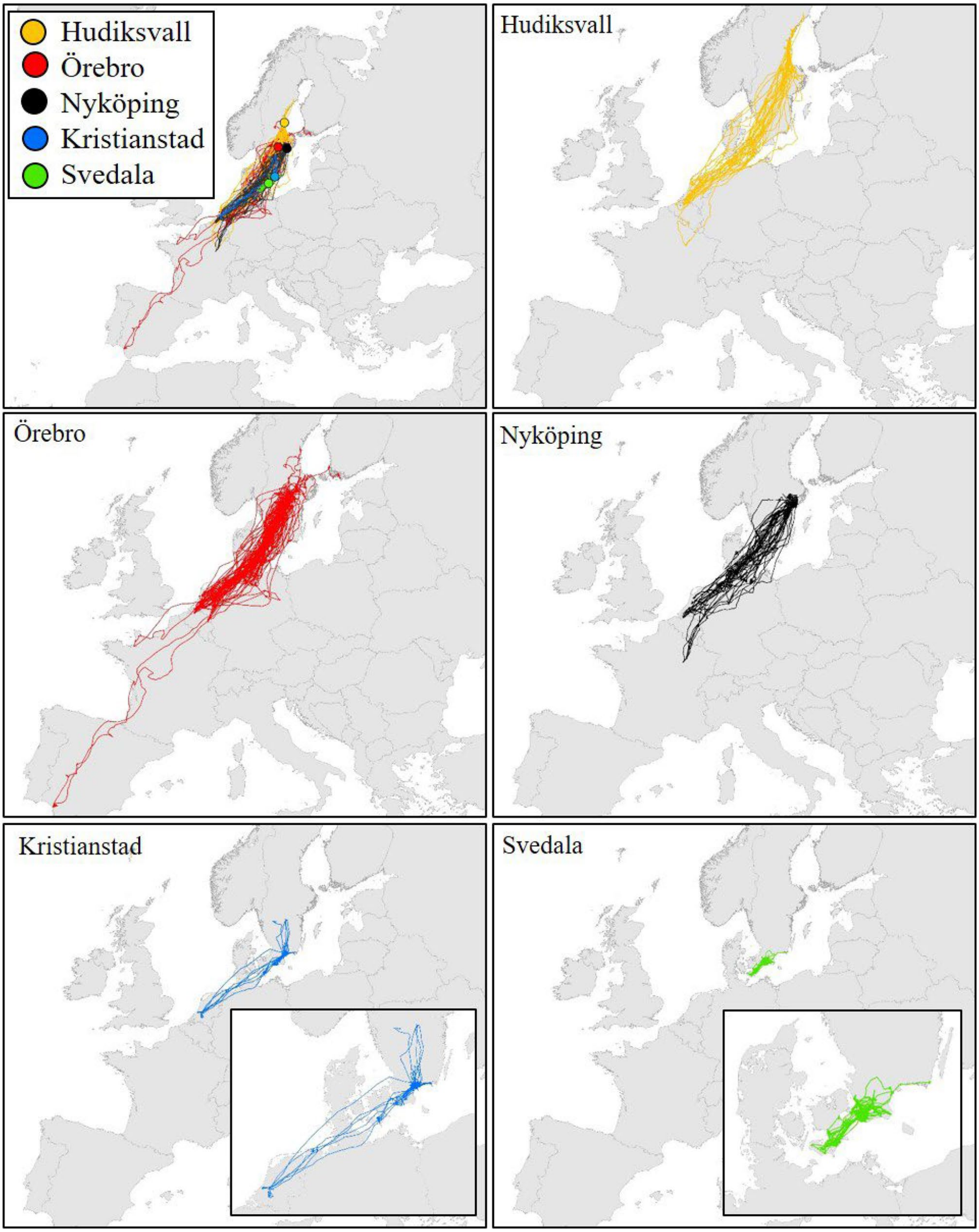

Fig. 2 Migration paths by GPS tracks for 76 Greylag geese caught at five sites in Sweden

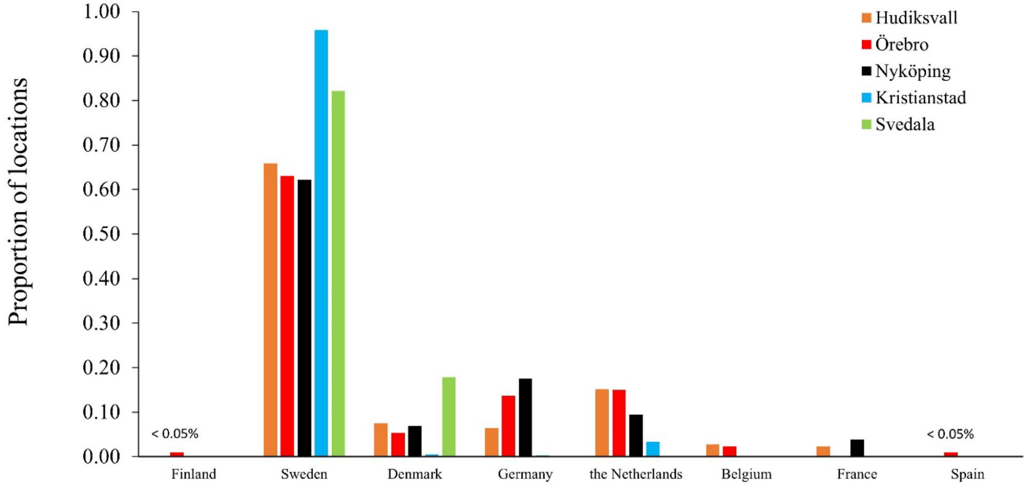

Fig. 3 Distribution of GPS locations by country in Greylag geese ($n=76$) originating from five catch sites in Sweden (see Fig. 1). Less than 0.05% of the positions were located in Spain and Finland, respectively

Discussion

A more detailed picture of the migration patterns of Greylag geese breeding in Sweden has been provided by the results from this study, with similarities as well as dissimilarities compared with previous studies. Although the general flyway outline has not changed, thus corresponding well to patterns described earlier (Fransson and Pettersson 2001), a much smaller fraction nowadays continues southwest to historical wintering areas in France and southern Spain. The main wintering area has shifted far to the northeast, to the Netherlands and Denmark. A sizeable proportion of the geese now winter in Sweden, where wintering Greylag geese were unknown 30–40 years ago (Andersson et al. 2001). Moreover, our study demonstrates geographical differences, i.e., that Greylag geese originating from different regions show not only different migration strategies but also a different degree of change.

Previous studies have described population growth and changes in distribution and migration patterns of Greylag geese in Europe (Fox and Madsen 2017; Nilsson and Kampe-Persson 2018; Boos et al. 2019). The present study, embracing much of the Swedish breeding range, implies that the change in migration patterns has continued and that it has been more pronounced in geese in the southernmost part of the country (cf. Andersson et al. 2001; Ramo et al. 2015; Nilsson and Kampe-Persson 2018). When comparing mean coordinates in winter (Dec–Jan) between earlier studies (based on tarsal rings and neck collars) and our recent GPS data, we did not find any profound difference in geese from our northernmost catch area, Hudiksvall, while there was a difference for geese tagged at Nyköping (Fig. 5; Andersson et al. 2001; Fransson and Pettersson 2001). The difference between “then” and “now” is even more pronounced for geese from our southernmost catch site (Svedala; Fig. 5). However, as earlier studies were based on tarsus ringed and neck collared birds, thus not on GPS locations, we cannot say for sure whether the differences are due to a true geographical shift, or to the methods used. Nevertheless, given that a general decrease in migration distance to more northerly wintering sites has been demonstrated also in earlier studies based solely on resightings of neck collars (Nilsson and Kampe-Persson 2018), and the profound differences in mean winter coordinates shown in Fig. 5, we are confident that our results show a continued northward shift, at least for Greylag geese originating from more southerly parts of Sweden. Future studies need to address to what extent spatiotemporal patterns obtained from neck collar readings are congruent with those from GPS data in the same species. The present study confirms the previously documented general SW-NE migration corridor, but based on GPS locations, we have found comparatively fewer individuals obviously deviating from the main corridor (cf. Andersson et al. 2001; Fransson and Pettersson 2001). We suggest that the higher variation in spatial distribution found in earlier studies can be explained, at least in part, by much larger samples than our 76 individuals. On the other hand, GPS tracking devices provide continuous data on a daily basis for all movements, and as a consequence, deviating patterns should be easier to detect in such data than in those derived from resightings

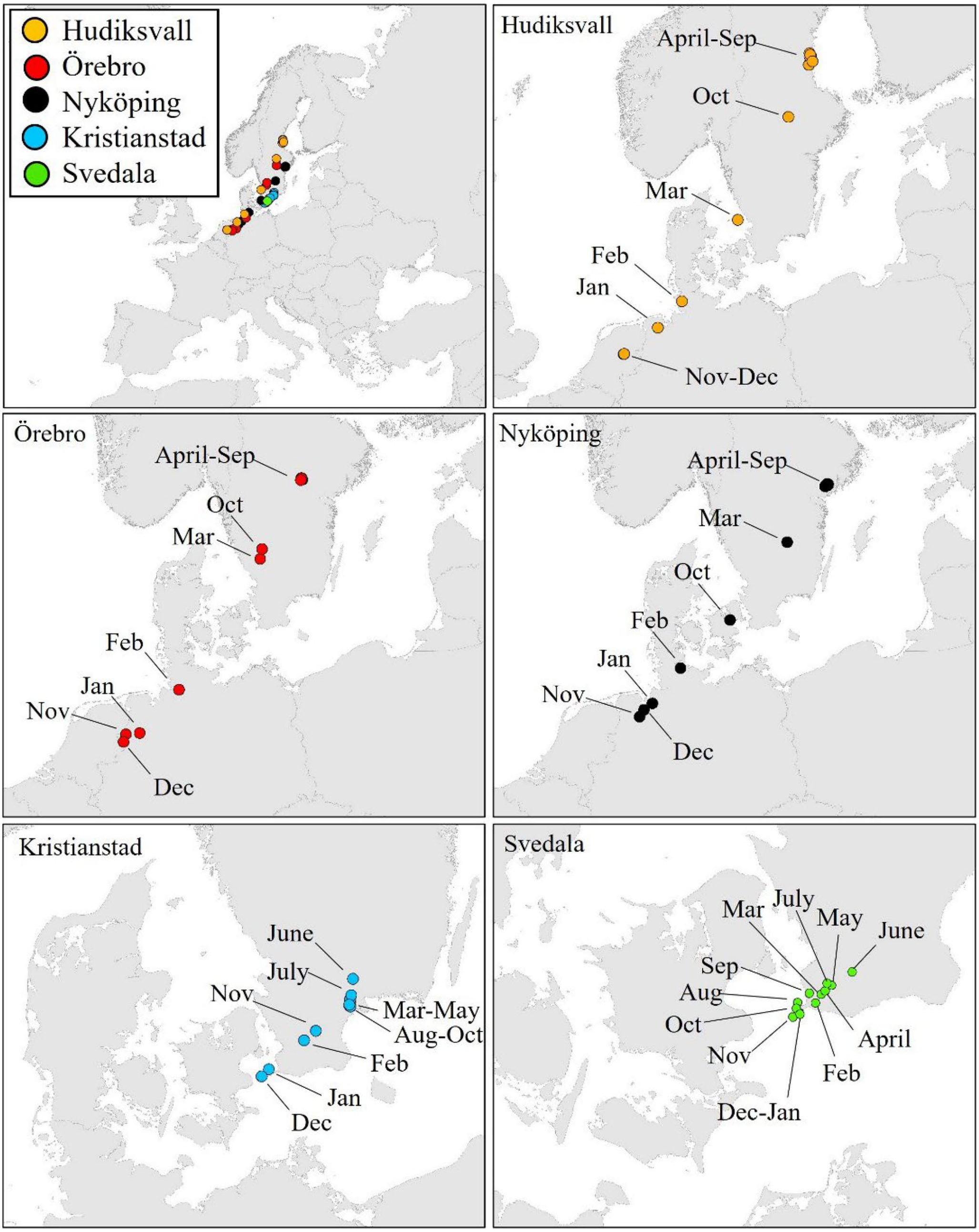

Fig. 4 Monthly mean coordinates based on GPS tracks from Greylag geese originating from five sites in Sweden. See Fig. 1 for catch site locations

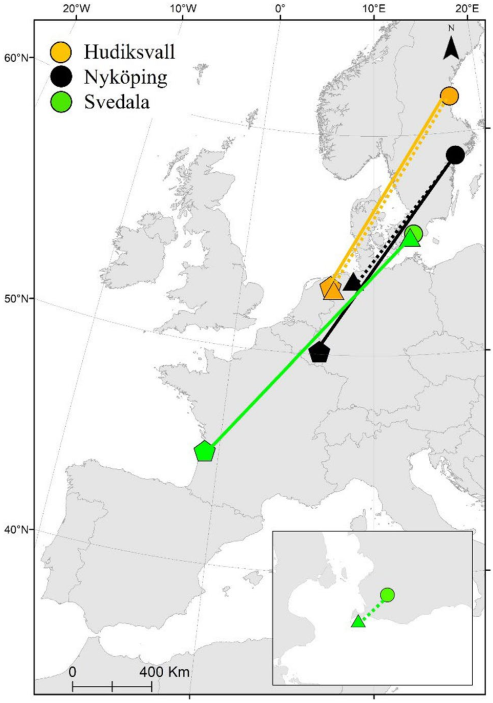

Fig. 5 In earlier studies Greylag geese were ringed 1940–1990 with standard tarsal rings at three out of five catch sites (circles) used in the present study. The map compares the two data sets with respect to mean winter (Dec–Jan) coordinates. Pentagons represent ring recoveries ($n = 80$) reproduced from Fransson and Pettersson (2001). Triangles denote mean coordinates from the present study (GPS positions). Greylag geese from the northernmost catch site (Hudiksvall) show similar migration patterns between the two time periods (~ 80 km further southeast in our study than earlier). On the other hand, data from geese ringed at Nyköping and Svedala (~ 440 km and ~ 1450 km further northeast in our study than earlier) imply a shortened migration distance, especially so birds from southernmost Sweden

of neck-banded birds (e.g. the two individuals in our study which swiftly passed Norway and Great Britain during migration would probably not have been detected by the neckband resighting technique).

Earlier studies show that Greylag geese from southernmost Sweden in general reached more southerly wintering sites compared to those ringed further north in the country (Andersson et al. 2001; Fransson and Pettersson 2001). In other words, it seems migration distance was previously rather equal in geese from different parts of the Swedish breeding range (Fig. 5), producing a classic ‘chain migration’ pattern (Berthold 2001). However, our results indicate a different pattern, as birds from southern sites in Sweden generally have abandoned former wintering sites and turned from being long-distance migrants to become residents or having a very short winter migration distance. This new pattern, in which migration distance increases with breeding latitude, instead recalls a ‘leapfrog migration’ pattern (Salomonsen 1955; Berthold 2001). Interestingly, Greylag geese breeding in the Netherlands have shifted from being migratory to being resident during the early 1990s, a change in accord with our results for birds in southernmost Sweden. This means that they, too, have been overflown by long-distance migrating Nordic Greylag geese to become part of an emerging ‘leapfrog migration’ pattern (Voslamber et al. 2010; Bacon et al. 2019). Our present results thus imply that Swedish Greylag geese now have migration strategies collectively creating a ‘leap-frog migration’ pattern rather than a chain migration pattern (Salomonsen 1955; Berthold 2001), but a more rigorous analysis is needed to draw such a conclusion. Specifically, the possible differences in distance and timing of migration among individuals from different breeding areas must be analyzed in a more formal and objective way. Regardless, with a continuous and expected climate change trajectory (Sorte et al. 2019) and an intensification of agriculture in Europe (Simoncini et al. 2019), we find it likely that our study gives a mere glimpse of an ongoing change in migration patterns in this population.

When the climate is changing, capacity to adapt to new conditions is key. Earlier studies have shown that some bird species have a limited capacity to adapt to new conditions, whereas others show swift changes such as range shifts in response to climate change (Böhning-Gaese and Lemoine 2004; Sekercioglu et al. 2008). Greylag geese seem to have a high degree of plasticity, be it phenotypic adaptation or evolutionary adaptation, or both. Obviously, in the era of the Anthropocene, they respond to widespread and significant human impact, for example, milder winters and increased availability of high-quality food due to changes in agricultural practices. This obviously includes the altered migration patterns of Greylag geese breeding in Sweden. When comparing our results to earlier findings, including data from 1984 to 1995, Swedish Greylag geese have radically changed their migration pattern on the population level in a mere 30–40 year period. This rapid change suggests altered behaviour within generations at the individual, family group, or flock level, rather than classical Darwinian adaptation across generations. Since we show that individuals may change migration strategies between years, the view of a phenotypic adaptation of the migration patterns of Greylag geese is to some extent supported by our study. Similar patterns of individual plasticity have been found in other studies of Nordic geese (Nilsson and Kampe-Persson 2018; Boos et al. 2019). Nilsson and Kampe-Persson (2018) also found that a higher proportion of Greylag geese ringed in southern Sweden changed wintering sites between years, compared to birds from more northern sites.

We acknowledge that a minor portion of the Swedish population of Greylag geese breeds north of our northernmost catch site Hudiksvall (61° 43′), but our study embraces the geographic area hosting the vast majority of the Swedish breeding population (Ottosson et al. 2012; Nilsson and Haas 2015). We nevertheless advocate complementary GPS tagging of Greylag geese breeding farther north, to challenge or confirm the patterns in the present study. For example, it has been shown in other waterbirds, breeding in the far north of Sweden, that at least a part of the population crosses the Gulf of Bothnia for a more easterly migration route southwards (e.g., Common crane: Skyllberg et al. 2014). Judging from the individual GPS data, the present study found little support for migration paths linking Swedish birds to Norway and Finland. However, it is known that bird breeding in northeastern Norway use stop-over sites in Sweden (Powolny et al. 2018; Boos et al. 2019). In addition, recent studies based on GPS tracking and neck collar readings show that Greylag geese breeding in Northeast Norway and Finland visit stop-over sites in certain regions of Sweden in September (Follestad and Piironen pers comm.). Moreover, Greylag geese originating from Denmark and eastern continental Europe (e.g. Poland) have been shown to perform a northbound moult migration to Sweden in summer (Nilsson and Hermansson 2019).

Management implications

Our study implies that Greylag geese breeding in Sweden have progressively abandoned former wintering sites in the southwest (Spain, France) and that individual birds may change migration strategy during their lifetime. The present study also shows that two radically different types of migration strategy occur within the Swedish population, depending on geographic origin. Such long-term change and plasticity in migration, and variation among regions create general challenges for management and conservation and thus a need for continuously updated knowledge, e.g. to coordinate monitoring, harvest quotas and networks of protected areas. Today, Greylag geese originating from the three northerly catch sites in our study area constitute a common management concern for all countries within the flyway, i.e., from Sweden to Spain, which then also in general terms supports the current delineation of the two management units (Powolny et al. 2018; Heldbjerg et al. 2021). Even so, and although the flyway embraces many countries, Greylag geese originating in these three northern catch sites spend much of their annual cycle within Sweden, and almost all of it in Sweden, Denmark, the Netherlands, and Germany. Greylag geese tagged at the two southernmost sites spent 97 and 100% of their time in Sweden and Denmark only. Consequently, the appropriate delineation of management units may vary from a regional to an international scale depending on the origin of geese and the migratory habits in specific areas. In other words, management strategies used for the Greylag geese treated as residents (i.e. MU2—Central European breeders) may actually also be applied to part of the Swedish population. The spatiotemporal patterns demonstrated in this study also reveal that Greylag geese seem to stay close to their respective catch site from April to September. This period would therefore be best suited for monitoring the population size of Greylag geese breeding in Sweden, if the aim is to estimate the national breeding population size, provided that a possible influx from Norway and/or Finland is either negligible or possible to control for. Since changes in migration strategy are likely to go on, continued mapping of movements and migration strategies of European Greylag geese is much needed for proper interpretation of collected data and for designing appropriate management and monitoring schemes.

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Declarations

Conflict of interest The authors declare no competing interests.

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Supplementary Information (SI)

European Journal of Wildlife Research

Migration patterns of Swedish Greylag geese *Anser anser* – implications for flyway management in a changing world

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SI 1. The table summarizes information about all Greylag goose individuals that are included in the present study.

Catch site	Sex	Age at tagging	Annual cycles	Individual
Hudiksvall	Female	2 cy+	2	D13
Hudiksvall	Female	2 cy+	2	D25
Hudiksvall	Female	2 cy+	1	D67
Hudiksvall	Female	2 cy+	2	D77
Hudiksvall	Female	2 cy+	2	D78
Hudiksvall	Female	2 cy+	2	D79
Hudiksvall	Female	2 cy+	2	DM3
Hudiksvall	Female	2 cy+	1	DM4
Hudiksvall	Female	2 cy+	1	DM5
Hudiksvall	Female	2 cy+	2	DM6
Örebro	Female	2 cy+	2	K03
Örebro	Female	2 cy+	2	K06
Örebro	Female	2 cy+	2	K09
Örebro	Female	2 cy+	1	K35
Örebro	Female	2 cy+	1	K36
Örebro	Female	2 cy+	1	K37
Örebro	Female	1 cy	3	S34
Örebro	Female	2 cy+	3	S57
Örebro	Female	2 cy+	1	S65
Örebro	Female	2 cy+	3	S66
Örebro	Female	2 cy+	1	S89

Örebro	Female	2 cy+	2	S96
Örebro	Male	2 cy+	2	K04
Örebro	Male	2 cy+	2	K05
Örebro	Male	2 cy+	1	K08
Örebro	Male	2 cy+	1	K31
Örebro	Male	2 cy+	1	K32
Örebro	Male	2 cy+	1	K34
Örebro	Male	1 cy	2	S38
Örebro	Male	1 cy	1	S41
Örebro	Male	1 cy	1	S51
Örebro	Male	2 cy+	1	S67
Örebro	Male	2 cy+	1	S68
Örebro	Male	2 cy+	2	S90
Örebro	Male	2 cy+	2	S91
Örebro	Male	2 cy+	2	S92
Örebro	Male	2 cy+	2	S93
Örebro	Male	2 cy+	2	S94
Örebro	Male	2 cy+	2	S99
Örebro	NA	2 cy+	2	S64
Nyköping	Female	2 cy+	3	D70
Nyköping	Female	2 cy+	2	D71
Nyköping	Female	2 cy+	1	D74
Nyköping	Female	2 cy+	1	K20
Nyköping	Female	2 cy+	1	K21
Nyköping	Female	2 cy+	1	K22
Nyköping	Female	2 cy+	1	K23
Nyköping	Female	2 cy+	1	S30
Nyköping	Female	2 cy+	1	S32
Nyköping	Female	2 cy+	2	S33
Nyköping	Female	2 cy+	2	S71
Nyköping	Female	2 cy+	2	S72
Nyköping	Female	2 cy+	2	S74
Nyköping	Female	2 cy+	2	S75
Kristianstad	Female	2 cy+	1	K43
Kristianstad	Female	2 cy+	1	K44
Kristianstad	Female	2 cy+	1	S78
Kristianstad	Female	2 cy+	2	S80
Kristianstad	Female	2 cy+	2	S85
Kristianstad	Female	2 cy+	1	S87
Kristianstad	Male	1 cy	1	K10
Kristianstad	Male	2 cy+	1	K42
Kristianstad	Male	2 cy+	3	S02
Kristianstad	Male	2 cy+	2	S77
Kristianstad	Male	2 cy+	2	S81
Kristianstad	Male	2 cy+	2	S83
Svedala	Female	2 cy+	1	K14

Svedala	Female	2 cy+	1	S06
Svedala	Female	2 cy+	3	S07
Svedala	Female	2 cy+	3	S14
Svedala	Female	2 cy+	1	S20
Svedala	Male	2 cy+	2	K18
Svedala	Male	2 cy+	1	S05
Svedala	Male	2 cy+	2	S25
Svedala	Male	2 cy+	1	S29
Svedala	NA	2 cy+	2	S12

II

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RESEARCH ARTICLE

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Leapfrog migration and residents: New migratory habits in Swedish Greylag geese

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Abstract

Knowledge about intraspecific and individual variation in bird migration behavior is important to predict spatiotemporal distribution, patterns of phenology, breeding success, and interactions with the surrounding environment (e.g., human livelihoods). Such variation is key to adaptive, evolutionary responses, i.e., how individuals respond spatiotemporally to the environment to maximize fitness. In this study we used GPS location data from one to three full annual cycles from 76 Greylag geese (*Anser anser*) to test the hypothesis that geese originating at five latitudinally separated capture sites in Sweden have different migration strategies. We also assessed individual consistency in movement strategy over consecutive annual cycles. We used the scale-independent net squared displacement modeling framework to quantify variables of autumn and spring migration for geese from each capture site: distance, timing, and duration. Our results demonstrate a positive correlation between migration distance and latitudinal origin. Geese from the northernmost site on average migrated farther south and about 15 times as far as the short-moving or resident geese from the two southernmost sites. Movement strategies of individual geese varied considerably both within and among capture sites. Individual consistency in movement strategy from one annual cycle to the consecutive was high in geese from the northern sites moving the farthest, whereas the resident or short-moving geese from the southernmost sites generally showed lower or no individual consistency. These changes have come about during a time span so short (i.e., ca. 35 years or 8–10 generations) that it can unlikely be explained by classical Darwinian between-generation adaptation. Consequently, and given that young geese follow their parents during their first migration, we presume an important role of within-family, inter-generation change as a driver behind the large-scale changed migration habits in Swedish Greylag geese.

