A cross-continental analysis of the habitat requirements for stable Black-tailed Godwit (*Limosa l. limosa*) populations in Europe

Miguel Silva-Monteiro

Propositions

1. The best breeding habitat for the Black-tailed Godwit is where its food resources thrive.
   (this thesis)

2. Cross-continental analyses are fundamental to unveiling the conservation needs of threatened species.
   (this thesis)

3. Effective science communication is as important as the science itself.

4. The best ecological research questions can only be formulated based on field observations, not in front of a computer.

5. Nature conservation science is unsustainable because it is based on short-term grants and projects.

6. Ecological anxiety and distress threatens the influx of young people into environmental careers.

7. It is vital to your health to find your balance between routine and adventure in life.

Propositions belonging to the thesis, entitled:

"A cross-continental analysis of the habitat requirements for stable Black-tailed Godwit (*Limosa l. limosa*) populations in Europe"

Miguel Silva-Monteiro

September 7th 2023, Wageningen

A cross-continental analysis of the habitat requirements for stable Black-tailed Godwit (*Limosa l. limosa*) populations in Europe

Miguel Silva-Monteiro

Thesis Committee

Promotor
Prof. Dr David Kleijn
Professor of Plant Ecology and Nature Conservation
Wageningen University & Research

Co-promotor
Dr Olavi Kurina
Senior Researcher, Chair of Biodiversity and Nature Tourism
Estonian University of Life Sciences

Other members
Dr R. Kentie, VU Amsterdam , the Netherlands
Dr M. Roodbergen, SOVON Dutch Center for Field Ornithology, add place, the Netherlands
Prof. Dr J. Gill, University of East Anglia, United Kingdom
Prof. Dr F. van Langevelde, Wageningen University & Research
This research was conducted under the auspices of the Graduate School Production Ecology & Resource Conservation (PE&RC).

A cross-continental analysis of the habitat requirements for stable Black-tailed Godwit (*Limosa l. limosa*) populations in Europe

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University,
by the authority of the Rector Magnificus,
Prof. Dr A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Thursday, September 7th, 2023
at 1:30 in the Omnia Auditorium.