KEYWORDS
animal movement, *Anser anser*, flyway management, GPS telemetry, individual variation, net squared displacement

TAXONOMY CLASSIFICATION
Applied ecology; Behavioural ecology; Conservation ecology; Evolutionary ecology; Population ecology; Zoology

1 | INTRODUCTION

Knowledge about intraspecific individual variation in migration behavior is vital to understand patterns of phenology, changes in breeding success, resource use, and interactions with the environment (e.g., habitats, other species, human livelihoods). Such variation is also key to adaptive responses studied within the evolutionary paradigm; i.e., how individuals respond spatiotemporally to selective regimes in an optimal way to maximize fitness (Alerstam & Hedenström, 1998). Accordingly, there has been a gradual historical shift in the general view on animal migration, from stereotyped patterns to a deeper appreciation of intraspecific variation as a driver of migration dynamics in populations. For example, migration distance in species in which all individuals migrate may vary by sex, age, or body condition; a process and pattern termed "differential migration" (Gauthreaux, 1982; Ketterson & Nolan, 1983; Newton, 2008). Similarly, some species are "partial migrants," where some individuals are true migrants, others do not migrate at all. In this case, migration strategy may differ by age, body condition, genetic constitution, or the frequency of a certain strategy in the population (Berthold, 2001; Newton, 2008).

Aside from short-term events (challenging weather, food shortage, etc.) that force individuals to change distance or timing of migration, it may also change because of evolutionary adaptation to long-term environmental change (e.g., land use, climate). Research accumulated over the last two decades documents significant changes in timing of migration in a wide range of avian species (Lehikoinen et al., 2019; Møller et al., 2010). This is mainly manifested by migrants arriving earlier than before to breeding grounds in spring, and in some species by a later departure in autumn (Jonzén et al., 2006; Lehikoinen et al., 2019; Mills, 2005). Migration distance per se has shrunk in several species, as witnessed by decreased mean recovery distance due to long-term climate change in 12 of 24 bird species ringed in the Netherlands (Visser et al., 2009). A related and widespread phenomenon is a northward shift in wintering range in medium- and short-distance migrants in temperate areas of the northern Hemisphere. This has been documented in passerines, shorebirds, raptors, and waterfowl (Pavón-Jordán et al., 2019; Potvin et al., 2016), and exemplifies "winter partial short-stopping" *sensu* Elmberg et al. (2014). However, less is known to what extent seasonal range shifts across a migratory flyway affect different populations or individuals within a population similarly. Previous research on differential and partial migration patterns as well as recent studies on range shifts are often based on crude arrival and departure dates or on census data. Consequently, they embrace little information about individual movements and intra-population differences, i.e., the potential drivers of the shift. Although time-series data collected over larger areas are crucial to infer changed migratory habits in the first place, such data inevitably contain noise and biases (Lehikoinen & Sparks, 2010). These deficiencies can be overcome by studying movements of individually tracked birds emanating from different source areas and followed throughout the annual cycle, an approach recently made possible for large- to medium-sized birds such as geese by solar-powered GPS technology.

Greylag geese breeding in Sweden were historically obligate long-distance migrants, wintering in Coto Doñana in Spain and to a lesser extent in France (Follestad et al., 2001; Fransson & Pettersson, 2001). Analyses in the 1990s of banding recoveries demonstrated a classical "chain migration pattern" (i.e., "parallel migration" *sensu* Salomonsen, 1955) in which migration distance does not differ among birds breeding at different latitudes, so that northern breeders winter north of southern breeders (Follestad et al., 2001; Fransson & Pettersson, 2001). The latter reference also reported a slight decrease in the relative share of recoveries from southern Europe in winter in the late 1900s. Later studies reported winter partial short stopping from more southern populations in the same flyway of Greylag geese (Månsson et al., 2022; Podhrázský et al., 2017; Ramo et al., 2015). In addition, there has been a recent and rapid increase in Greylag geese wintering in southern Sweden, some of which are known local breeders (Nilsson & Kampe-Persson, 2018a; Nilsson et al., 2020). Evidence from throughout the flyway thus indicates recent significant changes in migration habits in Greylag geese in Western Europe. These changes are often seen as an adaptive response to an increasingly benign environment with shorter and milder winters, reduced nutritional bottlenecks due to changed agricultural practices, and reduced per capita hunting mortality (Fox & Madsen, 2017; Fox et al., 2005). This provides opportunity to study adaptive changes in migration strategy in geese breeding at different latitudes within a flyway.

In this study, we provided Greylag geese caught on Swedish breeding grounds with neckbands equipped with solar-powered GPS-tracking devices. GPS location data from these birds not only confirmed a continued trend for winter short stopping but also showed that the change in migratory strategy differed depending on breeding latitude (Månsson et al., 2022). According to these data, northern breeders are still long-distance migrants, whereas birds from the two southernmost capture sites show more limited winter movements (Månsson et al., 2022). These findings indicate that Greylag geese breeding in Sweden may have switched from a "chain migration" to a "leapfrog" pattern, in which northern breeders overshoot southern breeders in autumn and winter, and migration distance increases with breeding latitude (*c.f.*, Salomonsen, 1955, Alerstam & Hedenström, 1998, Newton, 2008).

However, the mapped individual movement trajectories and the monthly mean locations for geese from different capture sites presented in Månsson et al. (2022) warrant evaluation by a more rigorous and objective analytical tool. The net squared displacement

(NSD) statistical framework sets out to“(i) separate migration from other movement behaviours, (ii) quantify migration parameters without the need for arbitrary cut-off criteria and (iii) test the predictability across individuals, time and space” (Bunnefeld et al., 2011). NSD has been used successfully to study drivers of migration in a wide range of taxa, mainly ungulates and carnivores, but also geese and cranes (Bunnefeld et al., 2011; Leopold & Hess, 2014; Smereka et al., 2021; Wolfson et al., 2020). For a Greylag goose population undergoing changes in migratory habits, NSD can be used to differentiate migrants from residents and to quantify key migration parameters (i.e., distance, timing, and duration). It can also be used to assess individual consistency in migratory habits between years.

In this study we used daily GPS location data from one to three full annual cycles obtained from 76 Greylag geese to test the hypothesis that birds originating at different latitudes have different migration strategies, so that the Swedish population have shifted from a chain migration to a leapfrog migration pattern. Based on the leapfrog hypothesis (Berthold, 2001; Salomonsen, 1955), we predicted that geese breeding the farthest north would winter the farthest south, whereas birds breeding the farthest south would move relatively shorter distances and winter the farthest north. The alternative hypothesis is that partial winter short stopping would affect all populations equally, leading to a retained pattern of chain migration. When it comes to individual consistency in migration strategy (i.e., distance, timing, and duration; Bunnefeld et al., 2011), we hypothesized that it would not change between years.

2 | METHODS

2.1 | Capture procedure and sites

The study is based on location data obtained 2017–2020 from 82 Greylag geese with GPS-equipped neckbands, made by either Ornitela (OT-N35 and OT-N44) or Made-by-Theo (Theo Gerrits) (Table 1 and Table S3), placed in June (2017–2019), focusing on breeding and molting adults and their unfledged goslings. Birds were caught early in the morning when foraging in fields, pastures, or lawns near water. They were herded slowly by foot or canoe via fences into net corrals, where they were immediately put in gunny sacks to keep calm until further handling. Handling protocols were approved by the animal ethics committee for central Sweden and fulfilled the ethical requirements for research on wild animals (decision Dnr 5.8.18-03584/2017).

TABLE 1 Number of Greylag geese ($n = 76$) with movement data (>349 locations per annual cycle) per capture site and annual cycle

	Number of individuals			
Capture site	**Total**	**2017/2018**	**2018/2019**	**2019/2020**
Hudiksvall	10	4	9	4
Örebro	30	10	18	22
Nyköping	14	4	8	10
Kristianstad	12	1	8	11
Svedala	10	5	8	4

Note: See Figure 1 for capture sites.

The five capture sites represent a latitudinal range from central to southern Sweden, embracing the main part of the national breeding range of Greylag geese (55°–61°N, Figure 1, Table 1). The northernmost site is an urban wetland surrounded by grasslands and lawns in a city park in Hudiksvall (N 61°43.96′, E 17°6.55′), located in the Southern boreal zone (Ahti et al., 1968; Hallanaro et al., 2002). This site mainly hosts molting geese, and less than five breeding pairs of Greylag geese. The site at Örebro (N 59°9.59′, E 15°22.86′) is part of a large wetland reserve situated close to the transition zone between the Southern boreal and Boreo-nemoral zones. The area is dominated by agricultural fields and attracts significant numbers of geese for breeding, as well as for staging in spring and autumn. Kvismare Bird Observatory estimated the minimum numbers of breeding pairs at 240 in 2017–2018. The site at Nyköping (N 58°58.17′, E 17°9.07′) is a wetland surrounded by a fragmented landscape of forests, extensively managed grasslands, agricultural fields, and lakes. This wetland is situated in the Boreo-nemoral zone and holds 10–20 breeding pairs, and ca. 80–110 molting Greylag geese. The two southernmost sites, at Kristianstad (N 56°4.98′, E 14°21.07′) and Svedala (N 55°33.34′, E 13°14.65′), are situated in the Nemoral zone. Some 20 pairs of Greylag geese breed at each site. The capture site at Kristianstad is in pastures on a narrow strip of land between two lakes, whereas the Svedala site comprises artificial wetlands on a golf course, surrounded by beech forest and agricultural fields.

2.2 | Data management

For the analyses, we used standardized data of one location per day and individual using the location closest to mid-day, i.e., 12:00 a.m. UTC (coordinated universal time). In total, 82 individuals from the five capture sites were tracked for at least one annual cycle. We defined the annual cycle as starting on July 1, when all geese were flightless and resident in a restricted area for breeding and molting. We only included individuals with location data for more than 349 days of the annual cycle (i.e., >90% data coverage; mean = 362.1 days of the annual cycle/individual). Locations for all geese were visually inspected in ArcGIS (vers. 10.7), and in cases where individuals obviously moved together in pairs or flocks, the individuals with the least number of locations ($n = 6$) were removed completely from the dataset to avoid inter-individual autocorrelation in movement. Consequently, data from 76 individuals were used in subsequent analyses (Table 1 and Table S3).

2.3 | Statistical modeling

We used the modeling framework developed by Bunnefeld et al. (2011) allowing scale-independent modeling and quantification of five migration variables: (1) migration distance, (2 and 3) timing of autumn and spring migration, and (4 and 5) duration of autumn and

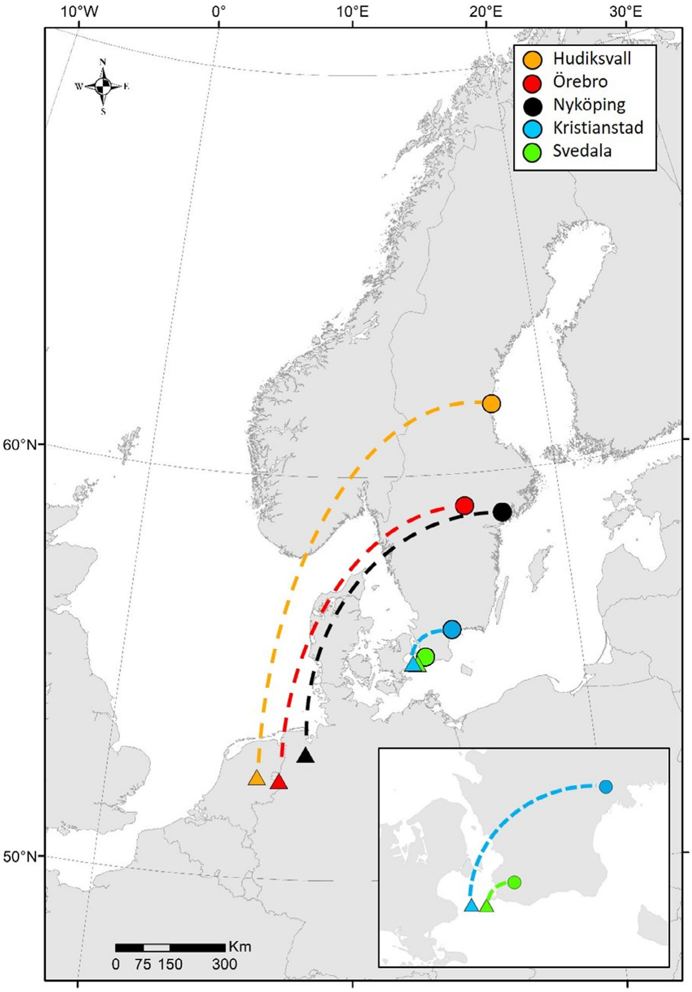

FIGURE 1 Capture sites (circles) and coordinates (triangles) for mean GPS locations at the predicted mean date when individuals from each capture site have reached the asymptotic migration distance (i.e., farthest distance from the capture sites). For modeling procedure, see Section 2.3. Dashed lines do not represent actual migration routes

spring migration. In addition, the framework allows modeling of the predictability of movement strategies over time and space for flocks and individuals originating at different capture sites. The analysis is based on data on spatiotemporal displacement (i.e., net squared displacement, "NSD") of individual geese during the annual movement cycle. The NSD value is calculated using the squared distance (km^2) based on a straight line from the starting location (July 1 each year) to all consecutive daily locations for each individual and annual cycle (July 1 year t to June 30 year $t+1$). These calculations were made in the R package *adehabitatLT* version 1.6 (Calenge, 2020). Specifically, we used a non-linear mixed model (package *nlme*) based on the following equation (derived from Bunnefeld et al., 2011):

$$\mathrm{NSD} = \frac{\delta_{\mathrm{a}}}{1 + \exp\left(\frac{\theta_{\mathrm{a}} - t}{\varphi_{\mathrm{a}}}\right)} + \frac{\delta_{\mathrm{s}}}{1 + \exp\left(\frac{\theta_{\mathrm{s}} - t}{\varphi_{\mathrm{s}}}\right)}$$

The terms δ_a and δ_s represent the asymptotic height of the annual movement cycle (i.e., movement distance during autumn and spring), θ_{a} the date of reaching half of the asymptotic distance during autumn migration, θ_{s} the date of reaching half of the spring migration distance to the sites of origin (i.e., timing), and φ_{a} and φ_{s} the number of days lapsed to cover a quarter of the distance moved (from 1/2 to 3/4 of the asymptotic migration distance) in autumn and spring (i.e., duration), respectively. The equation is divided into two subequations to allow for variation in movements in autumn versus spring (e.g., differences in timing and duration due to potential alteration of staging sites or migration triggers) (Bunnefeld et al., 2011).

To identify differences in migration strategy between geese of different origin, we used the NSD values for the full annual cycles as response variable, and explored the effect of capture site (five-level factor: Hudiksvall, Örebro, Nyköping, Kristianstad, Svedala) with the complement of annual cycle (three-level factor: 2017/2018, 2018/2019, 2019/2020) as explanatory variable for distance, duration, and timing of autumn and spring movement (see explored model structures in Table S1). To avoid pseudo-replication due to using data from individual geese from more than one annual cycle, we also explored the most parsimonious random-effect structure of goose ID on the defined migration variables. To define starting values for each respective variable in the model using the equation above, we plotted NSD data over the annual cycle (days lapsed from 1 July) and manually fitted a curve for each capture site to derive prior values to parameterize the equation above. Model exploration showed that only model 1 was supported by the data and converged accordingly (Table S1). In model 1, NSD values (km^2) were used as response variable, capture site as a fixed-effect variable of distance, duration and timing of autumn and spring movement, and goose ID as a random effect on migration distance.

To test if Swedish Greylag geese show a leapfrog migration pattern, we used model predictions to identify the month when geese from each capture site reached their asymptotic distance and calculated mean coordinates for geese from each capture site at that time. To obtain mean coordinates, we first calculated the mean value for each individual having data from multiple annual cycles and then estimated the grand mean for all individuals from each capture site. Maps were created in ArcMap (version 10.7).

To test for individual consistency in movement strategy over consecutive annual cycles, we extracted data from individuals that had NSD covering at least two consecutive annual cycles ($n = 43$, Table S2) and estimated the Pearson correlation between the NSD values for individuals at each given point in time (days since July 1) during an annual cycle and the following (i.e., 2017/2018 vs. 2018/2019 and 2018/2019 vs. 2019/2020). All statistical modeling was carried out in R (version 3.6.3; R Core Team, 2020).

3 | RESULTS

We found that variation in all migration variables, i.e., distance (km), timing of autumn and spring movement (dates), and duration of autumn and spring movement (days), was explained by the latitudinal origin of geese (i.e., capture site). Our results demonstrate a positive correlation between migration distance and latitudinal origin of geese. Geese from the northernmost site Hudiksvall (1207 km, CI: 985–1395) on average migrated 1.4 and 1.2 times as far as those from the more centrally located sites Nyköping (892 km, CI: *NA*–1388) and Örebro (1041 km, CI: 177–1462), and 15 and 4 times as far as those from the southernmost sites Svedala (82 km, CI: *NA*–1106) and Kristianstad (327 km, CI: *NA*–1121) (Figure 2, Table 2). Consequently, Greylag geese from northern capture sites migrated farther south than did the geese of more southern origin (Svedala and Kristianstad) (Figure 1).

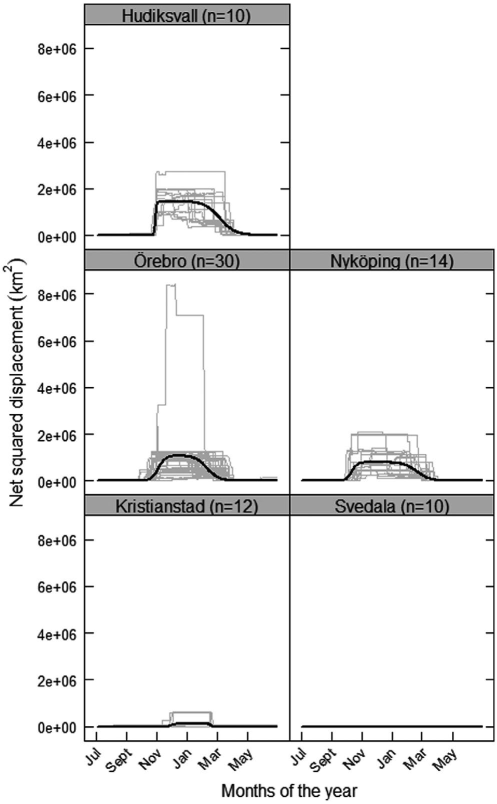

FIGURE 2 Net squared displacement based on GPS data over the annual cycles (July 1 to June 30, 2017–2020) for individual Greylag geese (grey lines) originating at five capture sites in Sweden; Hudiksvall ($n = 10$), Nyköping ($n = 14$), Örebro ($n = 30$), Kristianstad ($n = 12$), and Svedala ($n = 10$). Model predictions (black lines) show the mean movement strategy for geese from each capture site and are based on a non-linear mixed model with the net squared displacement distance (km^2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effects on the asymptotic migration distance. The *Y*-axis is kept constant for comparison; for detailed graphs with adjusted *Y*-axes for each capture site, see Figures S1–S5

Movement strategies of individual geese varied considerably both within and among capture sites, with particularly wide confidence intervals around the predicted migration distance (Figure 2, Table 2, for detailed graphs for each capture site, see Figures S1–S5). Geese from Svedala made only restricted, local movements (82 km, CI: *NA*–1106) and did not generate any distinct migration patterns (Figure 2 and Figure S5). As a result, there were wide confidence intervals around the predicted estimates of timing and duration of both autumn and spring movement, covering the full annual cycle of geese from Svedala (i.e., a poor fit of the non-linear mixed model; Figure 2, Table 3). For the second-most southern capture site, Kristianstad, our results show that many geese were relatively resident all year around, like the geese originating at Svedala, whereas

TABLE 2 Predicted model estimates (95% confidence intervals) based on GPS data of asymptotic migration distance (km), the start and end dates of the annual cycles (July 1 to June 30, 2017–2020) for individual Greylag geese originating at five capture sites in Sweden; Hudiksvall (n = 10), Örebro (n = 30), Nyköping (n = 14), Kristianstad (n = 12), and Svedala (n = 10). Predictions were derived from a non-linear mixed model with the net squared displacement distance (km^2) as response variable, capture site as fixed effect variable, and goose ID as random effect on the asymptotic migration distance

Migration variable	Hudiksvall	Örebro	Nyköping	Kristianstad	Svedala
Net squared distance (km^2)	1,457,388 (968,314–1,946,461)	1,085,376 (31,535–2,139,216)	795,883 (−333,536–1,925,302)	107,204 (−1,044,075–1,258,483)	6756 (−1,210,934–1,224,446)
Distance (km)	1207 (984–1395)	1041 (177–1462)	892 ([a]–1388)	327 ([a]–1121)	82 ([a]–1106)
Timing (days since July 1)					
Autumn	119 (119–120)	125 (125–126)	102 (101–103)	150 (148–152)	32 (0–1441)
Spring	250 (249–251)	224 (223–226)	234 (232–236)	232 (230–234)	154 (−10,226–10,534)
Timing (date)					
Autumn	28 Oct (28–29)	3 Oct (3–4)	10 Oct (9–10)	28 Nov (26–30)	1 Aug (1 Jul–[a])
Spring	7 Mar (6–8)	10 Feb (9–12)	20 Feb (18–22)	18 Feb (16–20)	2 Dec ([a])
Duration (days)					
Autumn	1.3 (1.1–1.4)	7.1 (6.7–7.6)	5.6 (4.9–6.3)	2.8 (1.2–4.4)	34.4 (−806–875)
Spring	15.5 (14.8–16.1)	12.0 (10.6–12.1)	13.1 (11.5–13.5)	1.3 (−1–1.8)	176.8 (−2364–2716)

Note: [a] It is not applicable to take the square root of the lower confidence interval of the net squared distance (km^2) for Nyköping (−333,536 km^2), Kristianstad (−1,044,075 km^2), and Svedala (−1,210,934 km^2). Confidence intervals for timing was out of bound to transform into dates for Svedala (upper confidence interval for autumn: 1442 days after Jul 1, and confidence intervals for spring: −10,226 to 10,534 days after Jul 1).

a few individuals displayed a more pronounced migration pattern (i.e., a net squared displacement curve, Figure 2) resulting in higher predicted migration distance in Kristianstad compared to Svedala (Table 3).

We found apparent patterns of timing of both autumn and spring migration in the individual geese that displayed a distinct migration pattern (i.e. a net squared displacement curve) for Hudiksvall, Nyköping, and Örebro, and for migrating individuals from Kristianstad. Geese from Örebro reached half their migration distance by the beginning of October (Oct 3, CI: 3–4), followed by those from Nyköping a week later (10 Oct, CI: 9–10), Hudiksvall by the end of October (Oct 28, CI: 28–29), and the few geese migrating from Kristianstad reaching half their migration distance by the end of November (Nov 28, CI: 26–30). Spring migration timing corresponded to the approximate order of autumn migration timing, i.e., geese had covered half of their migration distance back to Örebro by the second week of February (Feb 10, CI: 9–12), followed by geese from Kristianstad (Feb 18, CI:16–20) and Nyköping (Feb 20, CI: 18–22) roughly a week later, and geese from Hudiksvall by early March (Mar 7, CI: 6–8).

The general consistency in order of timing of autumn and spring migration for geese with different latitudinal origin indicates that the duration of the migration period is relatively similar in geese from all capture sites, except for those from Svedala and Kristianstad, which moved only locally. The geese from Hudiksvall, which migrated the farthest and fastest in autumn (1.3 days, CI: 1.1–1.4), were the ones with the longest migration duration (i.e., time to cover a quarter of the distance) in spring (15.5 days, CI: 14.8–16.1), followed by geese from Nyköping (13.1 days, CI: 11.5–13.5), and Örebro (12.0 days, CI: 10.6–12.1) (Figure 2, Table 2). The migration duration was consistently less in autumn than in spring for geese from Hudiksvall, Örebro, and Nyköping. For geese from Kristianstad, autumn migration duration was slightly longer (2.8 days, CI: 1.2–4.4) than in spring (1.3 days, CI: −1–1.8) (Figure 3, Table 2).

The individual consistency in movement strategy (i.e., the correlation in net squared displacement on a given day) from one annual cycle to the next was high in the geese migrating the farthest, i.e., the northernmost and central capture sites (Hudiksvall, Örebro, and Nyköping; correlation range: 0.63–0.96, Table 3). There were not any indications of differences depending on the specific annual cycles considered in geese from these sites (2017/2018 *vs.* 2018/2019 and 2018/2019 *vs.* 2019/2020). Resident or short-moving geese from the southern sites (Kristianstad and Svedala) generally showed lower or no individual consistency, with only a few individuals showing consistent movements from one annual cycle to the next (correlation range: −0.84–0.95, for details see Table 3).

4 | DISCUSSION

We found that migration distance increased with increasing latitude of origin in Swedish Greylag geese, and that the final wintering areas were generally located farther south for the geese migrating from the northern capture sites. Moreover, the migration strategies of geese from different capture sites differed in timing and in duration of autumn and spring movement, but with considerable individual variation within capture sites. Geese from the three northern capture sites (Hudiksvall, Nyköping, and Örebro) showed distinct migration patterns, whereas only a few individuals from the southern site Kristianstad migrated, albeit short distances, and the geese from Svedala were relatively resident, only displaying local movements. Taken together, these findings corroborate the hypothesis that present-day Swedish Greylag geese exhibit a leapfrog migration pattern *sensu* Salomonsen (1955) and Berthold (2001) and refute the alternative hypothesis of a retained chain migration pattern.

4.1 | Autumn migration was faster than spring migration in geese from the northernmost sites

Among the three northern capture sites, where all geese clearly migrated, the duration of autumn migration was rather similar despite differences in migration distance. The geese that migrated the farthest (Hudiksvall) thus also migrated the fastest. Yet, they did not start autumn migration earlier, as geese from Örebro and Nyköping had reached a quarter of their migration distance earlier than those from Hudiksvall. This pattern fits with findings from Greylag geese in Norway, where northern breeders migrated later than southern breeders. However, contrary to our results, northern breeders in Norway migrated slower than southern breeders (Andersson et al., 2001).

Interestingly, the time used to cover a quarter of the migration distance was consistently less in autumn than in spring for geese from Hudiksvall, Örebro, and Nyköping. This is in line with GPS location data from Greater white-fronted geese (*Anser albifrons*) (Kölzsch et al., 2014), but contrary to phenological patterns in many other waterfowl, in which spring migration is faster than autumn migration (Calenge et al., 2010; Nilsson et al., 2013). Drent et al. (1978) argued that herbivorous waterfowl time their spring migration to coincide with the flush of nutritious plant growth as spring progresses northwards, the so called “green wave hypothesis.” Kölzsch et al. (2014) suggested that the slower spring migration in greater white-fronted geese was a response to gradual northwards greening in spring, thus consistent with the “green wave hypothesis.” For any migration strategy, the high present-day all-winter abundance of autumn-sown winter green agricultural crops in the migration corridor of Greylag geese is a likely factor to counteract adaptive responses to phenology of natural vegetation, at least for most of the northward migration.

TABLE 3 Pearson correlation estimates (mean, min-max) of individual movement strategies of Greylag geese (i.e., net squared displacement value on each given day) between consecutive annual cycles (2017/2018 to 2018/2019 and 2018/2019 to 2019/2020). The correlation estimates only include individual geese with data from more than one annual cycle ($n = 43$)

	2017/2018 to 2018/2019		2018/2019 to 2019/2020	
Capture site	Mean (min–max)	*n*	Mean (min–max)	*n*
Hudiksvall	0.86 (0.84–0.90)	3	0.86 (0.79–0.95)	4
Örebro	0.89 (0.84–0.92)	5	0.85 (0.68–0.96)	15
Nyköping	0.93 (0.92–0.93)	2	0.81 (0.63–0.95)	8
Kristianstad	−0.84	1	0.38 (−0.10–0.83)	6
Svedala	0.24 (−0.17–0.84)	3	0.31 (−0.01–0.95)	4

4.2 | Non-migratory behavior is common in geese from the southernmost sites

Unlike geese from the three northern capture sites, most of those from the southern (Svedala and Kristianstad) were resident in a very restricted area, with only short-distance excursions locally or regionally. The number of Greylag geese wintering in southern Sweden has increased steadily from almost zero to ~60,000 during the last 30 years (Nilsson et al., 2020), but the origin of these birds has been largely unknown. The present study demonstrates that non-migratory behavior is common among Greylag geese breeding in southernmost Sweden, and that they do very limited movements overall during the annual cycle. Interestingly, we see a slight difference between the two southernmost capture sites; while all geese from Svedala were relatively resident, those from Kristianstad were either residents or short-distance migrants. However, Greylag geese from Kristianstad most probably do not fit the classical definition of “partial migrants”; it is not known whether individuals showing different strategies (i.e., those that only move locally and those that fly to nearby Denmark) differ with respect to age, body condition, or “genetic programming.”

4.3 | Individual consistency in movement strategy between years

Individual consistency in movement strategy from one annual cycle to the next was high in the distinctly migratory geese, i.e., those from Hudiksvall, Örebro, and Nyköping, whereas the short-moving geese with at least two annual cycles from the southern sites (Kristianstad and Svedala) indicated low or no individual consistency (Table 3). Our second hypothesis that individuals should show a consistency in movement habits between years was thus corroborated by the migratory geese from the three northern sites, whereas those from Kristianstad and Svedala in the south provided equivocal results or even refuted the predictions derived from this hypothesis. We interpret these results cautiously, however, as we only tested short-term individual consistency (i.e., from one annual cycle to the next) and the sample size in terms of both annual cycles (e.g., limited climatic variation) and individuals per capture site was limited.

4.4 | Leapfrog migration pattern and inter-individual variation

This study demonstrates a present-day leapfrog migration pattern in Swedish Greylag geese, and differences in migration strategy at the level of capture site (latitude of breeding or molting area). We argue this pattern is robust because: (a) it conforms to the spatial predictions of the leapfrog hypothesis; (b) at the level of capture site, migration distance increased with latitude; (c) only 2 of 22 geese from the two southern sites reached the winter areas of geese from the three capture sites farther north; and (d) only one bird from the three northern capture sites wintered in the core winter area of geese from the two southern sites.

At the same time, our data highlight notable within-site variation in timing, duration, and migration distance, as witnessed by the individual NSD curves (the grey lines in Figures S1–S5). In the following, we will argue that the large-scale leapfrog pattern and the within-site individual variability found need to be seen as complementary with respect to adaptation and the evolution of a new migration pattern. Consequently, we advocate against seeing the present spatial (leapfrog) pattern as a set of stereotypes by capture site, and instead wish to point out the variation within capture sites as an evolutionary "toolbox." Accordingly, individual variation in movement represents a multitude of sub-strategies open for evolutionary selection and different fitness outcomes; in other words a likely driver of long-term, adaptive, change at the level of breeding area. Work on Whooping cranes (*Grus americana*) highlights the importance of such variability by showing that older and innovative individuals attempting new strategies can be drivers of rapid change in migration patterns (Teitelbaum et al., 2016). Juvenile Greylag geese follow their parents during their first autumn and winter, making the early migration habits a socially learned trait (*c.f.*, Kölzsch et al., 2020). Sharing of information within flocks speed up adaptations in migration performance as well as feeding and site choice (Delgado et al., 2018; Mueller et al., 2013).

We acknowledge the fact that the previous chain migration pattern of Swedish Greylag geese was not documented by individual GPS location data, but rather by recoveries of geese with tarsus rings (n=80 individuals; Fransson & Pettersson, 2001). Nevertheless, our results imply that there has been an overall change in migration patterns. The historically most important winter site in Coto Doñana in Spain is nowadays rarely used by Swedish Greylag geese, and similar changes have occurred in other parts of the continental European flyway (Voslamber et al., 2010).

4.5 | Evolutionary perspectives

Greylag geese breeding in southernmost Sweden have gone from being long-distance migrants to being mainly non-migrants in less than 35 years, which is equivalent to 8–10 generations. This begs the question why geese in different parts of Sweden, within the same flyway, have responded so differently. To individual birds it is an asset to know an area well, e.g., where the best roost and foraging sites are, and where predation risk is low. Such advantages are especially important in lean times of nutritional bottlenecks and challenging weather, and favor resident individuals compared to migratory conspecifics that come to the area (Alerstam & Enckell, 1979). A side effect of residency ("prior occupancy" in many verbal models) is the lack of migration cost, and selection will favor residency if it confers higher fitness than adopting a migratory behavior. This scenario fits well with our result that Greylag geese in southernmost Sweden have become mostly resident. It also helps explain why conspecific migrants from the north, with little or no local knowledge, do not stop to winter in southern Sweden. The recent adoption of a resident strategy has likely conferred strong selective advantages in Greylag geese breeding in southernmost Sweden, due to mild winters reducing nutritional needs. In addition, the acreage of autumn-sown winter green crops has increased during the last 35 years, providing abundant predictable high-quality food the year around. In other words, there has not been any fitness penalty in pursuing a resident strategy.

In a theory based on the ideal despotic distribution, i.e., assuming that prior occupancy is an asset, Holmgren and Lundberg (1993) predicted that a leapfrog migration pattern is most likely to evolve when migration costs are high. Compared to the situation 35 years ago, we do not see that migration costs have remained high in terms of energy expenditure. On the contrary, Greylag geese from our three northerly sites have reduced their migration distance significantly, which should lead to lowered energetic costs. Lundberg and Alerstam (1986) presented the most explicit treatment of factors that may induce transition from chain to leapfrog migration pattern. Their theory, too, is based on migration being costly and on an advantage of priority (residents *vs*. migrants), leading to asymmetrical competition. Under these premises, a chain migration pattern will change into a leapfrog pattern if there is an accentuated increase in breeding suitability toward the north or in wintering suitability toward the south in the flyway (Lundberg & Alerstam, 1986). In the absence of data on possible changes in breeding suitability, per capita mortality, and a comprehensive measure of migration cost, it is, however, hard to say whether the theories offered by Lundberg and Alerstam (1986) and Holmgren and Lundberg (1993) explain the change from chain to leapfrog migration in Swedish Greylag geese. While the selective value of adopting residency in southernmost Sweden under recent and present condition is relatively obvious, it is harder to explain why geese breeding in central and northern Sweden continue to overshoot their southern conspecifics.

The three theories above, and for that matter most hypotheses about evolution of bird migration, are framed within the paradigm of resource limitation and competition (intraspecific and/or interspecific), assuming that density-dependent processes operate (Alerstam et al., 2003; Salomonsen, 1955). Assumptions and constraints within this paradigm are relaxed if populations are well below their carrying capacity, which may have been the case for some time for Greylag geese in Sweden and beyond. A combination of sustained population growth and improved body condition, the latter implied by lower age at first reproduction (Nilsson & Kampe-Persson, 2018b), points in this direction. Consequently, if food has long been superabundant, and the per capita hunting mortality rate has fallen as the population has grown, a more successful hypothesis to explain the changed migration pattern may need to be formulated within a paradigm that does not assume food resource limitation.

Although the arguments above are partly speculative, there is evidence that the environment in which European Greylag geese live has seen a reduced seasonality in food abundance, the latter in itself proposed as a key driver for a migratory strategy to evolve (Alerstam & Högstedt, 1982). Swedish Greylag geese nowadays find most of their food most of the year on cropland, instead of in natural habitats. There are indeed empirical reasons to question the omnipresence of resource limitation and density-dependent processes in geese, as in many other taxa (e.g., Rodhe, 2005). In a review of 54 studies explicitly testing for the occurrence of density-dependent patterns and processes in ducks, Gunnarsson et al. (2013) found that no less than 70 of 154 species-specific cases lacked evidence for density dependence. It can be argued that goose populations might be limited by other factors, e.g., availability of nest and molting sites, but no such scientific evidence is apparent for Greylag geese breeding in Sweden.

5 | CONCLUSIONS

The present study demonstrates significant variation in both movement pattern among individuals from a given capture site, and among capture sites. Greylag geese in W Europe may have lived largely unrestricted from food resource limitation and associated competition during the last decades, permitting rapid adoption of new migration strategies tuned to super-abundant food in the agricultural landscape and benign winters with low mortality. The change from a classic chain migration to the present leapfrog pattern has taken some 35 years. This time span and the number of generations involved might be too few to allow classical Darwinian between-generation adaptation to drive the change, even under assumptions of assortative mating. Consequently, and given that young geese follow their parents during their first migration, we presume an important role of within-family inter-generation change in migration habits as a driver behind the rapid change in migration patterns in Swedish Greylag geese.

Our study highlights the general value of collecting individual movement data over entire annual cycles from a variety of breeding sites within a population or flyway. It also emphasizes the need to think outside the paradigm of resource limitation, for population trajectories in ecological time as well as for adaptation in evolutionary time, to understand changed movement patterns in species that spend most of the annual cycle in anthropogenic habitats offering super-abundant food.

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CONFLICT OF INTEREST

None of the authors have any conflicts of interests to declare.

AUTHOR CONTRIBUTIONS

Lovisa Nilsson: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Visualization (lead); Writing – original draft (equal); Writing – review & editing (equal). **Camilla Olsson:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Writing – review & editing (equal). **Johan Elmberg:** Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Project administration (lead); Writing – original draft (equal); Writing – review & editing (equal). **Nils Bunnefeld:** Conceptualization (equal); Methodology (lead); Writing – review & editing (equal). **Niklas Liljebäck:** Conceptualization (equal); Funding acquisition (supporting); Project administration (supporting); Writing – review & editing (equal). **Johan Månsson:** Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Project administration (lead); Writing – review & editing (equal).

DATA AVAILABILITY STATEMENT

Data is available in Dryad: https://doi.org/10.5061/dryad.wh70rxwq3.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Supporting Information

Leapfrog migration and residents: new migratory habits in Swedish Greylag geese

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Table S1. Structure of the non-linear mixed models tested for convergence (see equation in Methods) based on different combinations of the fixed factors capture site (five-level factor: Hudiksvall, Örebro, Nyköping, Kristianstad, Svedala) and annual cycle (three-level factor: 2017/2018, 2018/2019, 2019/2020), and the random effect goose ID (76 levels) on the movement variables: distance, timing and duration of autumn and spring movement.

Model	Fixed effect	Random effect	Convergence
1	Capture site on distance, timing, duration	Goose ID on distance	Yes
2	Capture site on distance, timing, duration	Goose ID on distance, timing	No
3	Capture site on distance timing, duration	Goose ID on distance, timing, duration	No
4	Capture site and annual cycle on distance, timing, duration	Goose ID on distance	No
5	Capture site on distance, timing, duration	Goose ID and annual cycle on distance	No

Table S2. Individual geese with GPS location data covering two or three annual cycles, per capture site.

Capture site	Number of individuals	
	2 cycles	*3 cycles*
Hudiksvall	7	0
Örebro	14	3
Nyköping	6	1
Kristianstad	5	1
Svedala	3	2

Table S3. Individual information about Greylag goose individuals (n=76) included in the statistical modelling in the present study.

Catch site	Sex	Age at tagging	Annual cycles	Individual
Hudiksvall	Female	2 cy+	2	D13
Hudiksvall	Female	2 cy+	2	D25
Hudiksvall	Female	2 cy+	1	D67
Hudiksvall	Female	2 cy+	2	D77
Hudiksvall	Female	2 cy+	2	D78
Hudiksvall	Female	2 cy+	2	D79
Hudiksvall	Female	2 cy+	2	DM3
Hudiksvall	Female	2 cy+	1	DM4
Hudiksvall	Female	2 cy+	1	DM5
Hudiksvall	Female	2 cy+	2	DM6
Örebro	Female	2 cy+	2	K03
Örebro	Female	2 cy+	2	K06
Örebro	Female	2 cy+	2	K09
Örebro	Female	2 cy+	1	K35
Örebro	Female	2 cy+	1	K36
Örebro	Female	2 cy+	1	K37
Örebro	Female	1 cy	3	S34
Örebro	Female	2 cy+	3	S57
Örebro	Female	2 cy+	1	S65
Örebro	Female	2 cy+	3	S66
Örebro	Female	2 cy+	1	S89
Örebro	Female	2 cy+	2	S96
Örebro	Male	2 cy+	2	K04
Örebro	Male	2 cy+	2	K05
Örebro	Male	2 cy+	1	K08
Örebro	Male	2 cy+	1	K31
Örebro	Male	2 cy+	1	K32
Örebro	Male	2 cy+	1	K34
Örebro	Male	1 cy	2	S38
Örebro	Male	1 cy	1	S41
Örebro	Male	1 cy	1	S51
Örebro	Male	2 cy+	1	S67
Örebro	Male	2 cy+	1	S68
Örebro	Male	2 cy+	2	S90
Örebro	Male	2 cy+	2	S91
Örebro	Male	2 cy+	2	S92
Örebro	Male	2 cy+	2	S93
Örebro	Male	2 cy+	2	S94
Örebro	Male	2 cy+	2	S99
Örebro	NA	2 cy+	2	S64
Nyköping	Female	2 cy+	3	D70
Nyköping	Female	2 cy+	2	D71

Nyköping	Female	2 cy+	1	D74
Nyköping	Female	2 cy+	1	K20
Nyköping	Female	2 cy+	1	K21
Nyköping	Female	2 cy+	1	K22
Nyköping	Female	2 cy+	1	K23
Nyköping	Female	2 cy+	1	S30
Nyköping	Female	2 cy+	1	S32
Nyköping	Female	2 cy+	2	S33
Nyköping	Female	2 cy+	2	S71
Nyköping	Female	2 cy+	2	S72
Nyköping	Female	2 cy+	2	S74
Nyköping	Female	2 cy+	2	S75
Kristianstad	Female	2 cy+	1	K43
Kristianstad	Female	2 cy+	1	K44
Kristianstad	Female	2 cy+	1	S78
Kristianstad	Female	2 cy+	2	S80
Kristianstad	Female	2 cy+	2	S85
Kristianstad	Female	2 cy+	1	S87
Kristianstad	Male	1 cy	1	S84
Kristianstad	Male	2 cy+	1	K42
Kristianstad	Male	2 cy+	3	S02
Kristianstad	Male	2 cy+	2	S77
Kristianstad	Male	2 cy+	2	S81
Kristianstad	Male	2 cy+	2	S83
Svedala	Female	2 cy+	1	K14
Svedala	Female	2 cy+	1	S06
Svedala	Female	2 cy+	3	S07
Svedala	Female	2 cy+	3	S14
Svedala	Female	2 cy+	1	S20
Svedala	Male	2 cy+	2	K18
Svedala	Male	2 cy+	1	S05
Svedala	Male	2 cy+	2	S25
Svedala	Male	2 cy+	1	S29
Svedala	NA	2 cy+	2	S12

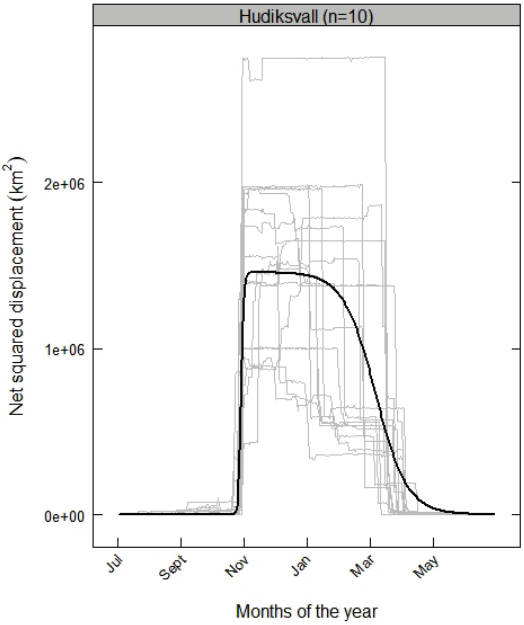

Figure S1. Net squared displacement over the annual cycles (1 July - 30 June, 2017-2020) for individual Greylag geese (grey lines) tagged with a GPS collar at Hudiksvall (n=10). The model prediction (black line) demonstrates the mean movement strategy of all geese from this capture site and is based on a non-linear mixed model with the net squared displacement distances (km^2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effect on the asymptotic migration distance. The y axis is adjusted to fit the specific results for this capture site. For a comparison among capture sites based on a common y axis scale, see Fig. 2.