Miguel Silva-Monteiro

Miguel Silva-Monteiro

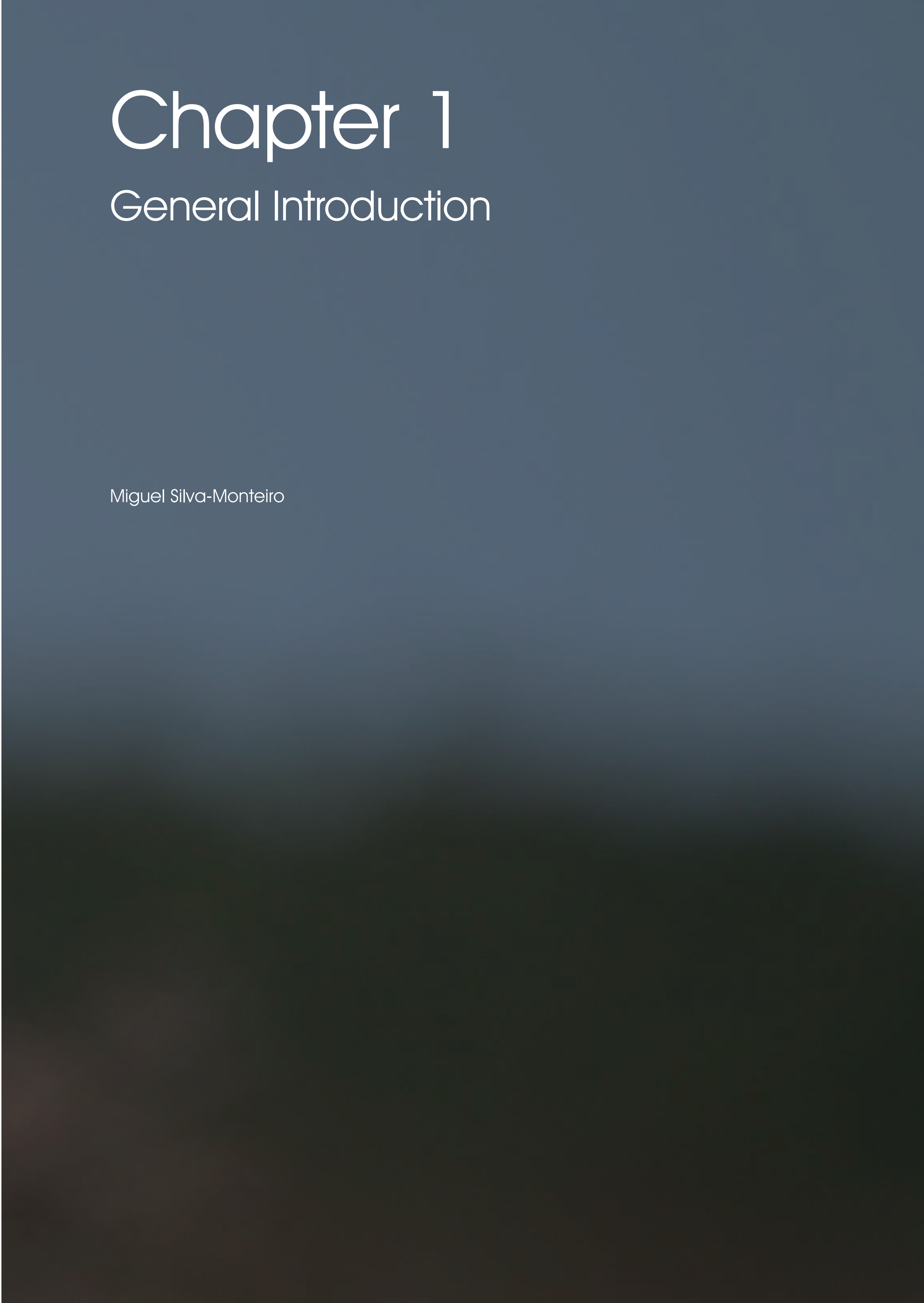
A cross-continental analysis of the habitat requirements for stable Black-tailed Godwit (*Limosa l. limosa*) populations in Europe,

198 pages.

PhD thesis, Wageningen University, Wageningen, the Netherlands (2023)
With references and summary in English

ISBN: 978-94-6447-710-8
DOI: https://doi.org/10.18174/630783

TABLE OF CONTENTS



Chapter 1

General Introduction

Miguel Silva-Monteiro

THE BLACK-TAILED GODWIT IN AN EVER-CHANGING EUROPE

Black-tailed godwit • Mustsaba-vigle • Barge à queue noire • Rycyk Mustapyrstökuiri •
Grutto • Skries • Maçarico-de-bico-direito

Many common names describe the scattered *Limosa limosa limosa* populations that breed or migrate throughout the European continent. The breeding area of the continental subspecies of the Black-tailed Godwit (Godwit from here on; Fig. 1.1a) is distributed across northern Europe, ranging from The United Kingdom and France in the west to Russia in the east (Keller *et al.* 2021). Small breeding populations of 400-1,000 pairs are dispersed in eastern countries such as Estonia, Hungary or Lithuania, while larger groups of up to 10,000 pairs are in Poland, Belarus, Ukraine and Russia (Jensen & Perennou 2007). However, the bulk of the European population breeds in north-western Europe, where up to 60,000 pairs (circa 65% of the global population) are located in areas surrounding the Wadden sea in the Netherlands, Germany and Denmark (Gill et al., 2007; Jensen and Perennou, 2007; Fig. 1.1a). The Godwit is able to breed in a myriad of wetland habitats, ranging from natural undisturbed bogs and fens, semi-natural extensive farmland such as coastal and floodplain grasslands (Jensen & Perennou 2007, Ławicki & Kruszyk 2011, Strus *et al.* 2018a) to intensive agricultural monocultures (Gill et al., 2007; Kleijn et al., 2010; Fig. 1.1b-e). Hence, as a breeding habitat generalist wader, it demonstrates flexibility in adapting to contrasting land-use intensity conditions. One could say that the iconic Godwit is a prime example of a bird that accompanied the fast man-made landscape transformations the European continent suffered during the last century.