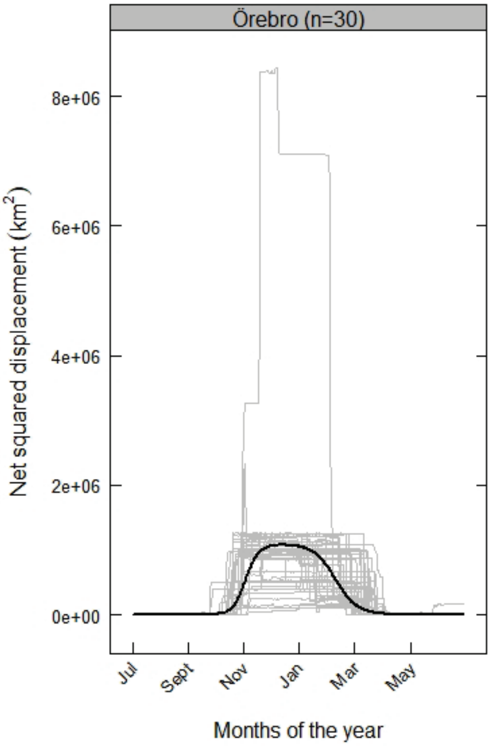

Figure S2. Net squared displacement over the annual cycles (1 July - 30 June, 2017-2020) for individual Greylag geese (grey lines) tagged with a GPS collar at Örebro (n=30). The model prediction (black line) demonstrates the mean movement strategy of all geese from this capture site and is based on a non-linear mixed model with the net squared displacement distances (km^2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effect on the asymptotic migration distance. The y axis is adjusted to fit the specific results for this capture site. For a comparison among capture sites based on a common y axis scale, see Fig. 2.

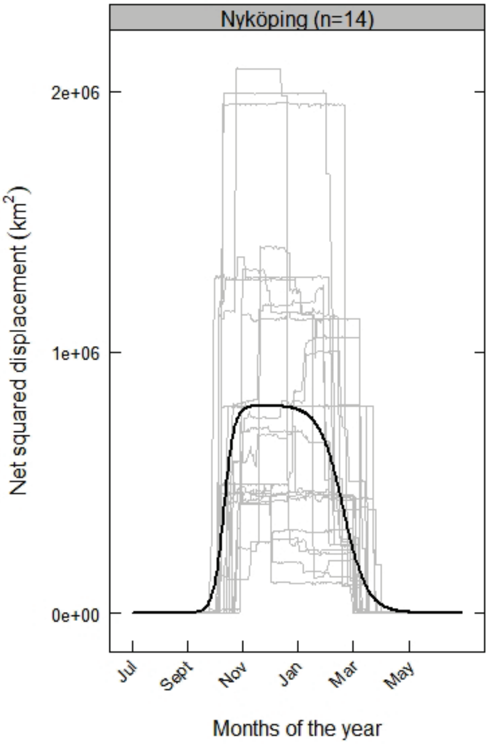

Figure S3. Net squared displacement over the annual cycles (1 July- 30 June, 2017-2020) for individual Greylag geese (grey lines) tagged with a GPS collar at Nyköping (n=14).The model prediction (black line) demonstrates the mean movement strategy of all geese from this capture site and is based on a non-linear mixed model with the net squared displacement distances (km^2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effect on the asymptotic migration distance. The y axis is adjusted to fit the specific results for this capture site. For a comparison among capture sites based on a common y axis scale, see Fig. 2.

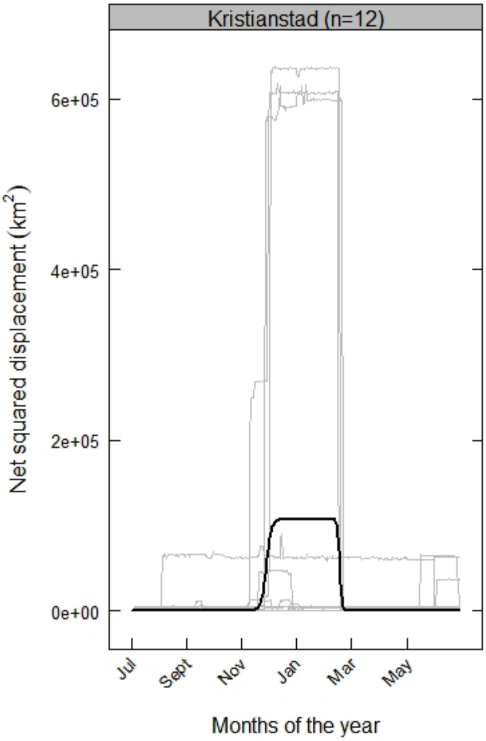

Figure S4. Net squared displacement over the annual cycles (1 July- 30 June, 2017-2020) for individual Greylag geese (grey lines) tagged with a GPS collar at Kristianstad (n=12). The model prediction (black line) demonstrates the mean movement strategy of all geese from this capture site and is based on a non-linear mixed model with the net squared displacement distances (km^2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effect on the asymptotic migration distance. The y axis is adjusted to fit the specific results for this capture site. For a comparison among capture sites based on a common y axis scale, see Fig. 2.

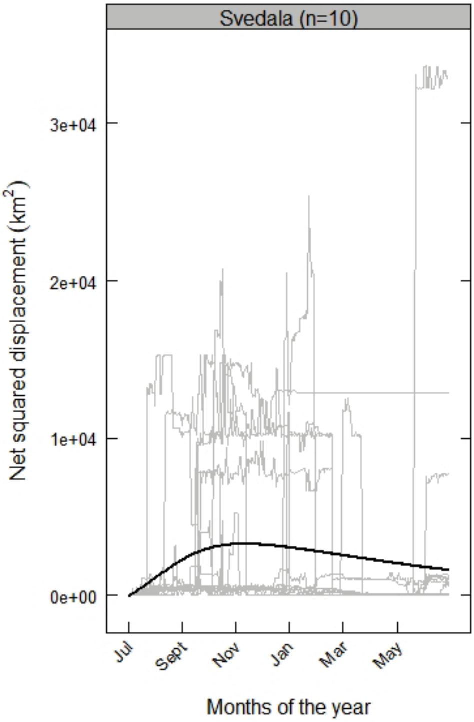

Figure S5. Net squared displacement over the annual cycles (1 July- 30 June, 2017-2020) for individual Greylag geese (grey lines) tagged with a GPS collar at Svedala (n=10). The model prediction (black line) demonstrates the mean movement strategy of all geese from this capture site and is based on a non-linear mixed model with the net squared displacement distances (km^2) as response variable, capture site as fixed effect variable on distance, duration and timing of autumn and spring movement, and goose ID as random effect on the asymptotic migration distance. The y axis is adjusted to fit the specific results for this capture site. For a comparison among capture sites based on a common y axis scale, see Fig. 2.

III

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Field selection in a guild of geese: Seasonal dynamics and implications for crop damage mitigation

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ABSTRACT

Goose management and crop damage mitigation are multi-species endeavors affected by agricultural practices and other environmental factors that vary in space and time. Yet, most previous studies concern single goose species and limited spatio-temporal scales. We analyzed selection of crop types in combination with field stages (pre- vs post-harvest) and assessed the probability of geese using different fields, in co-occurring goose species across seasons and over multiple years. The study was conducted in two landscapes differing in agricultural practices and seasonal composition of goose species and crops. We found several overarching trends in field selection and use of growing crops across species and study areas, but also considerable variability among seasons and species, highlighting the complexity goose management is facing. Fields used for livestock feed production, such as pastures and ley fields, were typically the most selected in spring and summer, as were post-harvest fields when and where available in summer. In autumn and winter geese mainly selected post-harvest fields. Selection for growing cereal crops was generally higher in winter and spring. A general advice for reducing goose grazing and potential damage to growing crops is to leave harvest residues in untilled fields for as long as possible in autumn and early winter. Sowing in spring rather than in fall is another way to reduce grazing, specifically on cereals during winter and early spring, if feasible given other factors affecting crop rotation. However, management needs to adopt adaptive strategies tailored to specific species, regions, and seasons to successfully reduce crop damage risk by grazing geese.

1. Introduction

Management of agricultural landscapes is increasingly challenged by the need to make trade-offs between economically sustainable food production for growing human populations and conservation of biodiversity and ecosystem services. While agricultural production continues to increase steadily, many wildlife species associated with agricultural landscapes have declined significantly (Hemminger et al., 2022; Lécuyer et al., 2022). Conversely, there are species that have benefited from modern agriculture, and increased dramatically to levels causing significant negative impact due to foraging, trampling, and grubbing (Düttmann et al., 2023; Fox and Madsen, 2017; Hemminger et al., 2022; Montràs-Janer et al., 2019).

Geese (*Anser*, *Branta*, *Chen*) are illustrative examples of such dilemmas. In the northern hemisphere, several goose species have long been considered symbols of conservation success, as their populations have been brought back from over-exploitation and historical lows to a favorable conservation status (Fox and Madsen, 2017; Hemminger et al., 2022). Today's agricultural landscapes offer predictable and nutritious food resources. In response, geese have largely shifted foraging habits from natural grasslands to cropland (Fox et al., 2016). The abundance and availability of these resources have supported population growth, as geese take advantage of its year-round availability. As a result, there are more geese than ever before sharing the agricultural landscape with humans (Fox and Abraham, 2017; Fox and Madsen, 2017).

With growing negative impact on agriculture, abundant goose populations have become the core of a conflict over agricultural and conservation interests over large parts of North America and Europe (Düttmann et al., 2023; Lefebvre et al., 2017; Montràs-Janer et al., 2019). The total negative impact caused by geese, swans, and cranes on agriculture is hard to gauge. Grazing does not necessarily result in damage leading to subsequent yield loss, as several factors potentially affect the extent of damage, such as grazing pressure, weather, crop type and level of vulnerability of crop along with its ability to compensate for

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damage (Clausen et al., 2022). Previous research highlights considerable variation in the extent to which goose grazing ultimately affects crop growth, yield and economic loss (review in Fox et al., 2016). Several studies indicate that the probability of damage increases as harvest approaches (Buitendijk and Nolet, 2023; Buitendijk et al., 2023), although grazing can have a pronounced impact on yield throughout the year (Montràs-Janer et al., 2020). Locally, grazing can challenge economic sustainability of agricultural practices, and cases of up to 50 % harvest loss due to goose grazing have been recorded recently, with millions of Euros spent annually in the European Union alone on reimbursement to farmers for harvest loss (Düttmann et al., 2023; Jensen et al., 2018; Montràs-Janer et al., 2019).

Management of geese on agricultural land and the related challenges farmers face have become increasingly complex; climate and landscapes are changing, and a greater number and diversity of goose species than before use agricultural land. Adding to the complexity, goose species are highly dynamic in dietary selection and migratory strategies over their annual cycle (Arzel et al., 2006; Nilsson et al., 2022). At the local level, several factors are known to influence field selection by foraging geese and thereby also the probability that geese select a certain field, e.g., crop type, crop stage, distance from roost site, disturbance, interspecific interactions and predation risk (Fox et al., 2016; McKay et al., 1996; Rosin et al., 2012; Tombre et al., 2019).

Hence, goose management is often a dynamic multi-species endeavor affected by agricultural practices and other environmental conditions that vary in space and time (Montràs-Janer et al., 2020). Yet, most previous studies on field use and selection by geese and related damage risk, concern single species and limited spatio-temporal scales and crop diversity. The generality of such studies is inherently limited, a problem exacerbated by the fact that damage mitigation, such as diversionary fields and alterations in cultivation practices in response to goose presence, may need to be tailored differently depending on species, season, and region (Nilsson et al., 2024; Teräväinen et al., 2022; Vickery and Gill, 1999). Some crops are less likely to be selected after they have reached a certain height, as they become less nutritious or hamper predator detection (Fox et al., 2016; Strong et al., 2021). Moreover, geese feeding on crop residues post-harvest cause no damage, highlighting the importance of considering field stage when assessing damage risk. A deeper understanding of the probability of geese using different fields, crop types, and field stages (pre- vs post-harvest) under various conditions will aid farmers and management to better predict crop damage risk and to prioritize preventive measures that are effective also in a multi-species context.

In this study, we studied selection by co-occurring goose species of crop type and field stage, across seasons over multiple years. The research was conducted in two landscapes characterized by intensive agriculture, but with distinct differences in crop diversity, phenology, farming practices, and seasonal composition of goose communities.

2. Methods

2.1. Study areas

This study was carried out in two areas in southern Sweden (Fig. 1); one at 59°10 N, 15°22 E (hereafter 'North') and one at 56°01'N, 14°09 E (hereafter 'South'). The northern is in the boreonemoral zone, whereas the southern study area is situated in the nemoral biotic zone, (Ahti et al., 1968). Both study areas are dominated by intensive agriculture but also contain shallow lakes, wetlands, grasslands, and forest patches. In both study areas, croplands and grasslands provide geese with abundant feeding opportunities, whereas lakes and wetlands serve as roost sites for all goose species present, and as recurrent breeding sites for greylag geese (Olsson et al., 2017; Waldemarsson, 2011). It should be noted that this study has an explicit focus on farmland, and that it does not embrace natural habitats sometimes used by geese for foraging. Accordingly, grasslands included in our analysis are all either grazed by livestock or otherwise actively managed and cannot be regarded as "natural" or "semi-natural" areas, as they are all subject to human management and hold economic value.

Main crops in both study areas are cereals *(i.e.,* wheat, barley, rye, oats), and potatoes. There are also considerable areas of ley fields and pastures for grazing livestock in both areas. South has a greater variety of crop types, including large areas of sugar beet, oilseed rape, maize, and vegetables such as beans, peas, onions, lettuce, kale, broccoli, cabbage, carrots and red beets. In total, more than 50 crop types were recorded during the field work conducted in South, a unique feature of our study providing geese opportunity to select among a wide range of crops. In both study areas, most crops are harvested from early August

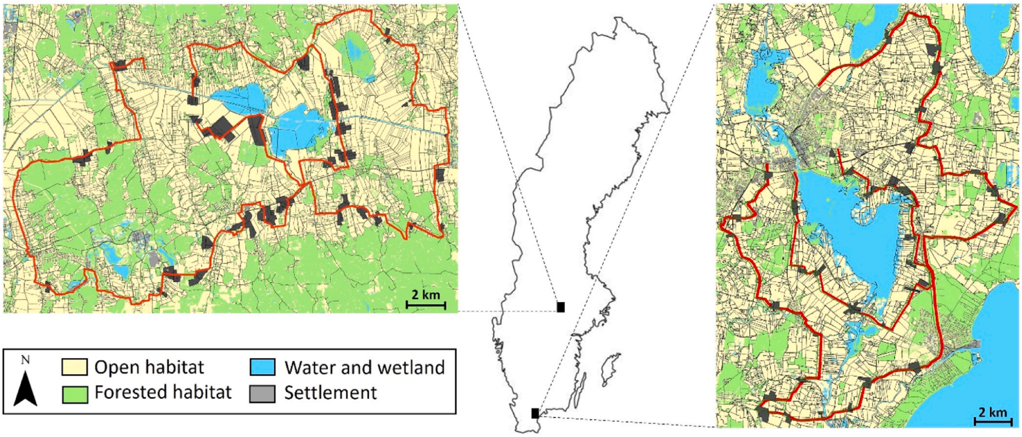


Fig. 1. Location of the study areas in Sweden (left map = 'North'; right map = 'South'). The legend box names the main habitat types. Red lines indicate the routes of monthly surveys conducted between 2017 and 2021. Along these routes, all geese present on agricultural fields and identifiable by species were counted, and the crop type and field stage were recorded. To assess field availability, data on crop type and field stage were also collected from randomly distributed reference fields (dark grey), which were surveyed on every occasion, regardless of goose presence.

through October, and winter-green crops (*e.g.,* some cereals, oilseed rape and newly established ley fields) are normally sown in August-October. However, in South some root crops are harvested also later, into December-January. Furthermore, fields with crops that are pre-germinated before planting or have a shorter growing season, as is the case for many vegetables, can be sown and harvested multiple times during a growing season. The same applies to ley fields, which may be cut up to five times per year in South, and up to three times in North. North offers stubble fields from mid-August until geese depart for southward migration, and green autumn-sown cereals in spring, in addition to pastures and other grasslands. In South, however, agricultural activities occur throughout winter, providing fresh harvest residues into January, and an uninterrupted supply of green forage (i.e., autumn-sown cereals, ley, pasture).

In North, there are both breeding (mainly greylag geese, April-August) and staging geese (March-April and September-November), but there are basically no geese present from December to February. The maximum numbers reported anytime during the study period were 14200 bean geese, 9300 greylag geese, 4000 barnacle geese, 2100 pink-footed geese, 1300 greater white-fronted geese, and 300 Canada geese ("Artportalen," 2024). Goose numbers in North peak in autumn (September-October).

In South, there are large numbers of geese year around, ranging from a few thousand in summer (locally breeding greylag geese and barnacle geese) to 15000—54000 from November through March. In South, the maximum numbers reported anytime during the study period were: 17200 bean geese, 9200 greylag geese, 44200 barnacle geese, 1400 greater white-fronted geese, 290 pink-footed geese, 3700 Canada geese, and 40 brent geese (Waldemarsson, 2011).

In addition to hosting numerous geese, there were thousands of other large herbivorous birds present in both study areas, e.g., common cranes (*Grus grus*) and whooper swans (*Cygnus cygnus*).

2.2. Data collection

Field surveys were carried out monthly in North from April 2018 to March 2021 (in total 27 months; no counts in December—February when geese were not present), and in South from October 2017 to September 2021 (48 consecutive months). In each study area surveys of geese and crops were done along two routes: one inner (nearer) and one outer (more distant) encircling major waterbodies used by geese as roost sites (Fig. 1). The inner routes were 29 km and 30 km, and the outer routes 70 km and 75 km in North and South, respectively. All geese observed on agricultural land (*i.e.,* cropland and pastures) along a survey route were counted and identified by species using binoculars and spotting scope.

In both study areas, bean geese are represented by two subspecies; taiga bean goose (*Anser fabalis fabalis*) and tundra bean goose (*Anser fabalis serrirostris*). In most cases it was possible to separate these taxa during the surveys and they were therefore kept separate also in the analyses. The combination of crop type and field stage (hereafter 'field type') in fields used by geese were noted. The maximum distance from the survey route at which records were included was set by the feasibility to define crop type and field stage and to identify geese to species in the field. Field stage was initially categorized as 'growing crop', 'stubble or harvested', or 'bare soil'.

We used a field tablet with digital maps to mark fields with goose presence (hereafter 'observation fields'). Data related to crop type and field stage collected during field surveys were later supplemented by official information regarding crop type and field size using field-level information obtained from the administrative database SAM14 (Swedish Board of Agriculture). However, for the variable field stage, the presence of cover crops, or cases where crop type changed during the growing season, we relied exclusively on own field survey data, as SAM14 only provides information on the main crop and lacks details on farming practices such as sowing and harvest timing. In addition to these observation fields, where goose presence differed among survey occasions (*i.e,* goose use of fields), 36 permanent survey points were distributed along the routes in each study area. These points were randomly distributed along the routes with a minimum distance of 1000 m between them (Fig. 1) and served as fixed locations for selecting permanent reference fields. Each point was adjacent to one or several agricultural fields (hereafter 'reference fields'), whose individual crop types and field stages were recorded on each survey occasion, regardless of goose presence, to quantify availability of different field types to geese. The total number of such reference fields along the survey routes was 134 in North and 93 in South. In cases when geese were observed in a reference field, the latter was simultaneously treated as both an observation field and a reference field.

In each monthly survey, one of the reference points was randomly assigned as a starting point. Surveys started within one hour after sunrise but were discontinued if weather conditions deteriorated to the extent that visibility declined substantially, or due to limited daylight hours in winter. Interrupted surveys were re-assumed as soon as conditions permitted the same or the following day. Field surveys ended when the inner and outer routes had been completed.

To ensure statistically manageable analyses, some field types (*i.e.* the combination of crop type and field stage) were subsequently pooled into new categories (hereafter 'field categories') for analyses (Table S1 in Supporting Information). The categorization was primarily based on agricultural and economic perspectives, focusing on perceived monetary value and relevance of each field type to the farmer, rather than their role as food sources for geese. For example, field types such as "bare soil," "fallow," and "buffer zone to watercourse (grassland)" were grouped into a single category (Table S1 in Supporting Information), as they all represent areas without direct economic value to the farmer, despite their differing ecological roles and forage potential for geese. Ley fields and pastures were treated as separate categories due to differences in management practices. Leys are intensively managed grasslands typically used for silage production, and they are harvested mechanically, whereas pastures are grazed directly by livestock. These differences imply variation in fertilization, disturbance, and harvesting/grazing regimes, which are relevant from both an agricultural and ecological perspective. In some cases, it was unavoidable to merge rare crop types that differ in both economic value and forage suitability, in order to keep the number of categories low enough for robust statistical analysis. However, we consistently distinguish between growing crops and post-harvest fields. It should be noted that the categories "other crop (harvested)" and "other crop (growing)" may differ among sites and seasons, due to spatial and temporal variation in crop availability (see Table S1 in Supporting Information). These categories include all crops not classified under specific field type (e.g. barley, ley, pasture) and their composition may therefore vary. Distance from night roost sites has been established as an important predictor of field use across several goose species and seasons (e.g., Fox et al., 2016), and particularly during the breeding period when geese are spatially constrained by nesting and brood-rearing (Olsson et al., 2017). However, due to the presence of multiple water bodies of varying suitability as potential roost sites within our study areas, and uncertainty regarding which of these were actually used as night roosts by the observed geese, we were unable to incorporate this variable without introducing bias.

The original dataset included observations from eight goose species, observed in the following number of fields: greylag goose (*Anser anser*, n = 757), taiga bean goose (*Anser fabalis fabalis*, n = 184), barnacle goose (*Branta leucopsis*, n = 173), white-fronted goose (*Anser albifrons*, n = 101), Canada goose (*Branta canadensis*, n = 96), tundra bean goose (*Anser fabalis rossicus*, n = 73), pink-footed goose (*Anser brachyrhynchus*, n = 19), and brent goose (*Branta bernicla*, n = 1). Due to very low number of observations, pink-footed goose and brent goose were excluded from all statistical analyses. Although barnacle geese breed locally in the southern study area, they do so primarily on offshore islands in the Baltic and only rarely visit agricultural fields on the mainland during the nesting season. During the summer season in South, only a single observation was made of barnacle geese; hence it was not included in the summer analyses. We defined seasons as: 'spring' = March-May, 'summer' = June-August, 'autumn' = September-November, and 'winter' = December-February.

2.3. Statistical analyses

Field selection by different goose species was analyzed by comparing field use in relation to availability of that field type in the landscape (*i.e.,* relative probability of goose presence at fields) (Lele and Keim, 2006). Due to the spatial aggregation of geese, extensive variation in flock size, and a substantial proportion of fields without goose presence, data exhibited pronounced zero-inflation and overdispersion. Generalized linear models were thus performed in R package lme4 (Bates et al., 2025) with binomial error structures and logit link functions. Study area (North *versus* South), season (spring, summer, autumn, winter), and goose species (barnacle goose, Canada goose, greater white-fronted goose, greylag goose, taiga bean goose, and tundra bean goose) were treated separately to avoid overfitting of models. Consequently, 17 separate global models were assessed, each comprising a unique combination of study area, season, and goose species (see Table S2 in Supporting Information). All 17 global models had the same setup, with goose presence (binomial) as the response variable, and field type and size (km^2) as explanatory variables. Field size was included in the models to account for larger fields having higher probability of goose presence due to their larger area. Since field size did not meet the criteria of normality in any of the models, values were log-transformed prior to analysis. As a continuous (and log-transformed) variable, field size was included as a fixed effect, as it was not suitable for inclusion as a random factor. We initially considered including "year" as a random effect to account for potential interannual variation. However, since the variance explained by year was non-significant and the sampling was balanced across years, we excluded "year" from the final models to improve model stability. Model assumptions were checked as outlined in Zuur et al. (2010). We compared all models with null models (intercept only, i.e. the response variable, with all other variables excluded) using AIC (see Table S2 in Supporting Information; (Burnham and Anderson, 2002)). We applied the "dredge" function in R (MuMIn package) to the global model to generate and compare models based on different combinations of fixed effects. The model with the lowest AIC for each of the 17 global models was considered the best-supported model for that specific combination of study area, season, and goose species (Table 2). Parameter estimates are presented with 95 % confidence intervals and reflect comparisons of each field type against the category "bare soil and fallow, " which served as the intercept. This category was retained as the reference level as it appeared in all models and thus provided a consistent basis for comparison across species, seasons, and sites. To evaluate model validity, we compared model deviance to the degrees of freedom. In all cases, deviance values were close to or well below the number of degrees of freedom, and all models were thus deemed valid.