Before the expansion of modern human land uses, it is believed that the Godwit strictly inhabited natural regularly flooded areas that were common throughout Europe (Bostrom & Nilsson 1983, Dugan 1993). Together with the drainage of the majority of existing mires in the 20th century (Fluet-Chouinard *et al.* 2023), followed by the development of agricultural practices that promoted the cultivation of croplands (Dugan 1993, Hartig *et al.* 1997, Zedler & Kercher 2005, An & Verhoeven 2019), the species was able to colonise these newly formed farmland habitats (Pain & Pienkowski 1997, Donald *et al.* 2002). Similarities between its previous natural breeding habitat and the newly-formed rural landscape were probably the reason for their successful colonisation: landscape openness, the presence of wet features, and heterogeneous and structurally diverse vegetation. Additionally, the low-intensity grazing or cutting regimes practised at that time maintained the farmland in the ideal conditions the species required year after year (Milsom *et al.* 2000, Durant *et al.* 2008a). In this new and expanding breeding habitat throughout Europe, where rural settlements dominated the landscape (European Environment Agency 2017), many farmland species, including the Godwit, flourished with increasing populations (Lebedeva

1998). It is believed that the population reached its peak during the 1960s with an estimated 125,000 breeding pairs in its key Dutch breeding areas alone (SOVON 2001, Teunissen & Soldaat 2006).

However, in order to sustain the increasingly growing human population, the industrialization of agriculture took off around the 1960s in north-western countries, bringing the end to what was coined as the “meadow bird golden era” (Cramp & Perrins 1983). The deployment of nitrogen fertilizers and high-power pumps to control water table levels together with the use of pesticides became the standard procedures to meet the high demand for more fertile and productive grasslands (Donald *et al.* 2001). Semi-natural, low land-use intensity grasslands, often rich in both plants and animals, quickly transformed into vast monocultures (Sutcliffe *et al.* 2015). Nevertheless, either by its plasticity or lack of alternative, more suitable habitats, the Godwit was able to persist and currently mostly breeds in those high land-use intensity locations (Thorup 2018, Roodbergen & Teunissen 2019).

Yet, despite its flexibility towards increasing land-use intensity habitats, we cannot describe the Godwit as a resilient species in recent decades. Throughout the last half of the 20th century, the species sharply declined, with an overall 60% population loss (EBCC 2016). The observed decline occurred throughout the European continent together with many other farmland bird species (Duncan *et al.* 1999, Benton *et al.* 2002, Donald *et al.* 2006, Flade *et al.* 2006). North-western European countries, where agricultural industrialization predominated, suffered the heaviest impact. The previously large Dutch breeding population currently has little over 30,000 pairs (Kentie *et al.* 2016). Grassland mowing by heavy machinery caused direct clutch and chick mortality of this ground-nesting species (Schekkerman *et al.* 2009). Additionally, due to more productive crops, the mowing date advanced faster than the species could cope with its clutch laying and chick-rearing timings (Schekkerman *et al.* 2009, Kentie *et al.* 2013). Furthermore, grassland monocultures transformed open vegetation types into dense swards where chicks couldn’t forage for invertebrate food or hide from predators, indirectly increasing their mortality probability (Schekkerman & Boele 2009, Kleijn *et al.* 2010).

In more extensive farmland habitats that remained in central and eastern European countries, the species was confronted with the polar opposite: the massive farmland abandonment and abrupt end of traditional agricultural practices led to many breeding areas becoming unsuitable as breeding areas (Leito *et al.* 2014, Kamp *et al.* 2018, Lesiv *et al.* 2018, Mischenko *et al.* 2019) due to tree and shrub encroachment (Verhulst *et al.* 2004, Sanderson *et al.* 2013, Kamp *et al.* 2018). Clutch mortality by both native and invasive mammal predators also substantially increased in the eastern region of Europe (Ławicki & Kruszyk 2011, Brzeziński *et al.* 2019), a similar trend to what has been observed in some western European locations (Teunissen *et al.* 2005). Very little is known about the overall ecology of these eastern European populations that breed in extensive farmland habitats and how they differ from the western European populations. Some breeding populations in Ukraine or Russia have only been recently described (Popov & Starikov 2015, Strus *et al.* 2018a). Similarly, little is known about the particularly small populations that potentially remained in the natural undisturbed mires (Leivits *et al.* 2013). Nonetheless, it is speculated that great losses occurred also there, similar to other wader species that rely upon those habitats (Fraixedas *et al.* 2017), with the reduction of habitat area and quality pointed out as possible causes (Hancock *et al.* 2009, Fraixedas *et al.* 2017).

Thus, the identified key cause for the species' population losses lies in its European breeding grounds, mainly affecting the nest and chick survival (Roodbergen *et al.* 2012), while adult survival rates remained high (Roodbergen *et al.* 2008). It became evident that many biological taxa dependent on farmland habitats were at severe risk of disappearing (Gregory *et al.* 2005), with the Godwit obtaining a near-threatened status (BirdLife International 2017). Research focusing on the specific habitat requirements necessary to revert negative population trends became an essential topic in the farmland biodiversity conservation field (Kleijn *et al.* 2011b). Yet, current research on the Godwit habitat requirements is heavily biased towards north-western European countries, where Godwits mostly breed in high land-use intensity habitats. Hence, many of the suggested conservation actions have been based on knowledge gathered solely from those populations. The remaining, central and eastern European Godwit populations are assimilated within different bird communities and habitats (Keller *et al.* 2021), with contrasting causes for their poor breeding success (Tryjanowski *et al.* 2011). The feasibility of the currently suggested conservation actions for the species might be heavily compromised in such locations. Successful cross-European conservation for the species requires a full understanding of its habitat requirements along its whole distribution.