Based on each of the 17 top-ranked models, predicted relative probabilities of goose presence were calculated with a 95 % confidence interval for each of the different field categories, study area, season, and goose species, using the ggpredict function in R (ggeffects package). In cases where field size was included in the top-ranked model, it was set to the mean value for each respective site and season in the predictions (Fig. 3).

To support interpretation of the ranking (Table 3), we conducted a supplementary post-hoc comparison of field types. While the ranking captures the overall patterns of field selection, it does not reflect whether specific field types differ significantly from one another with respect to probability of goose presence. Therefore, we performed pairwise comparisons using the "marginaleffects" function in R, applying a Bonferroni correction for multiple testing, for each of the 17 model outcomes (see Fig. S3a–q in Supporting Information). Field size was held constant at its predicted mean for each study site and season. Model estimates are presented with 95 % confidence intervals. These comparisons were included as a descriptive complement to the ranking presented in Table 3.

3. Results

3.1. Numbers and relative abundance of geese

In total, 237105 geese were counted across study areas, years, and seasons (Table 1, Fig. 2). Slightly more than one third (37 %) were found in post-harvest fields, 32 % were found in fields used for livestock feed production (growing ley and pasture), and 31 % in fields with other types of pre-harvest crops grown for human consumption. Goose numbers, species composition, and flock size all varied across seasons and study areas (Table 1). The median number of geese counted over the years per survey occasion (i.e., once a month) in North was 1892 in spring, 943 in summer, and 5482 in autumn. The corresponding values for South were 2002 in spring, 345 in summer, and 3703 in autumn, and 7471 in winter. The number of fields with goose presence, for each of the surveys conducted, varied among species and seasons, ranging from 35 to 326 (Table 1). Geese were observed at distances of up to 1326 m from the survey route in North (mean distance 294 m (±212 m SD)). In South, the maximum observation distance was 1480 m (mean 313 m (±228 m SD)). The number of geese observed in individual fields ranged from a single or a few birds to 18000 (in any of all surveys; Table 1). When geese were present in a field, median flock size ranged from 5 to 158 depending on season and species (Table 1). Taiga bean goose and barnacle goose were the most numerous species in North and South, respectively. Greylag goose was the only species occurring in significant numbers in all surveyed seasons in both study areas. In spring, the latter species, unlike the others, tended to occur in very small groups, resulting in a large number of observations.

3.2. Probability of goose presence in relation to crops and growth stages

3.2.1. Spring

In spring, the probability of goose presence in fields with different field categories (Table S1 in Supporting Information) differed slightly between the two study areas, as well as among goose species (Fig. 3). For all species in both areas, the probability of presence showed close to or partially overlapping confidence intervals for most field categories, except for those with a generally low probability of goose presence (*i.e.,* bare soil and fallow).

In North, the highest ranked fields with respect to probability of presence by greylag geese were the categories harvested crops (*e.g.,* including cereal mixtures, potatoes, and oilseed rape) and growing barley, followed by pasture, and ley (Table 2 & 3, Fig. 3). In taiga bean goose, ley fields and pastures ranked highest, followed by the category other growing crops and by growing wheat.

In South, pastures ranked highest in both greylag and barnacle geese, followed by ley fields and growing wheat. For greater white-fronted goose, ley ranked highest, followed by growing wheat and harvested crops (Table 2 & 3, Fig. 3).

3.2.2. Summer

There were some differences in the ranking of field categories between the two study areas. However, a common feature was a comparatively high probability of greylag goose presence in fields used for livestock feed production (ley and pasture) and on harvested crops, but a low probability of presence in fields with growing crops intended for human consumption (Fig. 3).

In North, fields with harvested crops ranked highest in greylag geese, followed by pasture and ley (Table 2 & 3; Fig. 3). In South, the highest ranked field categories by greylag geese were pasture followed by harvested crop and ley (Table 2 & 3; Fig. 3).

Table 1
Number of fields with goose presence (n_{fields}) by season, study area, and goose species in monthly field surveys conducted in two study areas (North=27 months and South=48 months) in Sweden. 'Number of geese' shows median, range (minimum-maximum), and total number of geese observed. See Methods for definitions of 'season'.

Season	Species	Study area	n_{fields}	Number of geese		
				median	range	total
Spring	Greylag	North	163	18	1–290	5852
	Taiga bean	North	37	112	1–1700	11179
	Greylag	South	326	7	1–264	6942
	Barnacle	South	37	20	1–3700	14411
	Gr. white-fronted	South	35	31	1–690	2676
Summer	Greylag	North	60	63	2–1150	8484
	Greylag	South	43	28	1–780	4136
Autumn	Greylag	North	61	38	2–3000	18583
	Taiga bean	North	41	70	1–18000	30754
	Greylag	South	86	50	1–1550	12014
	Barnacle	South	58	158	1–5000	32420
Winter	Greylag	South	53	25.0	1–1900	15268
	Barnacle	South	95	100	1–1500	33453
	Gr. white-fronted	South	188	5	1–300	1291
	Taiga bean	South	124	56	1–2320	21917
	Tundra bean	South	72	40	1–1370	10491
	Canada	South	44	30	1–1400	7234

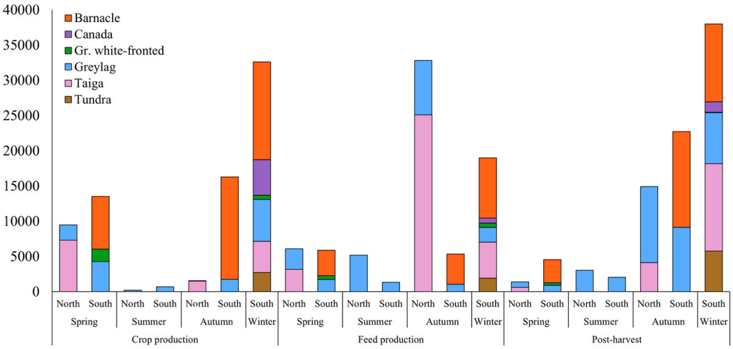


Fig. 2. Total number of counted geese in fields with crop production (pre-harvest, intended for human consumption), livestock feed production (ley and pastures), and post-harvest crops presented by season and study area (study areas North versus South). Colors denote different goose species (legend above). Samples include 27 monthly surveys in North and 48 in South.

3.2.3. *Autumn*

During this season the availability of different field categories differed considerably between the two study areas, but harvested crops had the highest probability of goose presence overall, irrespective of goose species and study area (Table 2 & 3, Fig. 3).

In North, the highest ranked field categories by both greylag geese and taiga bean geese were those with harvested barley, followed by pasture, and harvested wheat (Table 2 & 3, Fig. 3). In South, harvested root crops and maize was the highest ranked field category in greylag and barnacle geese, followed by harvested wheat and harvested barley in greylag geese, and ley along with growing cereals in barnacle geese (Table 2 & 3, Fig. 3).

3.2.4. *Winter (South only)*

Although the order of the top-ranked field categories differed slightly in terms of probability of presence across species, harvested root crops and maize along with winter-green crops, such as autumn-sown cereals and ley fields, generally ranked high among the six species present (Table 2 & 3, Fig. 3).

Fields with harvested root crops and maize were the highest ranked field category, followed by either ley, growing wheat or other growing cereals in four of six species (barnacle goose, greylag goose, taiga bean goose, and tundra bean goose; Table 2 & 3, Fig. 3). In greater white-fronted goose, ley fields were top-ranked followed by harvested root crops and maize. Growing cereals had the highest probability of Canada goose presence in winter, with wheat being top-ranked among them, followed by barley and other cereals.

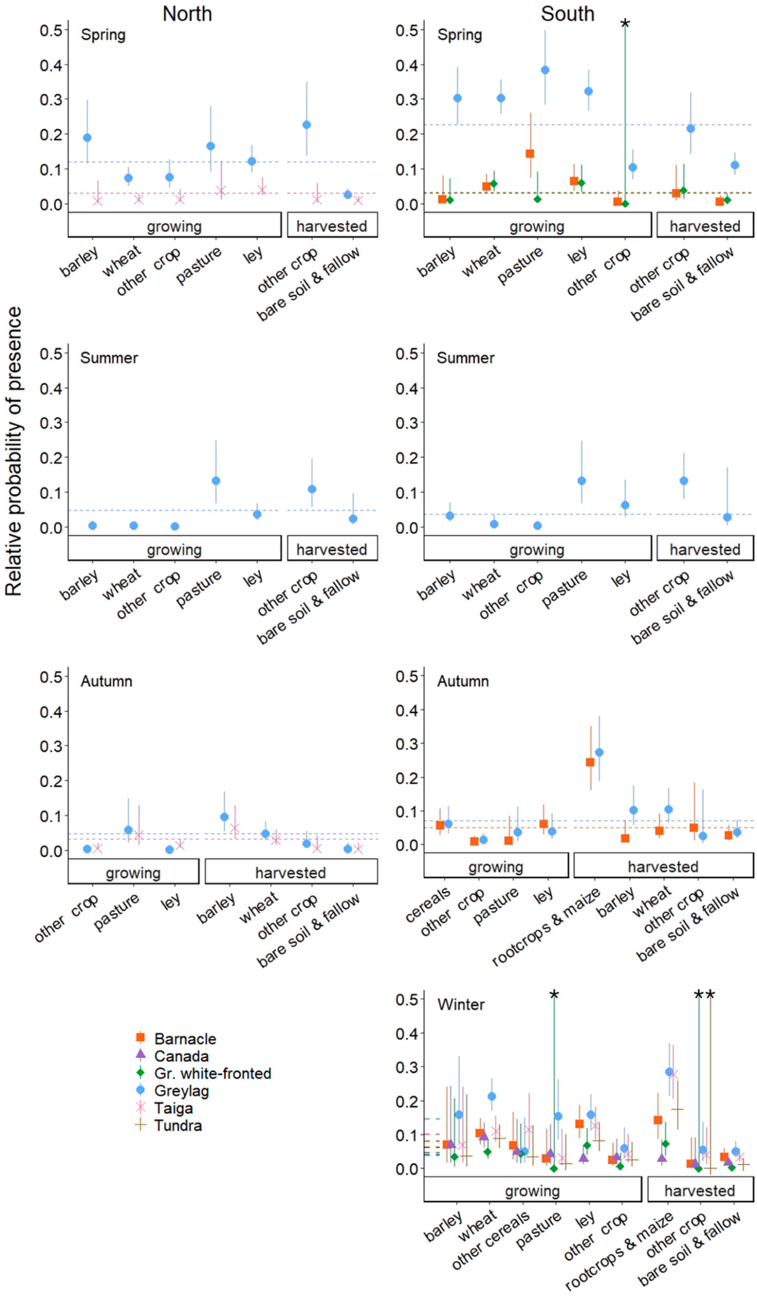
4. Discussion

Our study revealed several overarching trends in seasonal field selection by geese across multiple species and two diverse agricultural landscapes. Though our study identified several general patterns in field selection across species and study areas, it also demonstrates extensive variability among seasons. This is in line with previous research demonstrating such patterns, which are often related to shifts in nutritional needs between seasons (e.g., protein *versus* carbohydrates; for a review see Fox et al., (2016).

4.1. *Patterns by season*

4.1.1. *Spring*

Overall, field selection in spring, when geese are fueling for northward migration and in particular for breeding, was generally biased



(caption on next page)

Fig. 3. Predicted relative probabilities of goose presence and 95 % confidence intervals for different field categories (combinations of crop type and field stage, merged into overarching field categories, see Table S1) by study area (North, left panel, South, right panel), season, and goose species derived from the models (see Table 2). When field size was included in the top-ranked model, it was set to its mean in the predictions. Note that the graphs include estimates from independent models. Dashed lines in all panels, except for winter where the lines are restricted to the y-axies for clarity,indicate use of field categories in proportion to availability in the landscapes (a value above this indicates an over-use and vice versa). Asterisks (*) indicate a confidence interval reaching a relative probability of presence of 1 (i.e. beyond the limit of the axis).

towards green biomass of growing pasture, ley, and cereals, as shown also by Fox (1993) and Olsen et al., (2017). This was true for greylag and barnacle goose in the South. Similar tendencies could be seen for taiga bean goose in North, and greater white-fronted goose in South, although the large confidence intervals warrant caution in interpreting these results (Fig. 3). However, greylag geese in North differed from this general pattern, as the field categories with the highest presence of this species were: a) post-harvest fields, and b) growing barley (Table 3, Fig. 3). Compared to growing grasses and cereals, where the green plant parts are being consumed, most post-harvest residues such as grains and leftover root crops have a considerably higher crude protein content (Sedinger, 1997). Whilst taiga bean geese in spring in North were exclusively staging, most adult greylag geese were preparing for breeding locally after recently arriving from wintering areas in central Europe (Månsson et al., 2022; Nilsson, 2011). An extra need for high protein and energy content to prepare for breeding could be one explanation as to why the dietary needs of the latter species at this time can be expected to differ from those of taiga bean geese (Fox et al., 2016; Giroux and Patterson, 1995; Sedinger, 1997)

In South, the patterns of goose presence on various field categories were broadly similar among three species present, with one notable exception; pasture was top-ranked by greylag and barnacle geese, but low ranked by greater white-fronted geese. Pasture has previously been shown to be highly selected in spring by adult greylag geese when breeding and rearing goslings (Olsson et al., 2017; Strong et al., 2021; Teräväinen et al., 2022). Our pairwise comparisons (Fig. S3a-e in Supporting Information) revealed a significant difference for pasture compared to other field categories only for greylag geese, which showed a consistently higher probability of presence in this field category. In contrast, although pasture was also ranked high by barnacle geese, the pairwise differences were not statistically significant for pasture compared to other field categories, indicating greater variation in field selection. This weaker selection pattern in barnacle geese for pasture in South is likely due to the fact that almost the entire population breeds on offshore Baltic islands, outside the delineation of our study area. This likely reduces their reliance on pastures. Whilst greylag geese are known to breed in considerable numbers within the South study area, greater white-fronted geese are exclusively staging in spring. This could explain why pastures were less favored by greater white-fronted geese in South. In contrast to their migrating conspecifics in North, greylag geese in South are resident in the area all year (Nilsson et al., 2022), thus the dietary needs of this species may differ between the two study areas in spring.

Our results of partially overlapping probability of goose presence for most field categories in spring may come about if several of the studied species have largely overlapping dietary demands at this time. However, it may also be due to the dynamic availability and abundance of specific crop types, heights, and field stages during this season. Notably, temporal patterns of growth in autumn-sown crops differ, and spring-sown crops become available at different times and rates. The dependence on agricultural crops in wintering geese, especially in early spring, makes current farming practices a major determinant of food abundance and availability in terms of specific field categories (Gill, 1996). Furthermore, breeding and non-breeding geese of the same species were present simultaneously in our study and these categories may differ in their selection of crops and fields (Olsson et al., 2017), which could add to the variation within, as well as between, species.

Despite the selection bias towards fields used for livestock feed production (ley and pasture), there was still a significant number of geese using fields with crops intended for human food production in spring. In fact, looking at use alone, a greater number of geese were found on food crops (~9500 in North and ~13500 in South) than on crops grown for livestock feed (~6100 in North and ~5900 in South), such as ley fields and pastures (Fig. 2).

4.1.2. *Summer*

Summer data, concerning greylag geese only, demonstrate a continued selection for grasses. This is in line with several earlier studies showing that pasture and ley fields are selected by greylag geese in late spring and summer (Nilsson et al., 2024; Olsson et al., 2017; Teräväinen et al., 2022). This might be an effect of recurring cutting and/or livestock grazing, keeping sward height low and hence attractive to geese throughout summer (Strong et al., 2021). Another reason might be that greylag geese with goslings at this time remain close to open waterbodies and wetlands, whose closest neighboring fields are often pastures and ley fields (Olsson et al., 2017). The notable overlap in probability of presence across field categories (Fig. 3 & Fig. S3f-g in Supporting Information) may be influenced by the fact that our sample includes both breeding and non-breeding individuals, which could not be separated in the analyses due to restrictions in sample size of breeding geese. In North and South, 25 % and 11,6 %, respectively, of summer observations involved adult geese accompanied by goslings. It has been shown in previous studies that field selection of breeding greylag geese differs from that of their non-breeding conspecifics, and that other factors such as distance to water and sward height become increasingly important during breeding and nesting (Olsson et al., 2017). Thus, field type might be of subordinate importance for field selection by breeding individuals, whose choices are likely constrained by other ecological requirements.

Due to some being flightless, we cannot assume that all fields are equally available to breeding individuals, as it is for the non-breeding segment of the population. If breeding birds select fields based on proximity to nesting sites or on sward height rather than field type, this could dilute the differences among field categories in our data, emphasizing the importance of distinguishing between breeding status in future analyses when possible. Harvested fields become increasingly available from August and onwards. Although we did not analyze field selection on a monthly basis, stubble fields with residual grain are previously known to be selected by geese and are therefore likely to be gradually more utilized as they become increasingly available in late summer, coinciding with increased mobility among breeding geese and their young (Teräväinen et al., 2022).

4.1.3. *Autumn*

Although the availability of several field types differed a lot between the two study areas in autumn, the most selected categories – irrespective of goose species and study area – were different types of harvested crops, especially barley and wheat. This is quite a contrast from field selection patterns in spring and summer, also representing a shift to a diet with higher carbohydrate content (for review see Fox et al., 2016). However, even though harvested crops were generally selected, a significant number of geese used unharvested fields (i.e. growing crops, intended for either human consumption or livestock feed) in autumn (Fig. 2). This was especially true for barnacle geese in South, where they were mainly found on autumn-sown cereals, and for taiga bean geese frequently using ley fields in North.

The extent to which goose foraging might cause damage to these

Table 2
Estimates, standard error and p-value for each of the 17 individual and top-ranked models and their related explanatory variables. All in all, 17 separate models were assessed using AIC. The p-values are estimated with a 95 % confidence interval. Each model constituted a unique combination of season, study area, and goose species, along with the null models (see Table S2 in Supporting Information for detailed information on model setup). The column "Top-ranked model" includes abbreviations indicating season (1 = spring, 2 = summer, 3 = autumn, 4 = winter), study area (S = South, N = North), and species (gg = greylag, bar = barnacle, wf = greater white-fronted, tai = taiga bean, tun = tundra bean, can = Canada goose).

Top-ranked model	Explanatory variable	Estimate	S.E.	p-value
1S-gg	bare soil & fallow (intercept)	−2.08	0.16	< 0.001
	barley (G)	1.24	0.26	< 0.001
	wheat (G)	1.25	0.2	< 0.001
	other crop (H)	0.8	0.31	0.01
	ley (G)	1.34	0.21	< 0.001
	other crop (G)	−0.6	0.28	0.83
	pasture (G)	1.61	0.28	< 0.001
1S-bar	bare soil & fallow (intercept)	−5.12	0.71	< 0.001
	barley (G)	0.71	1.23	0.56
	wheat (G)	2.15	0.77	0.005
	other crop (H)	1.64	1.01	0.1
	ley (G)	2.45	0.77	0.002
	other crop (G)	−0.11	1.23	0.93
	pasture (G)	3.33	0.81	< 0.001
1S-wf	bare soil & fallow (intercept)	−2.83	0.77	< 0.001
	field area(log)	0.65	0.25	0.011
	barley (G)	0.02	1.12	0.98
	wheat (G)	1.75	0.56	0.002
	other crop (H)	1.32	0.78	0.088
	ley (G)	1.81	0.62	0.003
	other crop (G)	−15.15	772.39	0.98
	pasture (G)	0.24	1.14	0.83
2S-gg	bare soil & fallow (intercept)	−2.2	1.19	0.065
	field area(log)	0.52	0.22	0.02
	barley (G)	0.19	1.09	0.86
	wheat (G)	−1.18	1.24	0.34
	other crop (H)	1.69	1.06	0.11
	ley (G)	0.88	1.1	0.42
	other crop (G)	−1.92	1.24	0.12
	pasture (G)	1.7	1.09	0.12
3S-gg	bare soil & fallow (intercept)	−1.33	0.53	0.01
	field area(log)	0.72	0.17	< 0.001
	cereals (G)	0.52	0.48	0.28
	rootcrops & maize (H)	2.25	0.42	< 0.001
	ley (G)	0.035	0.57	0.95
	other crop (G)	−1.07	0.57	0.06
	other crop (H)	−0.41	1.08	0.7
	pasture (G)	−0.06	0.7	0.94
	barley (H)	1.05	0.46	0.02
	wheat (H)	1.09	0.44	0.01
3S-bar	bare soil & fallow (intercept)	−1.07	0.65	0.009
	field area(log)	0.73	0.21	< 0.001
	cereals (G)	0.81	0.54	0.14
	rootcrops & maize (H)	2.5	0.49	< 0.001
	ley (G)	0.9	0.56	0.1
	other crop (G)	−1.18	0.72	0.1
	other crop (H)	0.69	0.84	0.41
	pasture (G)	−0.77	1.11	0.49
	barley (H)	−0.32	0.83	0.7
	wheat (H)	0.48	0.59	0.42
4S-gg	bare soil & fallow (intercept)	−1.72	0.36	< 0.001
	field area(log)	0.45	0.11	< 0.001
	barley (G)	1.26	0.55	0.02
	wheat (G)	1.62	0.28	< 0.001
	rootcrops & maize (H)	2,00	0.31	< 0.001
	ley (G)	1.26	0.31	< 0.001
	cereals (G)	0.01	0.64	0.98
	other crop (G)	0.16	0.46	0.73
	other crop (H)	0.07	0.57	0.9
	pasture (G)	1.22	0.42	0.004
4S-bar	bare soil & fallow (intercept)	−1.99	0.47	< 0.001
	field area(log)	0.51	0.16	< 0.001
	barley (G)	0.75	0.79	0.34
	wheat (G)	1.19	0.36	< 0.001
	rootcrops & maize (H)	1.54	0.4	< 0.001
	ley (G)	0.45	0.37	< 0.001
	cereals (G)	0.7	0.6	0.24
	other crop (G)	−0.31	0.66	0.63
	other crop (H)	−0.92	1.06	0.38
	pasture (G)	−0.15	0.79	0.85
4S-wf	bare soil & fallow (intercept)	−3.55	1.12	0.002
	field area(log)	0.92	0.24	< 0.001
	barley (G)	2.63	1.43	0.066
	wheat (G)	3.05	1.03	0.003
	rootcrops & maize (H)	3.43	1.06	0.001
	ley (G)	3.38	1.05	0.001
	cereals (G)	2.9	1.67	0.01
	other crop (G)	0.95	1.42	0.5
	other crop (H)	−13.81	1312.06	0.99
	pasture (G)	−14.24	1498.46	0.99
4S-tai	bare soil & fallow (intercept)	−2.12	0.46	< 0.001
	field area(log)	0.46	0.14	0.001
	barley (G)	0.73	0.79	0.34
	wheat (G)	1.23	0.35	< 0.001
	rootcrops & maize (H)	2.37	0.35	< 0.001
	ley (G)	1.39	0.37	< 0.001
	cereals (G)	1.28	0.5	0.01
	other crop (G)	0.22	0.55	0.69
	other crop (H)	0.18	0.66	0.79
	pasture (G)	−0.14	0.79	0.86
4S-tun	bare soil & fallow (intercept)	−3.09	0.67	< 0.001
	field area(log)	0.51	0.19	0.006
	barley (G)	1.15	1.14	0.31
	wheat (G)	2.1	0.55	< 0.001
	rootcrops & maize (H)	2.88	0.56	< 0.001
	ley (G)	2.04	0.58	< 0.001
	cereals (G)	1.1	0.88	0.21
	other crop (G)	0.78	0.78	0.32
	other crop (H)	−14.22	808.45	0.99
	pasture (G)	0.24	1.14	0.84
4S-can	bare soil & fallow (intercept)	−2.58	0.63	< 0.001
	field area(log)	0.56	0.2	0.006
	barley (G)	1.47	0.85	0.08
	wheat (G)	1.77	0.46	< 0.001
	rootcrops & maize (H)	0.5	0.72	0.49
	ley (G)	0.57	0.62	0.36
	cereals (G)	1.11	0.73	0.13
	other crop (G)	0.66	0.66	0.32
	other crop (H)	−0.22	1.09	0.84
	pasture (G)	0.95	0.73	0.2
1N-gg	bare soil & fallow (intercept)	−0.78	0.37	0.04
	field area (log)	0.96	0.11	< 0.001
	barley (G)	2.19	0.4	< 0.001
	wheat (G)	1.11	0.33	< 0.001
	other crop (H)	2.41	0.41	< 0.001
	ley (G)	1.67	0.33	< 0.001
	other crop (G)	1.15	0.38	0.003
	pasture (G)	2.02	0.43	< 0.001
1N-tai	bare soil & fallow (intercept)	−0.92	0.61	0.13
	field area (log)	1.28	0.21	< 0.001
	barley (G)	−0.039	1.13	0.97
	wheat (G)	0.3	0.57	0.6
	other crop (H)	0.25	0.9	0.78
	ley (G)	1.58	0.51	0.002