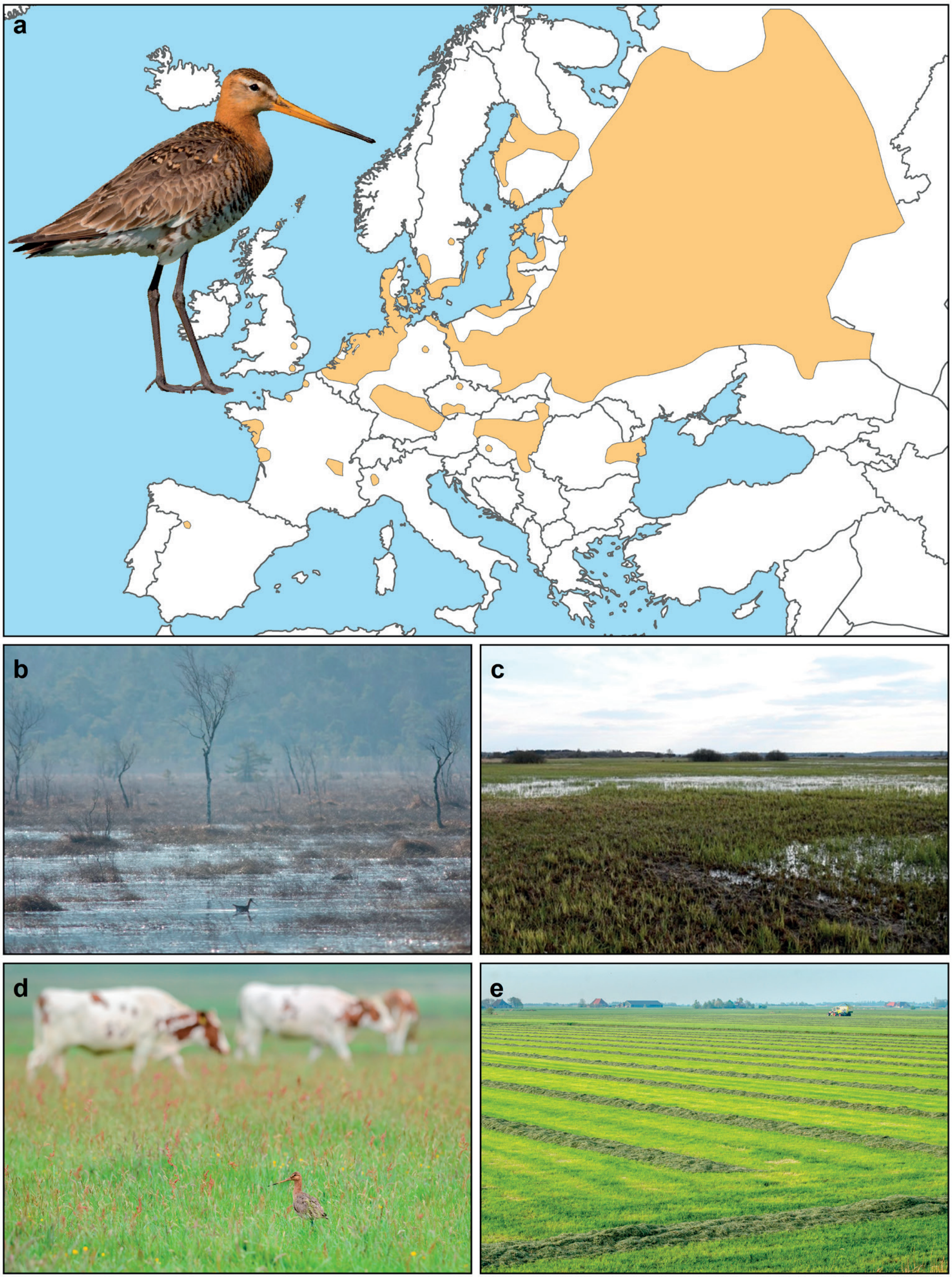


Figure 1.1. (**a**) The Black-tailed Godwit, *Limosa l. limosa* (Linnaeus, 1758) and its current breeding distribution across the European continent in orange, adapted from BirdLife International (2017) and Keller et al. (2021); Contrasting Godwit breeding habitats widely varying in their land-use intensity: (**b**) an Estonian fen with no human disturbance; (**c**) a Polish flooded grassland where low densities of cattle graze the land; (**d**) a Dutch bird meadow managed through AES; (**e**) a Dutch grassland monoculture that is mowed several times a year due to fertilizer's enhanced productivity. Photos (d) and (e) by Marycha Franken.

PICKY BIRD? UNDERSTANDING THE BLACK-TAILED GODWIT'S HABITAT REQUIREMENTS ACROSS EUROPE

In order to halt or revert the observed decline of the Godwit population, it is important to identify site-specific or general breeding habitat requirements and to explore how the key factors in bird habitat selection differ along the land-use intensity range. Habitat selection factors can be divided into proximate factors, which drive the species to perceive certain conditions as beneficial (as a cue or stimuli) and actively select them to lay their clutches, and ultimate factors, which limit individual fitness and the population dynamics through survival (Fuller 2012). However, it is important to note that proximate factors often correlate with the ultimate factors. This is especially important for migratory and ground-nesting birds, such as the Godwit, which rely on vegetation cues at early spring arrival that can indicate their suitability or unsuitability as a nest site later in the breeding season (Klomp 1954). Following Fuller (2012), we can describe five factors that may influence the Godwit's habitat selection: (i) Food supply for both adults and chicks; (ii) Predation pressure, mainly affecting nest and chick survival (iii) Structural and functional habitat characteristics, that allow the species to adapt to certain macro or micro-habitat characteristics (e.g. vegetation height, soil moisture); (iv) The presence of other birds, creating inter- or intraspecific competition or mutualistic relations and; (v) Space, the necessary area to accomplish all the previous conditions.

Food Supply

Arguably one of the essential factors for habitat selection is food availability and quality. If selected locations would be free of other limiting factors, populations would grow until they reach their maximum carrying capacity (Goss-Custard & West 1997), or in this case, the maximum number of Godwit breeding couples and respective families a location can provide food for. Surprisingly, there is little research on food resources and respective carrying capacities for waders in their European breeding grounds. Most of the studies focusing on the potential carrying capacity for a wader species or community were conducted in limited geographical ranges and mostly in wintering non-breeding areas (Goss-Custard 1991, Zharikov & Skilleter 2003, Piersma 2012, Bakker *et al.* 2021). At Godwit breeding sites, food abundance depends on the suitable foraging habitat available, which differs between adults and chicks (Struwe-Juhl 1995a). While adults probe the ground for soil-dwelling invertebrates using their long, sensitive beaks, their chicks mainly search for active above-ground and flying arthropods in tall open vegetation swards (Schekkerman & Beintema 2007). Due to the increased fertilizer application of grasslands in northwestern countries, the soil-dwelling invertebrate abundance (e.g. earthworms) has increased in those locations (Atkinson *et al.* 2005), benefiting adult Godwits (Kleijn *et al.* 2009a). However, the abundance and biomass of above-ground invertebrates, such as arthropods, are thought to have declined across all European grasslands that have intensified their management (Hallmann *et al.* 2017, Seibold *et al.* 2019). It is feared that higher taxa depending on them, as Godwits are in their pre-fledgling phase, might suffer heavy population declines because of this (Lister & Garcia 2018, Goulson 2019). However, studies looking into Godwit chick growth in varying land-use intensity habitats, pointed out that growth was not significantly lower in grassland monocultures compared to much less intensive meadow reserves (Kentie *et al.* 2013, Loonstra *et al.* 2017). Then again, those studies were done in breeding sites located within the same modern Dutch agricultural landscape and did not assess invertebrate abundances directly. Therefore, the assessment of the invertebrate community across other key breeding locations for the species, together with an exploration of the environmental conditions responsible for their abundance and quality is missing. Such knowledge may contribute to our understanding of how resource availability limits Godwit breeding populations and if it is a vital requirement for habitat selection and population growth.

Predator Pressure

Equally important for breeding site selection and limiting population size is predator pressure (Fuller 2012). For Godwits, low clutch and chick survival rates have been pointed out as the main sources for population declines in Europe (Roodbergen *et al.* 2012, Kentie *et al.* 2013), while adult survival remains high and stable (Roodbergen *et al.* 2008). In the last decades, both nest and chick predation pressure has increased all over Europe (Macdonald & Bolton 2008). In north-western European countries most nest and chick mortality was believed to be mainly caused by intensified agricultural practices (Teunissen *et al.* 2008b), but currently, predators such as the Stoat (*Mustela ermine*) and the Red Fox (*Vulpes vulpes*), are another important cause for the demise of the species, accounting for up to 50% of all nest and chick mortality (Teunissen *et al.* 2008a, Schekkerman *et al.* 2009). In eastern Europe, invasive and native mammals are likewise the current main culprits of the poor breeding success, with the Red Fox or the American Mink (*Neovison vison*) predating over 70% of Godwits nests in most countries (Ławicki & Kruszyk 2011, Niemczynowicz *et al.* 2017, Kaasiku *et al.* 2022). While in western European countries, predator abundance has been demonstrated to have increased and especially impacted ground-nesting birds (Roos *et al.* 2018), in eastern European countries wader nest predation seemed to have increased due to forest encroachment on grasslands, which promotes predator presence in nearby grasslands (Kaasiku *et al.* 2022). In both regions, predation might have been potentially enhanced due to the lack of top predators, which alters the behaviour and abundance of those mesopredators (Ritchie & Johnson 2009). However, Godwit nest survival continues to be highly variable between countries, and in some populations, such as the population of the Oulu region in Finland, nest predation is virtually non-existent with very high breeding success rates (Timonen personal observations). Predator fauna, abundance and related landscape movement dynamics are, therefore, highly variable across the Godwit distribution, and their impacts on breeding couples are often difficult to assess (Ibáñez-álamo *et al.* 2015, Laidlaw *et al.* 2021). Beyond causing clutch mortality, predation pressure can also impact bird behaviour while on breeding grounds or even lead breeding birds to disperse to other areas (Krebs & Davies 1997). After an unsuccessful breeding attempt, Dutch Godwits often lay a second, replacement clutch within 200m of the previous clutch (Verhoeven *et al.* 2020). Similarly, breeding dispersal between years is also about the same distance (Kentie *et al.* 2014). Thus, due to their high breeding site fidelity (Kruk *et al.* 1998), Godwit breeding dispersal movements might not be representative of local predation pressures. Nonetheless, predator pressure can also be assessed by inspecting incubation behaviour disruptions as seen in other wader species, which leave the nest untended for longer periods whenever predators are near, which may consequently increase their incubation duration, hatching failure or predation probability (Cervencl *et al.* 2011). However, once again, little is known about whether eastern European Godwits react differently in their breeding dispersal or incubation behaviours, with no broader patterns between habitats or countries investigated. Provisory and short-term solutions to increase breeding success by mammal exclusion have recently been experimented with in both western and eastern European countries, such as fencing areas (Smith *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022b) or culling mammal populations (Bolton *et al.* 2007, Fletcher *et al.* 2010a). However, without a better understanding of how predation pressure affects nest and chick survival or breeding adults, the implementation of truly effective conservation plans remains difficult (Laidlaw *et al.* 2021).