(*continued on next page*)

Table 2 (*continued*)

Top-ranked model	Explanatory variable	Estimate	S.E.	p-value
	other crop (G)	0.39	0.72	0.59
	pasture (G)	1.52	0.72	0.04
2N-gg	bare soil & fallow (intercept)	0.88	0.92	0.34
	field area(log)	1.53	0.21	< 0.001
	barley (G)	−1.9	1.08	0.08
	wheat (G)	−2,00	0.93	0.03
	other crop (H)	1.62	0.83	0.05
	ley (G)	0.48	0.81	0.55
	other crop (G)	−2.69	1.27	0.03
	pasture (G)	1.86	0.83	0.03
3N-gg	bare soil & fallow (intercept)	−1.13	0.82	0.17
	field area (log)	1.38	0.18	< 0.001
	ley (G)	−0.97	1.24	0.43
	other crop (G)	−0.46	1.02	0.65
	other crop (H)	1.37	0.89	0.12
	pasture (G)	2.51	0.86	0.004
	barley (H)	3.04	0.77	< 0.001
	wheat (H)	2.28	0.75	0.002
3N-tai	bare soil & fallow (intercept)	−2.13	1.09	0.05
	field area (log)	1.23	0.19	< 0.001
	ley (G)	1.55	1.09	0.16
	other crop (G)	0.69	1.17	0.57
	other crop (H)	0.71	1.43	0.62
	pasture (G)	2.8	1.14	0.014
	barley (H)	3.19	1.07	0.003
	wheat stubble (H)	2.38	1.05	0.02

unharvested crops is, however, difficult to gauge. Autumn-sown cereals, oilseed rape and ley fields have a long growing period still ahead, which may allow for recovery if weather and other conditions permit, but grazing could still pose a risk of yield reduction year around (Montràs-Janer et al., 2020). Similarly, the harvest season for ley fields extends well into autumn, and in some cases the final harvest may not yet have been taken, meaning that geese grazing on such fields close to harvest may have a notable impact on the total yield meant for livestock feed.

4.1.4. *Winter (South only)*

As a foraging guild, geese showed a strong selection for harvested fields with root crops and maize in winter, followed by fields dominated by various winter-green crops (autumn-sown cereals, pastures and ley fields). Fields with abundant residual grain may permit effective foraging, as in barnacle geese foraging on maize spill (Clausen et al., 2018). Although not analyzed on a month-by-month basis, winter marked a gradual within-season shift from foods rich in carbohydrates (for example root crop spill) in December to crops high in protein (such as grasses, autumn-sown cereals and oilseed rape) in February, probably in preparation for migration and/or breeding, as well as a response to depletion of harvest residues over the course of the winter season. While the ranking of crops is strikingly similar across most species in winter, Canada geese were an exception by not being observed on the otherwise top-ranked crops, i.e., root crops and maize. Instead, they were mainly found on autumn-sown cereals (wheat and barley) as also previously shown by Flegler et al. (1987). Geese primarily used post-harvest fields during winter. However, when combining the number of geese observed on growing crops intended for human consumption and livestock feed, the total number of geese present on growing crops well exceeded those of post-harvest fields in winter (Fig. 2).

This extensive use of growing crops suggests that the potential for agricultural conflict in winter should not be underestimated. However, assessing the actual damage caused by goose foraging remains challenging, as other factors such as crop growth dynamics and weather conditions influence the extent to which grazing translates into subsequent economic loss. Some crops may tolerate a certain degree of defoliation without yield reduction, while others – especially in the early stages of regrowth – may be more vulnerable to repeated grazing.

4.2. *Species-specific patterns in field selection*

In the statistical sense the present study does not provide proper tests of interspecific differences in field selection, but some species-specific patterns are evident (Table 3 & Fig. 3). Greylag goose and barnacle goose selection overlap widely in all seasons, and with most other species by selecting grasses and cereals (pasture, ley, wheat, and barley) in spring and summer, and by consuming a much broader variety of crops in fall and winter. However, three species stand out as deviating more in their selection in winter; Canada geese appear to be selecting winter-green autumn-sown cereals, greater white-fronted geese have the strongest selection for 'lawn-like' grasslands (i.e., ley), as do also taiga and tundra bean geese in spring (i.e., ley and pasture). These observed interspecific differences in field selection may reflect variation in migratory strategy, breeding status, or habitat preference among species (Fox et al., 2016). However, as our study did not formally test for either interspecific differences or such underlying drivers, such interpretations remain speculative and warrant further investigation in future research.

4.3. *Differences between study areas*

Comparing results between the two study areas is important to assess the generality of field selection patterns observed in the present and other studies. We found very similar selection patterns between the study areas in summer but diverging patterns in spring and autumn (Table 3 & Fig. 3). A plausible explanation for this is that seasonal species composition of the goose guild differed between study areas. Accordingly, interspecific competition or differences in food selection could lead to such patterns (Fox et al., 2016; Tombre et al., 2019). Although the main field categories analyzed were largely the same in the two study areas, there are notable differences in field types and the availability of fields within certain main categories (Table S1 in Supporting Information), and this is especially true for spring and autumn. Hence, the difference in selected field categories between the two study areas could also be partly attributed to such variations. This is to say that from a farming perspective the likelihood of a field type attracting foraging geese can differ between areas in these seasons, a difference that became even more pronounced in winter when there were no geese at all in the northern area. This naturally creates entirely different conditions for agriculture in South and other areas hosting geese year around. Summer data, on the other hand, concern only one and the same species (greylag goose) in both study areas, as well as less variation in availability of different crop stages, as most crops have sprouted and few are ready for harvest. Here, the three most selected field categories were the same (Table 3 & Fig. 3), thus corroborating the generality of this pattern.

4.4. *Understanding field selection to predict damage risk*

We studied field selection of geese using binomial data, i.e. presence *versus* absence of geese in a field. This means 'presence' can be anything from one to several thousand geese (Boyce et al., 2016). From a damage risk perspective, it is thus important to consider flock size along with the overall distribution of geese within a certain field category, i.e. whether they tend to occur aggregated or more evenly distributed. When comparing the number of fields where geese occurred and the total goose counts, we saw indications of variation among species; compared to the other species, barnacle goose and taiga bean goose tended to occur in larger numbers distributed across fewer fields. There were also indications of intraspecific variation in median flock size among seasons. For example, in both study areas greylag geese tended to spread out over a larger number of fields in spring, despite being considerably fewer individuals in total, compared to a more clumped distribution in autumn

Table 3

Ranking (numbers and colors) of selection of field categories by season, goose species, and study area. (G) denotes a growing crop and (H) a harvested crop, i.e. geese feeding on harvest residues. Rankings are based on model predictions, see Table 3 and Fig. 3. It is important to note that this table is intended only to provide a general pattern of crop selection ranking and that the model estimates for selection, and thus the ranking between categories presented here, are not always statistically significantly different from each other. For a detailed view of which categories differ significantly, pairwise comparisons can be found in Figures S3a-q in the Supporting Information. Due to sample size restrictions in certain seasons, some field types were occasionally merged into categories consisting of several field types (see Table S1). Accordingly, OH denotes that the crop was merged into the category 'other crops' (H), OG into 'other crops' (G), CG into 'cereals' (G). No root crops or maize were available in the northern study area in summer (NA).

Season	Species	Study area	Bare soil & Fallow	Barley (G)	Barley (H)	Cereals (G)	Ley (G)	Other crop (G)	Other crop (H)	Pasture	Rootcrops & Maize (H)	Wheat (G)	Wheat (H)
Spring	Greylag	North	7	2	OH	OG	4	5	1	3	OH	6	OH
	Taiga bean	North	7	6	OH	OG	1	3	5	2	OH	4	OH
	Greylag	South	7	4	OH	OG	3	6	5	1	OH	2	OH
	Barnacle	South	7	5	OH	OG	2	6	4	1	OH	3	OH
	Gr. White-fronted	South	6	5	OH	OG	1	7	3	4	OH	2	OH
Summer	Greylag	North	4	6	OH	OG	3	7	1	2	NA	5	OH
	Greylag	South	7	4	OH	OG	3	6	2	1	OH	5	OH
Autumn	Greylag	North	7	OG	1	OG	6	5	4	2	OH	OG	3
	Taiga bean	North	7	OG	1	OG	4	5	6	2	OH	OG	3
	Greylag	South	9	CG	3	4	6	8	7	5	1	CG	2
	Barnacle	South	9	CG	6	3	2	8	4	7	1	CG	5
Winter	Greylag	South	9	3	OH	8	4	6	7	5	1	2	OH
	Barnacle	South	9	4	OH	5	2	7	8	6	1	3	OH
	Gr. White-fronted	South	7	5	OH	4	1	6	8	9	2	3	OH
	Taiga bean	South	9	5	OH	3	2	6	7	8	1	4	OH
	Tundra bean	South	8	4	OH	5	3	6	9	7	1	2	OH
	Canada	South	9	2	OH	3	4	5	8	6	7	1	OH

when the total count was much higher. Such aspects are important to consider in addition to field selection when assessing damage risk.

Worth considering is also that damage risk may be scale-dependent, differing between the field and landscape level, and vary depending on whether it is viewed from the perspective of selection or actual use. Since selection accounts for availability, certain rare but selected crops may have a high selection index, indicating that individual fields with these crops are at high risk of damage. On the other hand, the use by geese and total grazing pressure and biomass consumption on the landscape level may be much higher for common crops. Our data illustrates this complexity. Although our data indicates a long period of selection of harvest residues, a significant number of geese still utilized unharvested fields where they either constitute a damage risk or compete with livestock for forage. Focusing on single species and the entire annual period, barnacle goose was the main 'culprit' in South, as was taiga bean goose in North, in terms of number of geese using unharvested fields and thus posing a damage risk to growing crops (Fig. 2; cf. Brazaitis et al., 2023). For example, in the present study barnacle geese selected harvested crops and ley in winter, but 30 % and 65 % more geese were actually found in pre-harvest fields with growing crops than in harvested and ley fields, respectively (compare Fig. 2 & 3). This discrepancy illustrates that the total damage risk or potential biomass loss at the landscape scale is better captured by measures of use rather than selection alone.

Moreover, the timing of grazing also affects the damage risk. Research has shown that the risk of grasses failing to compensate for grazing increases later in spring compared to winter and early spring (Buitendijk and Nolet, 2023; Buitendijk et al., 2023). Spring grazing can impact harvest yields of ley fields and the availability of grass for livestock in pastures later in the season (Buitendijk and Nolet, 2023; Buitendijk et al., 2023). In summary, the risk of damage from grazing geese is multifaceted. While their presence on arable land does not always result in damage (Fox, 1993), both the intensity and timing of use, as well as the field type and scale of analysis, must be considered to predict their full impact.

4.5. Management implications and conclusion

The ranking of field categories by goose species as demonstrated in this study may offer promise for effective management strategies. Accordingly, such information can be used to adapt farming practices, when feasible given other constraints, to avoid the presence of strongly selected crops in a vulnerable stage at times when goose presence peaks in a certain area. This may apply to choice of crop for a certain field as well as to time of harvest or tillage. The present study clearly demonstrates that harvest residues are important and highly selected foods in autumn in both study areas and throughout winter when available (e.g., in South). Accordingly, cereal stubble and fields with root crop spill (potatoes, carrots, sugar beets etc.) may serve as diversionary food sources for geese during these seasons, when mitigation of damage risk to autumn-sown crops may be required (Gill et al., 1996; Kubasiewicz et al., 2015, Montràs-Janer et al., 2020). To make use of this opportunity, fields with stubble and harvest residues should be left untilled as long as possible, ideally spanning the local staging period of geese in autumn, and throughout winter in areas where geese occur all year. This supposes such practices do not conflict with regulations for farming, for subsidies, or other important aspects of agricultural management, such as crop rotation or practical constraints related to soil and weather conditions.

The overall high selection for grasses and cereals in late autumn, winter, and early spring makes the time of sowing a crucial aspect. Since too intense goose grazing can become a serious and costly problem any time during this period (Montràs-Janer et al., 2020, 2019), sowing cereals in spring may eliminate or reduce grazing problems during the months goose numbers in some areas peaks. Furthermore, by postponing the time of sowing the total amount of time the crop is potentially subjected to grazing, and possibly damaged, is reduced. The same argument can be applied to oilseed rape. However, changes in sowing time must be assessed in the context of local feasibility, as crop-specific growth requirements, soil conditions, and potential impact on economic returns may limit the extent to which sowing time can be adjusted. In some cases, crop rotation planning to alternate autumn-sown and spring-sown crops—as successfully applied in Japan to reduce goose damage (Amano et al., 2007)—may offer a feasible compromise, provided it aligns with broader agronomic constraints and subsidy requirements. Alternatively, if sowing is done at a time that is likely to later lead to increased damage risk by intense grazing, it is advisable to be prepared to implement other means of management such as scaring practices, diversionary fields and/or derogation shooting (Jager et al., 2023; Simonsen et al., 2017; Teräväinen et al., 2022). These options, too, must be considered within the regulatory and logistic framework of local farming systems.

This study demonstrates general patterns of selection and use of different crop types and field stages by the goose foraging guild as a whole, while also revealing considerable variability among species, seasons, and between study areas. These findings highlight the complexity of goose foraging behavior on agricultural land, where variation in species composition and the selection and use of different field types over the annual cycle influences the risk of damage to agricultural crops. In our study, we focused on crop type and crop stage selection across species and seasons. However, additional factors beyond those examined may further explain the spatial distribution and behavioral complexity of geese. For example, proximity to roosting sites and human disturbance may influence field selection (Fox et al., 2016; Olsson et al., 2017). The variability observed in our study underscores the need for adaptive strategies in damage mitigation efforts and that such strategies need to be tailored to specific species, regions, and seasons. For instance, knowledge of species-specific field selection and patterns of use in different seasons is crucial for effectively planning and establishing diversionary fields as a means to reduce crop damage by geese (Jensen et al., 2008; Teräväinen et al., 2022).

CRediT authorship contribution statement

Camilla Olsson: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lovisa Nilsson:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Johan Elmberg:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Johan Månsson:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Johan Elmberg reports financial support was provided by Swedish Environmental Protection Agency. Johan Mansson reports financial support was provided by Swedish Environmental Protection Agency. Lovisa Nilsson reports financial support was provided by Swedish Research Council Formas. Johan Mansson reports financial support was provided by Swedish Association for Hunting and Wildlife. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109913.

Data availability

Data will be made available on request.

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SUPPORTING INFORMATION

Table S1. Crop types and field stages as categorized into field categories.

Season	Study area	Field category	Crop types included
Spring	North	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (growing)	barley
		other crop (harvested)	barley, cereal mixtures, cereal/legume mixtures, oat, oilseed flax, oilseed rape, other cereals, potatoe, triticale, wheat
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley
		other crop (growing)	cereal/grass mixtures (>50% cereal), cereal/legume mixtures, faba bean, oat, oilseed flax, oilseed radish, oilseed radish/grass mixtures (>50% oilseed radish), oilseed rape, other cereals, other legumes, pea, potatoe, rye, triticale, turnip rape
		pasture (growing)	permanent grassland for grazing livestock
		wheat (growing)	wheat
Spring	South	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (growing)	barley
		other crop (harvested)	broccoli, barley, brussel sprout, carrot, cereal mixtures, cereal/legume mixtures, faba bean, maize, other cabbages, other cereals, other legumes, pea, potatoe, sugarbeet, triticale, wheat
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley
		other crop (growing)	broccoli, brussel sprout, carrot, cereal/grass mixtures (>50% cereal), cereal/legume mixtures, faba bean, lettuce, maize, oilseed radish, oilseed radish/grass mixtures (>50% oilseed radish), oilseed rape, onion, other cabbages, other cereals, other legumes, pea, potatoe, rye, strawberries, sugarbeet, triticale, white cabbage
		pasture (growing)	permanent grassland for grazing livestock, wetland
		wheat (growing)	wheat

Summer	North	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (growing)	barley
		other crop (harvested)	barley, cereal mixtures, cereal/legume mixtures, faba bean, oat, oilseed rape, other cerelas, other legumes, pea, rye, triticale, wheat
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley
		other crop (growing)	cereal/grass mixtures (>50% cereal), cereal/legume mixtures, faba bean, oat, oilseed flax, oilseed rape, other cereals, other legumes, pea, potatoe, rye, triticale, turnip rape
		Pasture (growing)	permanent grassland for grazing livestock
		wheat (growing)	wheat
Summer	South	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (growing)	barley
		other crop (harvested)	broccoli, barley, brussel sprout, carrot, cereal mixtures, cereal/legume mixtures, oilseed rape, onion, other cabbages, other cereals, lettuce, rye, triticale, wheat, white cabbage
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley
		other crop (growing)	broccoli, brussel sprout, carrot, cereal/grass mixtures (>50% cereal), cereal/legume mixtures, faba bean, lettuce, maize, oilseed rape, onion, other cabbages, other cereals, other legumes, pea, potatoe, redbeet, rye, strawberries, sugarbeet, triticale
		pasture (growing)	permanent grassland for grazing livestock
		wheat (growing)	wheat
Autumn	North	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (harvested)	barley
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley

		other crop (growing)	barley, cereal/legume mixtures, faba bean, oat, oilseed flax, oilseed radish, oilseed radish/grass mixtures, oilseed rape, other cereals, other legumes, pea, potatoe, rye, turnip rape, wheat.
		other crop (harvested)	cereal mixtures, cereal/legume mixtures, faba bean, oat, oilseed flax, oilseed rape, other cereals, other legumes, pea, potatoe, rye, triticale
		pasture (growing)	permanent grassland for grazing livestock, wetland
		wheat (harvested)	wheat
Autumn	South	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (harvested)	barley
		cereals (growing)	barley, cereal/grass mixtures (>50% cereals), cereal/legume mixtures, other cereals, rye, wheat
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley
		other crop (growing)	broccoli, brussel sprout, carrot, faba bean, lettuces, maize, onion, oilseed radish, oilseed radish/grass mixtures, oilseed rape, other cabbages, other legumes, pea, potatoe, redbeet, strawberries, sugarbeet
		other crop (harvested)	broccoli, brussel sprout, cereal mixtures, cereal/legume mixtures, faba bean, lettuce, onion, oilseed rape, other cabbages, other cereals, other legumes, pea, rye, triticale, white cabbage
		pasture (growing)	permanent grassland for grazing livestock
		rootcrops & maize (harvested)	carrot, maize, potatoe, sugarbeet
		wheat (harvested)	wheat
Winter	South	bare soil & fallow	bare soil, fallow, buffer zone to watercourse (grassland)
		barley (growing)	barley
		ley (growing)	annual or cultivated grassland for forage, forage mixtures dominated by grasses, intercrops dominated by grasses, ley
		cereals (growing)	cereal/grass mixtures (>50% cereals), cereal/legume mixtures, other cereals, rye, triticale
		other crop (growing)	carrot, oilseed radish, oilseed radish/grass mixtures (>50% oilseed radish), oilseed rape, potatoe, strawberries

other crop (harvested)	barley, broccoli, brussel sprout, cereal mixtures, cereal/legume mixtures, onion, other cabbages, other cereals, rye, triticale, wheat, white cabbage
pasture (growing)	permanent grassland for grazing livestock
rootcrops & maize (harvested)	carrot, maize, potatoe, sugarbeet
wheat (growing)	wheat

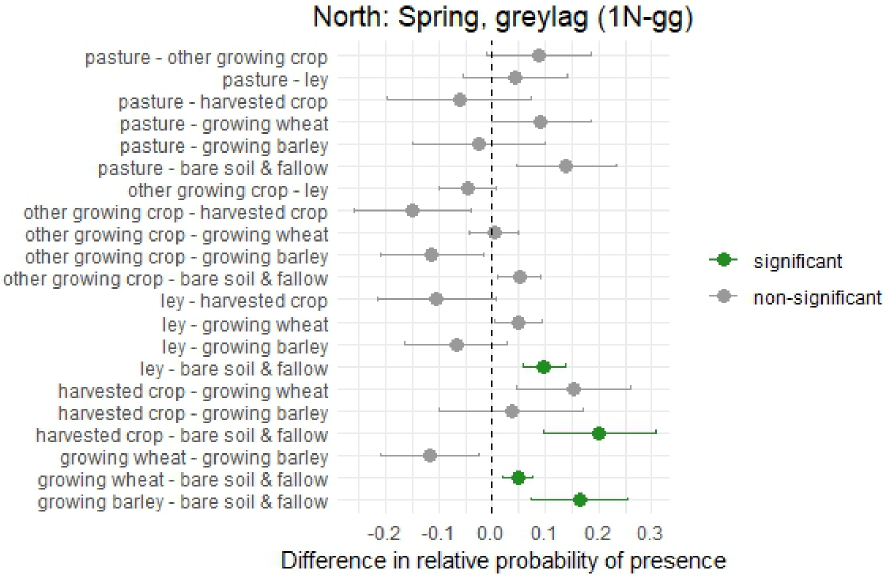
Table S2. Multi-model interference from binomial generalized models assessing the probability of goose presence in relation to field category and size, conducted separately for each combination of study area (North and South), season and goose species. Field size was log-transformed to meet model assumptions. The "Model" column includes abbreviations indicating season (1 = spring, 2 = summer, 3 = autumn, 4 = winter), study area (S = South, N = North), and species (gg = greylag, bar = barnacle, wf = greater white-fronted, tai = taiga bean, tun = tundra bean, can = Canada goose).

Study area	Season	Species	Model	Variables	AIC	DeltaAIC	Model weight
South	Spring	Greylag	1S-gg	field type	1464.2	0	0.71
				field type+field size (log)	1466.0	1.8	0.29
				null model	1541.9	77.7	0
				field size (log)	1543.7	79.5	0
South	Spring	Barnacle	1S-bar	field type	303.4	0	0.69
				field type+field size (log)	305.0	1.66	0.3
				null model	329.1	25.73	0
				field size (log)	330.8	27.38	0
South	Spring	White-fronted	1S-wf	field type+field size (log)	292.2	0	0.93
				field type	297.5	5.23	0.07
				field size (log)	311.8	19.6	0
				null model	315.3	23.03	0
South	Summer	Greylag	2S-gg	field type+field size (log)	313.9	0	0.88
				field type	317.9	3.95	0.12
				field size (log)	363.5	49.56	0
				null model	369.5	55.56	0
South	Autumn	Greylag	3S-gg	field type+field size (log)	548.0	0	1
				field type	565.9	17.87	0
				field size (log)	603.8	55.77	0
				null model	620.9	72.86	0
South	Autumn	Barnacle	3S-bar	field type+field size (log)	408.6	0	1
				field type	420.1	11.45	0
				field size (log)	456.2	47.51	0
				null model	463.7	55.03	0
South	Winter	Greylag	4S-gg	field type+field size (log)	992.5	0	1
				field type	1008.0	15.4	0
				field size (log)	1055.0	62.47	0
				null model	1076.5	83.95	0
South	Winter	Barnacle	4S-bar	field type+field size (log)	637.1	0	0.99
				field type	647.0	9.9	0.01
				field size (log)	660.5	23.41	0
				null model	667.3	30.19	0
South	Winter	White-fronted	4S-wf	field type+field size (log)	333.4	0	1
				field type	348.1	14.66	0
				field size (log)	365.0	31.65	0
				null model	375.9	42.53	0
South	Winter	Taiga	4S-tai	field type+field size (log)	741.7	0	0.99
				field type	750.5	8.88	0.1
				field size (log)	795.2	53.53	0

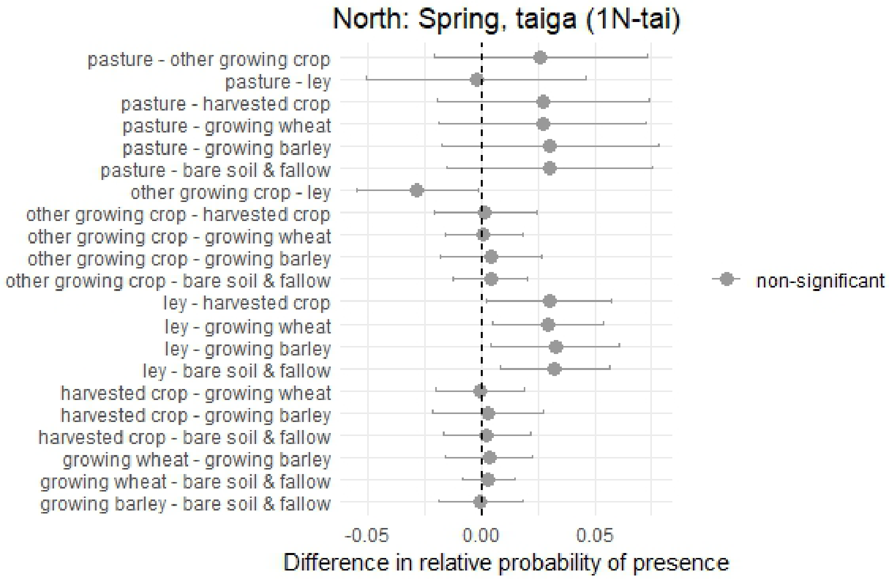
				null model	807.4	65.69	0
South	Winter	White-fronted	4S-tun	field type+field size (log)	492.3	0	0.96
				field type	498.6	6.29	0.04
				field size (log)	537.1	44.8	0
				null model	544.7	52.46	0
South	Winter	Canada	4S-can	field type+field size (log)	416.7	0	0.94
				field type	423.1	6.4	0.04
				field size (log)	424.7	8.02	0.02
				null model	433.1	16.39	0
North	Spring	Greylag	1N-gg	field type+field size (log)	824.9	0	1
				field size (log)	875.7	50.84	0
				field type	918.7	93.82	0
				null model	1001.5	176.65	0
North	Spring	Taiga	1N-tai	field type+field size (log)	292.3	0	0.81
				field size (log)	295.2	2.92	0.19
				field type	333.9	41.92	0
				null model	335,0	42.67	0
North	Summer	Greylag	2N-gg	field type+field size (log)	300.5	0	1
				field type	371,0	70.5	0
				field size (log)	394.7	94.23	0
				null model	485,0	184.52	0
North	Autumn	Greylag	3N-gg	field type+field size (log)	335,0	0	1
				field size (log)	395.2	60.20	0
				field type	404.1	69.11	0
				null model	491.1	156.08	0
North	Autumn	Taiga	3N-tai	field type+field size (log)	284.5	0	1
				field size (log)	303.1	18.60	0
				field type	331,0	46.48	0
				null model	362.7	78.13	0

Figure S3a-q. Pairwise comparisons using the ”marginaleffects function” in software R, with Bonferroni correction applied for multiple comparisons within each of the 17 models. When field size was included in the top-ranked model, it was held constant at its predicted mean for each site and season. These figures provide complement the ranking presented in Table 3, by allowing direct comparisons between specific field types. Estimates are presented with 95% confidence intervals. See Table S2 in Supporting Information for information on multi-model interference. Each point represents the estimated difference in relative probability of presence between two field categories, where the first category (to the left of the “–” symbol) is the reference. A positive value thus indicates a higher probability of goose presence on the first field type compared to the second, while a negative value indicates a comparably lower probability of presence. Comparisons with statistically significant differences are displayed in green, while non-significant differences are displayed in grey. The vertical dashed line at zero indicates no difference in estimated relative probability between the two field types.

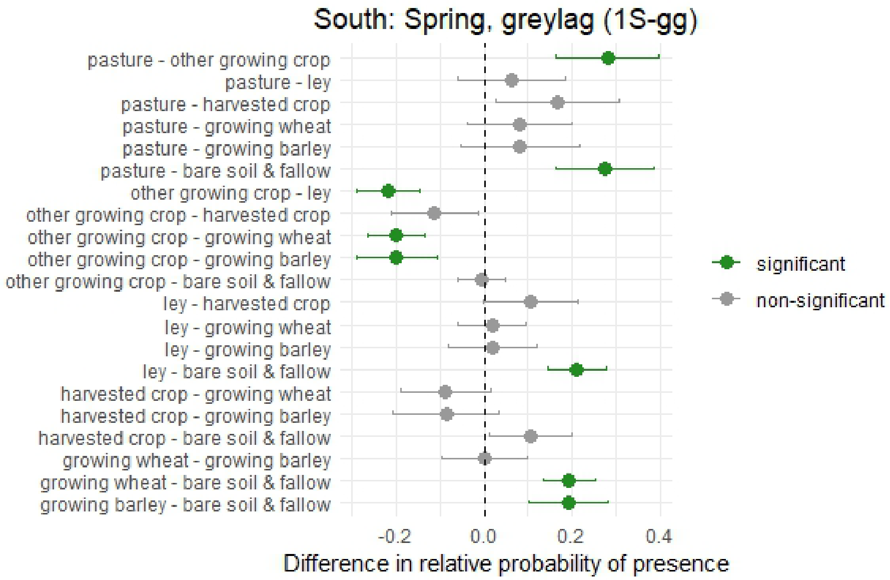
S3a



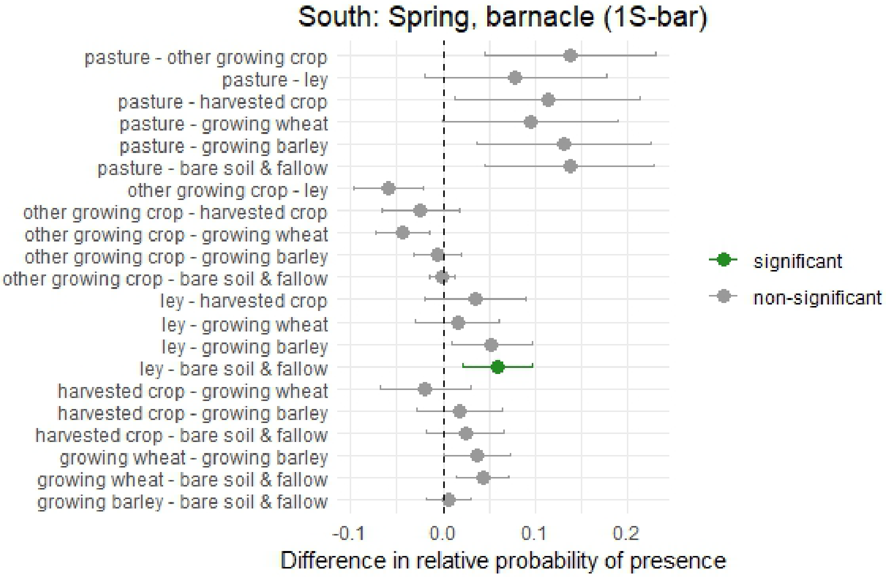
S3b


North: Spring, taiga (1N-tai)
pasture - other growing crop
pasture - ley
pasture - harvested crop
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other growing crop - ley
other growing crop - harvested crop
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
ley - harvested crop
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested crop - growing wheat
harvested crop - growing barley
harvested crop - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.05
0.00
0.05
Difference in relative probability of presence
non-significant

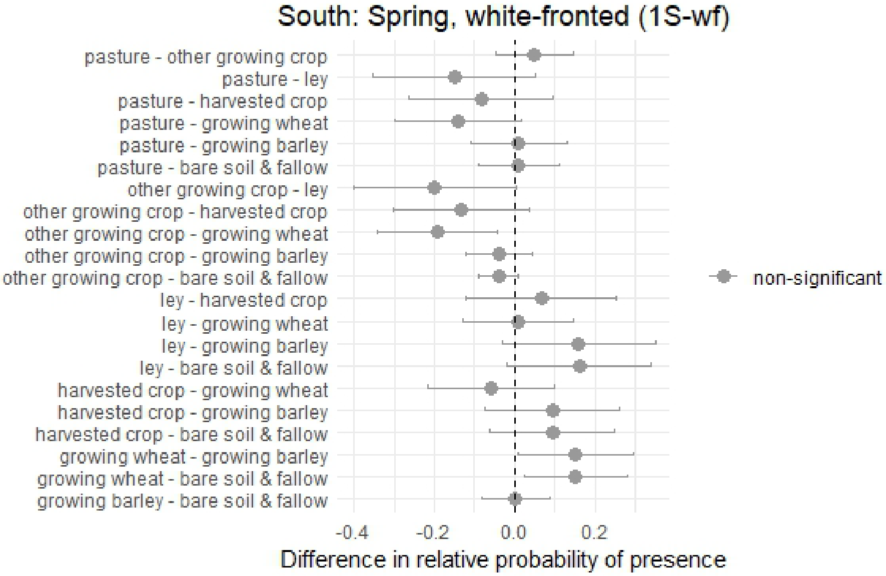
S3c


South: Spring, greylag (1S-gg)
pasture - other growing crop
pasture - ley
pasture - harvested crop
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other growing crop - ley
other growing crop - harvested crop
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
ley - harvested crop
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested crop - growing wheat
harvested crop - growing barley
harvested crop - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.2
0.0
0.2
0.4
Difference in relative probability of presence
significant
non-significant

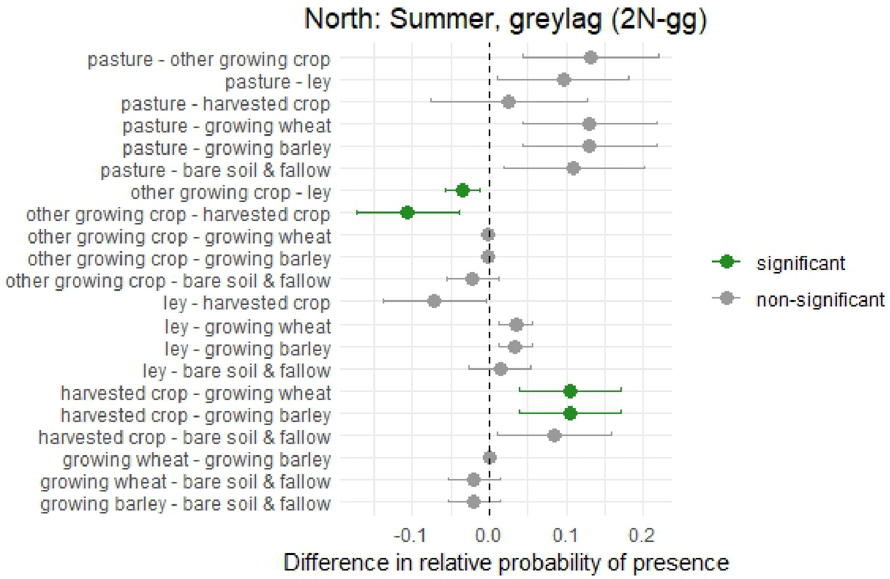
S3d


South: Spring, barnacle (1S-bar)
pasture - other growing crop
pasture - ley
pasture - harvested crop
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other growing crop - ley
other growing crop - harvested crop
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
ley - harvested crop
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested crop - growing wheat
harvested crop - growing barley
harvested crop - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.1
0.0
0.1
0.2
Difference in relative probability of presence
significant
non-significant

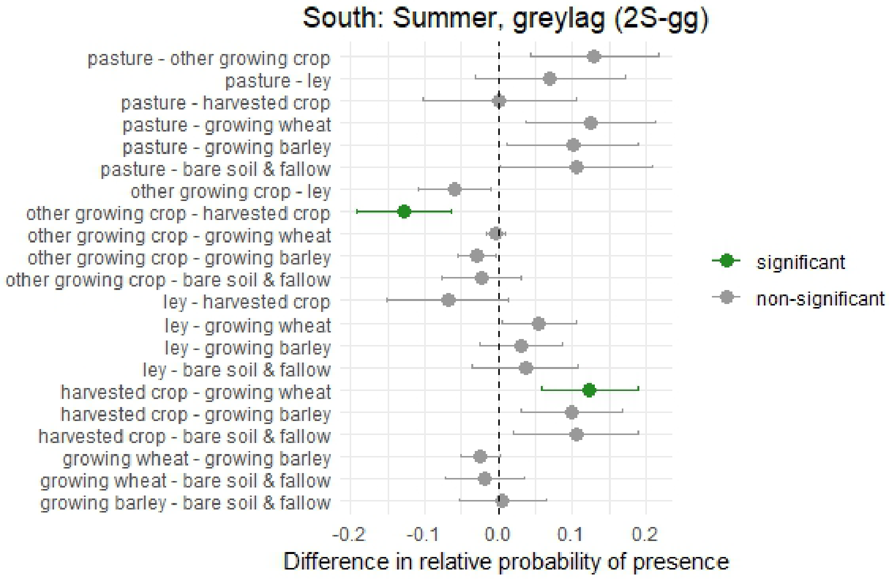
S3e


South: Spring, white-fronted (1S-wf)
pasture - other growing crop
pasture - ley
pasture - harvested crop
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other growing crop - ley
other growing crop - harvested crop
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
ley - harvested crop
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested crop - growing wheat
harvested crop - growing barley
harvested crop - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.4
-0.2
0.0
0.2
Difference in relative probability of presence
non-significant

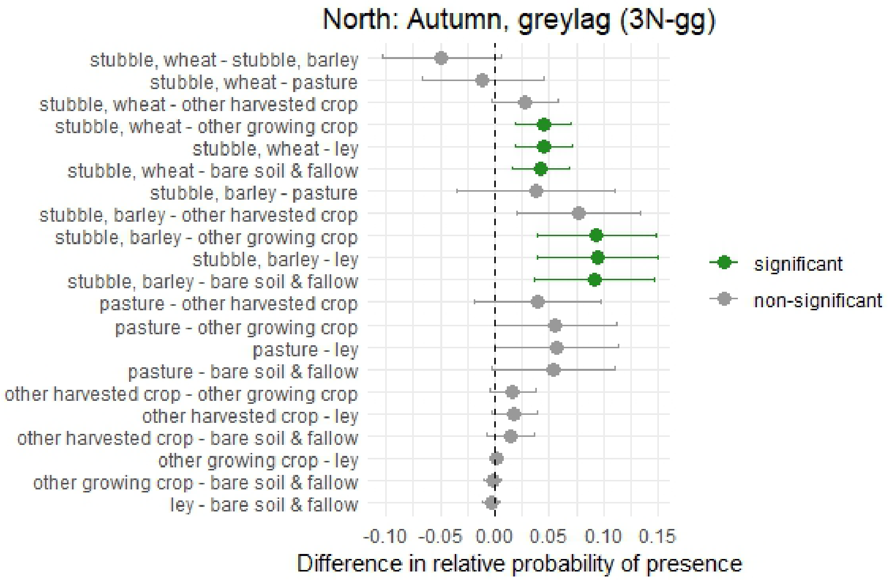
S3f


North: Summer, greylag (2N-gg)
pasture - other growing crop
pasture - ley
pasture - harvested crop
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other growing crop - ley
other growing crop - harvested crop
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
ley - harvested crop
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested crop - growing wheat
harvested crop - growing barley
harvested crop - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.1
0.0
0.1
0.2
Difference in relative probability of presence
significant
non-significant

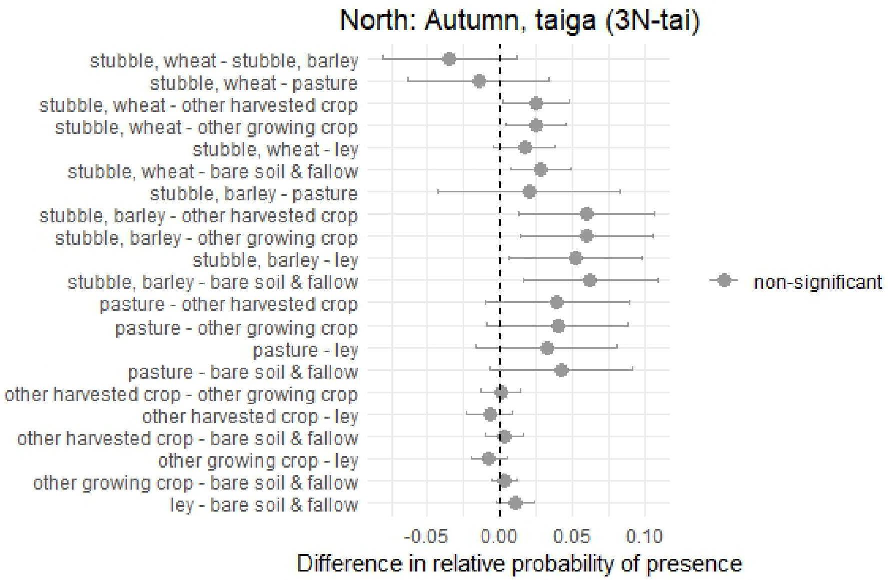
S3g


South: Summer, greylag (2S-gg)
pasture - other growing crop
pasture - ley
pasture - harvested crop
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other growing crop - ley
other growing crop - harvested crop
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
ley - harvested crop
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested crop - growing wheat
harvested crop - growing barley
harvested crop - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.2
-0.1
0.0
0.1
0.2
Difference in relative probability of presence
significant
non-significant

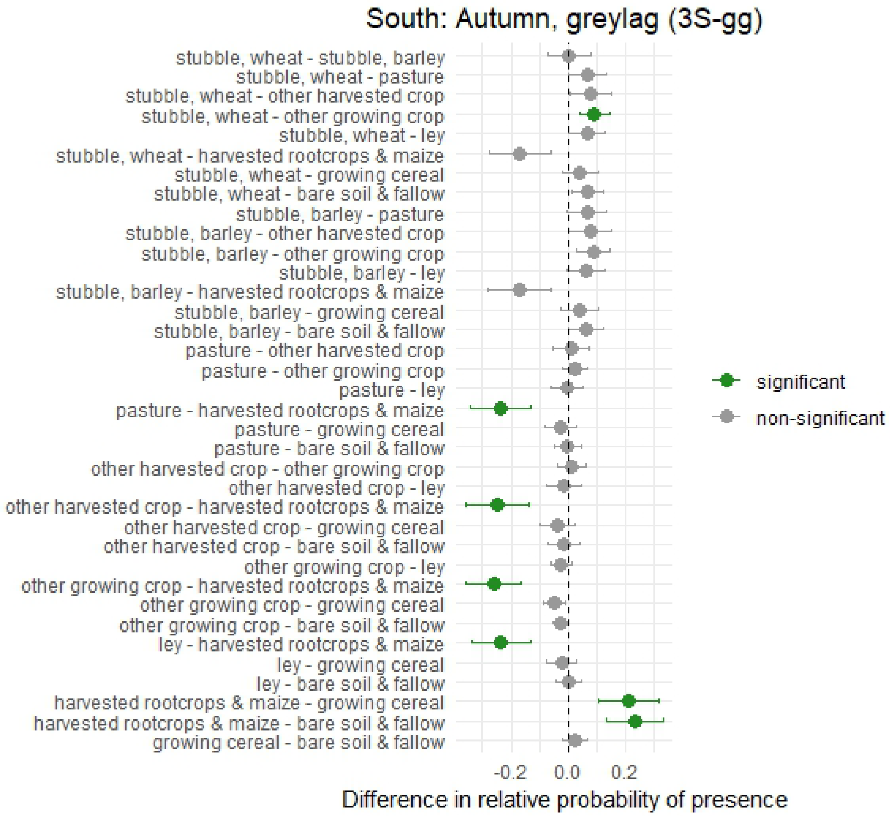
S3h


North: Autumn, greylag (3N-gg)
stubble, wheat - stubble, barley
stubble, wheat - pasture
stubble, wheat - other harvested crop
stubble, wheat - other growing crop
stubble, wheat - ley
stubble, wheat - bare soil & fallow
stubble, barley - pasture
stubble, barley - other harvested crop
stubble, barley - other growing crop
stubble, barley - ley
stubble, barley - bare soil & fallow
pasture - other harvested crop
pasture - other growing crop
pasture - ley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - ley
other harvested crop - bare soil & fallow
other growing crop - ley
other growing crop - bare soil & fallow
ley - bare soil & fallow
-0.10
-0.05
0.00
0.05
0.10
0.15
Difference in relative probability of presence
significant
non-significant

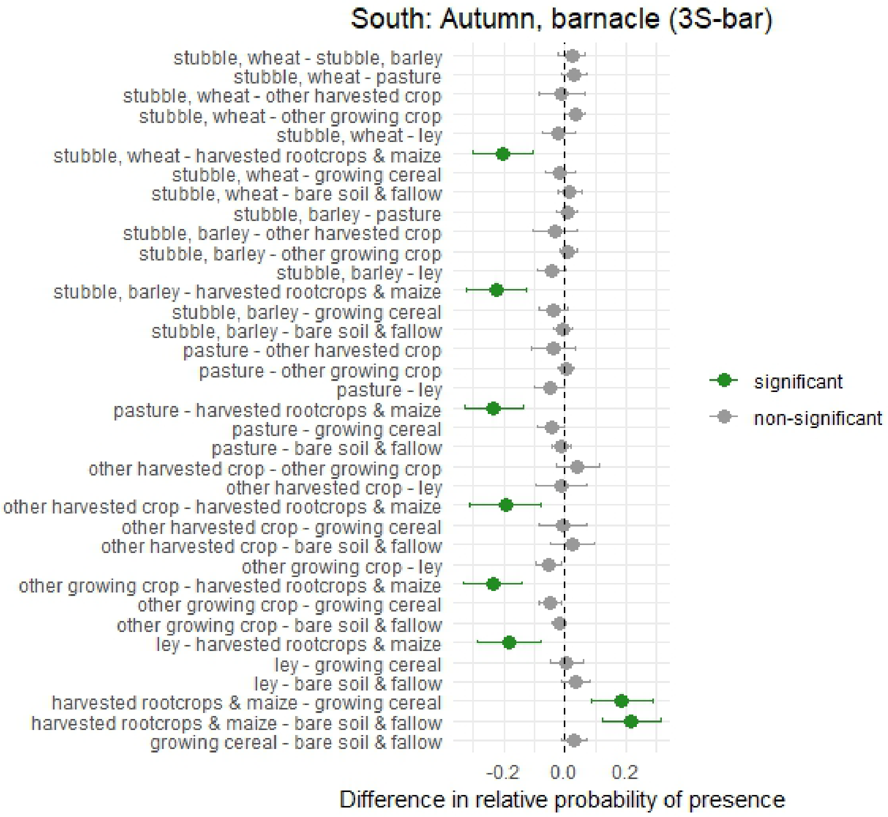
S3i


North: Autumn, taiga (3N-tai)
stubble, wheat - stubble, barley
stubble, wheat - pasture
stubble, wheat - other harvested crop
stubble, wheat - other growing crop
stubble, wheat - ley
stubble, wheat - bare soil & fallow
stubble, barley - pasture
stubble, barley - other harvested crop
stubble, barley - other growing crop
stubble, barley - ley
stubble, barley - bare soil & fallow
pasture - other harvested crop
pasture - other growing crop
pasture - ley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - ley
other harvested crop - bare soil & fallow
other growing crop - ley
other growing crop - bare soil & fallow
ley - bare soil & fallow
-0.05
0.00
0.05
0.10
Difference in relative probability of presence
non-significant

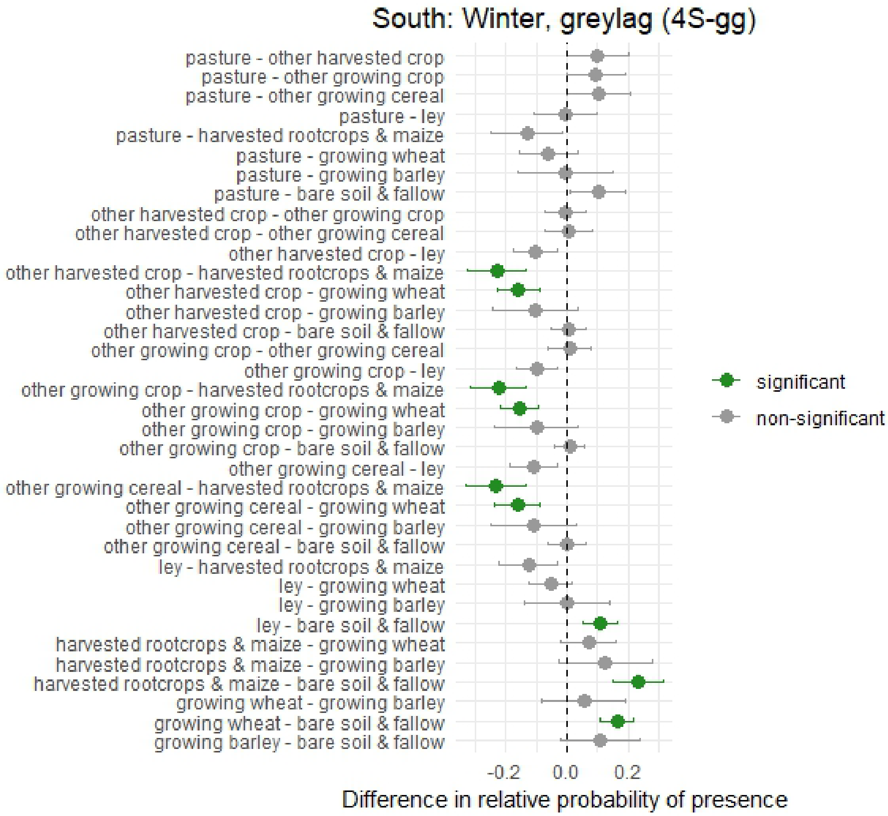
S3j


South: Autumn, greylag (3S-gg)
stubble, wheat - stubble, barley
stubble, wheat - pasture
stubble, wheat - other harvested crop
stubble, wheat - other growing crop
stubble, wheat - ley
stubble, wheat - harvested rootcrops & maize
stubble, wheat - growing cereal
stubble, wheat - bare soil & fallow
stubble, barley - pasture
stubble, barley - other harvested crop
stubble, barley - other growing crop
stubble, barley - ley
stubble, barley - harvested rootcrops & maize
stubble, barley - growing cereal
stubble, barley - bare soil & fallow
pasture - other harvested crop
pasture - other growing crop
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing cereal
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing cereal
other harvested crop - bare soil & fallow
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing cereal
other growing crop - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing cereal
ley - bare soil & fallow
harvested rootcrops & maize - growing cereal
harvested rootcrops & maize - bare soil & fallow
growing cereal - bare soil & fallow
-0.2
0.0
0.2
Difference in relative probability of presence
significant
non-significant

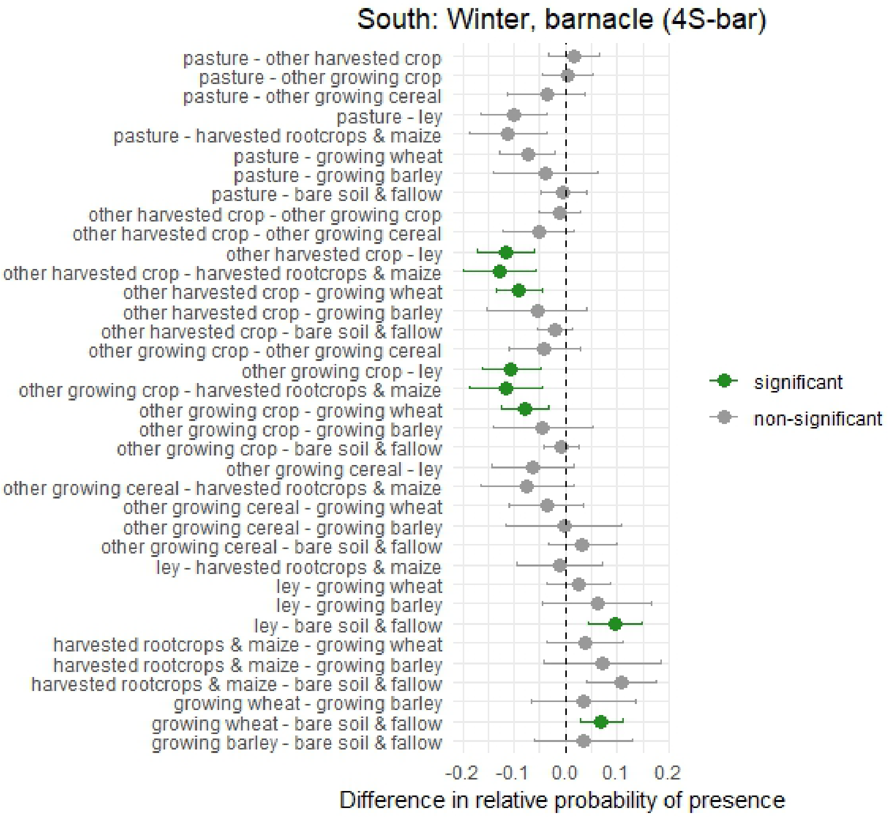
S3k


South: Autumn, barnacle (3S-bar)
stubble, wheat - stubble, barley
stubble, wheat - pasture
stubble, wheat - other harvested crop
stubble, wheat - other growing crop
stubble, wheat - ley
stubble, wheat - harvested rootcrops & maize
stubble, wheat - growing cereal
stubble, wheat - bare soil & fallow
stubble, barley - pasture
stubble, barley - other harvested crop
stubble, barley - other growing crop
stubble, barley - ley
stubble, barley - harvested rootcrops & maize
stubble, barley - growing cereal
stubble, barley - bare soil & fallow
pasture - other harvested crop
pasture - other growing crop
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing cereal
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing cereal
other harvested crop - bare soil & fallow
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing cereal
other growing crop - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing cereal
ley - bare soil & fallow
harvested rootcrops & maize - growing cereal
harvested rootcrops & maize - bare soil & fallow
growing cereal - bare soil & fallow
-0.2
0.0
0.2
Difference in relative probability of presence
significant
non-significant

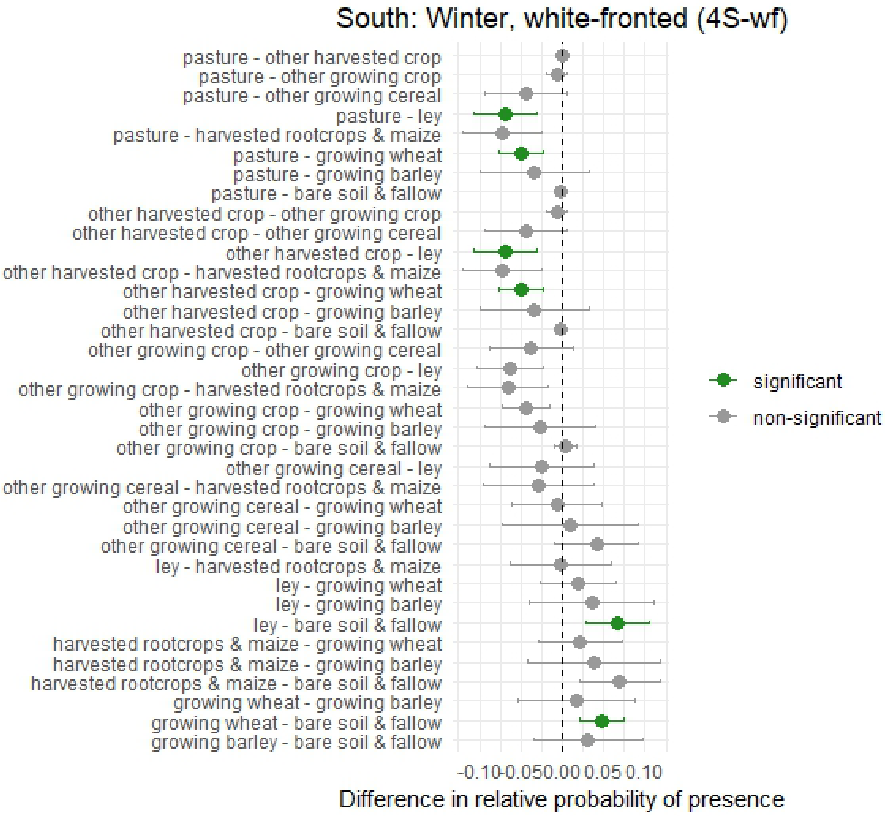
S31


South: Winter, greylag (4S-gg)
pasture - other harvested crop
pasture - other growing crop
pasture - other growing cereal
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - other growing cereal
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing wheat
other harvested crop - growing barley
other harvested crop - bare soil & fallow
other growing crop - other growing cereal
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
other growing cereal - ley
other growing cereal - harvested rootcrops & maize
other growing cereal - growing wheat
other growing cereal - growing barley
other growing cereal - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested rootcrops & maize - growing wheat
harvested rootcrops & maize - growing barley
harvested rootcrops & maize - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.2
0.0
0.2
Difference in relative probability of presence
significant
non-significant

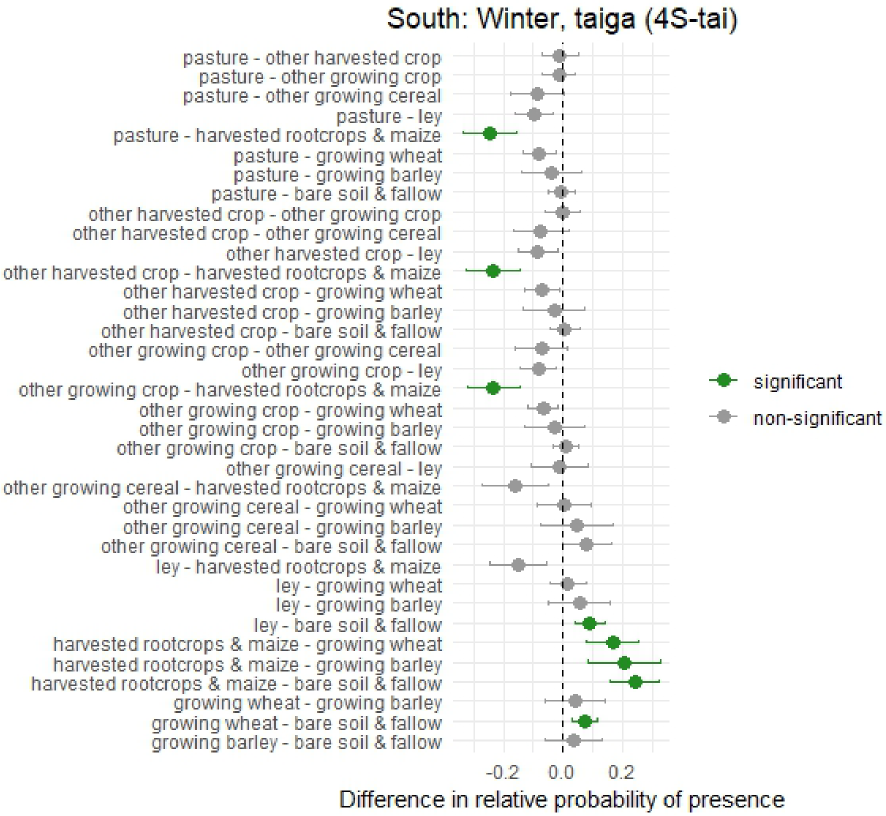
S3m


South: Winter, barnacle (4S-bar)
pasture - other harvested crop
pasture - other growing crop
pasture - other growing cereal
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - other growing cereal
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing wheat
other harvested crop - growing barley
other harvested crop - bare soil & fallow
other growing crop - other growing cereal
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
other growing cereal - ley
other growing cereal - harvested rootcrops & maize
other growing cereal - growing wheat
other growing cereal - growing barley
other growing cereal - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested rootcrops & maize - growing wheat
harvested rootcrops & maize - growing barley
harvested rootcrops & maize - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.2
-0.1
0.0
0.1
0.2
Difference in relative probability of presence
significant
non-significant

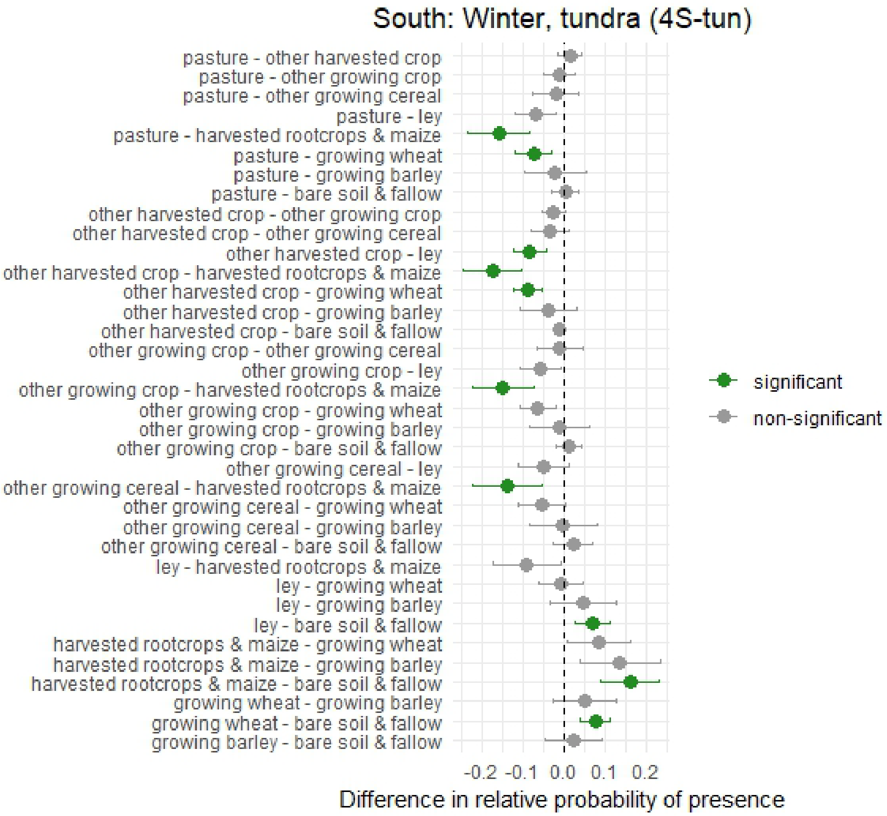
S3n


South: Winter, white-fronted (4S-wf)
pasture - other harvested crop
pasture - other growing crop
pasture - other growing cereal
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - other growing cereal
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing wheat
other harvested crop - growing barley
other harvested crop - bare soil & fallow
other growing crop - other growing cereal
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
other growing cereal - ley
other growing cereal - harvested rootcrops & maize
other growing cereal - growing wheat
other growing cereal - growing barley
other growing cereal - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested rootcrops & maize - growing wheat
harvested rootcrops & maize - growing barley
harvested rootcrops & maize - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.10
-0.05
0.00
0.05
0.10
Difference in relative probability of presence
significant
non-significant

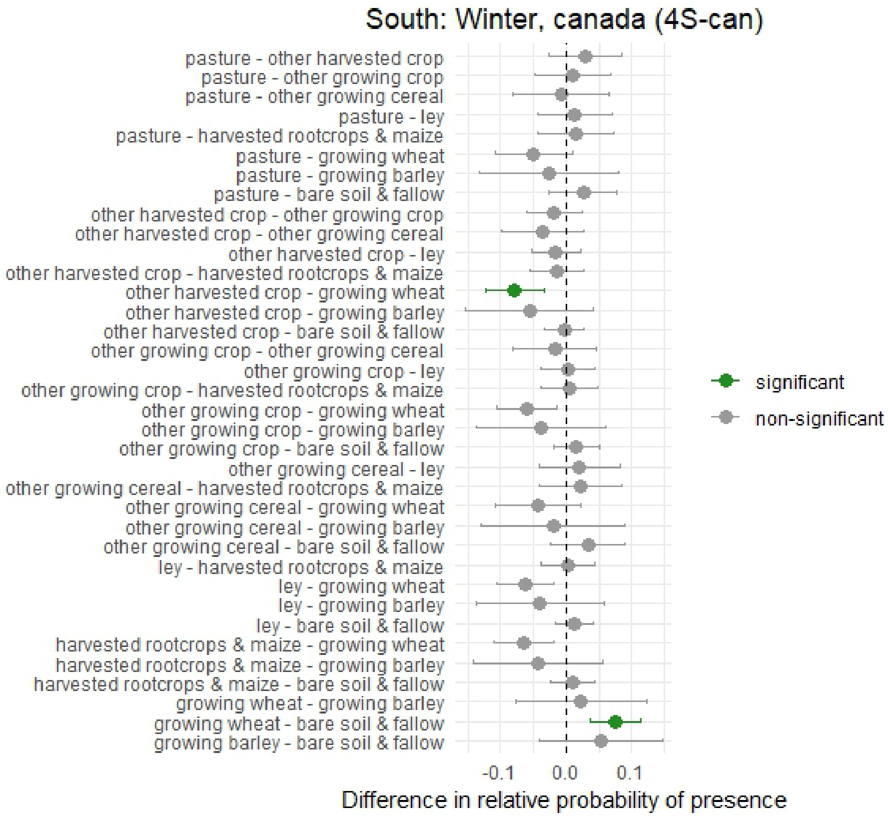
S3o


South: Winter, taiga (4S-tai)
pasture - other harvested crop
pasture - other growing crop
pasture - other growing cereal
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - other growing cereal
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing wheat
other harvested crop - growing barley
other harvested crop - bare soil & fallow
other growing crop - other growing cereal
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
other growing cereal - ley
other growing cereal - harvested rootcrops & maize
other growing cereal - growing wheat
other growing cereal - growing barley
other growing cereal - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested rootcrops & maize - growing wheat
harvested rootcrops & maize - growing barley
harvested rootcrops & maize - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.2
0.0
0.2
Difference in relative probability of presence
significant
non-significant

S3p


South: Winter, tundra (4S-tun)
pasture - other harvested crop
pasture - other growing crop
pasture - other growing cereal
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - other growing cereal
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing wheat
other harvested crop - growing barley
other harvested crop - bare soil & fallow
other growing crop - other growing cereal
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
other growing cereal - ley
other growing cereal - harvested rootcrops & maize
other growing cereal - growing wheat
other growing cereal - growing barley
other growing cereal - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested rootcrops & maize - growing wheat
harvested rootcrops & maize - growing barley
harvested rootcrops & maize - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.2
-0.1
0.0
0.1
0.2
Difference in relative probability of presence
significant
non-significant

S3q


South: Winter, canada (4S-can)
pasture - other harvested crop
pasture - other growing crop
pasture - other growing cereal
pasture - ley
pasture - harvested rootcrops & maize
pasture - growing wheat
pasture - growing barley
pasture - bare soil & fallow
other harvested crop - other growing crop
other harvested crop - other growing cereal
other harvested crop - ley
other harvested crop - harvested rootcrops & maize
other harvested crop - growing wheat
other harvested crop - growing barley
other harvested crop - bare soil & fallow
other growing crop - other growing cereal
other growing crop - ley
other growing crop - harvested rootcrops & maize
other growing crop - growing wheat
other growing crop - growing barley
other growing crop - bare soil & fallow
other growing cereal - ley
other growing cereal - harvested rootcrops & maize
other growing cereal - growing wheat
other growing cereal - growing barley
other growing cereal - bare soil & fallow
ley - harvested rootcrops & maize
ley - growing wheat
ley - growing barley
ley - bare soil & fallow
harvested rootcrops & maize - growing wheat
harvested rootcrops & maize - growing barley
harvested rootcrops & maize - bare soil & fallow
growing wheat - growing barley
growing wheat - bare soil & fallow
growing barley - bare soil & fallow
-0.1
0.0
0.1
Difference in relative probability of presence
significant
non-significant

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Climate change and new agricultural practices have driven a rapid increase in numbers of most European goose populations and a northward expansion of their wintering range. This has escalated crop damage and conservation conflicts. Managing geese is challenging, involving different species, stakeholders and competing interests along the flyway. This thesis provides ecological insights to guide management and damage prevention, from flyway to field level. Specifically, it addresses migratory patterns, foraging site selection, and local movements by geese in agricultural landscapes.

Camilla Olsson received her graduate education at the Department of Ecology, Swedish University of Agricultural Sciences (SLU), where she also obtained her MSc degree in Agricultural Sciences. She holds a BSc in Biology from Kristianstad University.

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