Structural and Functional Habitat Characteristics

Two central habitat requirements common throughout all breeding areas are landscape openness and wetness (Beintema *et al.* 1995, Söderström & Pärt 2000). As a ground-nesting species, the Godwit actively selects open areas by avoiding upgoing structures (e.g. trees, shrubs, houses) that might obstruct its surrounding vision, which consequently reduces predator detection (Van Der Vliet *et al.* 2010). Areas with the presence of trees might also be additionally avoided due to their potential to enhance the clutch and chick predator abundance, as a perching or nesting site for avian predators (Van Der Vliet *et al.* 2008, Woud 2014), or by enlarging the foraging roaming area for mammal predators (Kaasiku *et al.* 2022). Moreover, overall habitat wetness might be selected due to promoting a similar unobstructed, predator-free environment. Sites with high soil moisture content, the presence of many dispersed water bodies or completely flooded, are less prone to tree growth or shrub encroachment, keeping them open (Smardon 2014). Also, mammal predators might avoid wetter areas due to reduced site accessibility and difficult mobility (Berg *et al.* 1992, Bellebaum & Bock 2008, Laidlaw *et al.* 2017).

Within an open and wet landscape, Godwits tend to prefer short vegetation swards (usually <10cm) surrounded by a heterogeneous landscape to lay their clutches (Verhulst *et al.* 2011, Groen *et al.* 2012, Rannap *et al.* 2017). Vegetation patches with diverse sward heights and structures are important for several aspects of its breeding ecology: while short vegetation swards are necessary for the nest site selection and surrounding visual predator detection, patches of taller, open vegetation are crucial as chick foraging area and cover against predators (Schekkerman & Beintema 2007, Kleijn *et al.* 2010). The maintenance of these key structural and functional habitat characteristics differs along the land-use intensity gradient, due to striking differences in soil moisture and vegetation productivity. In managed grasslands of western European countries, wetness and sward height heterogeneity are currently largely dependent on agri-environment schemes (AES) and protected areas in which management is aiming to slow down vegetation growth and create a heterogenous sward mosaic by reducing fertilizer inputs, delaying the grazing and mowing dates (Breeuwer *et al.* 2009), and keeping high water table levels (Groen *et al.* 2012). However, the success of AES is limited and unable to revert the negative population trend, with breeding numbers not substantially increasing (Kleijn *et al.* 2001, Schekkerman *et al.* 2008, Breeuwer *et al.* 2009). AES sites are often oases surrounded by intensively managed monocultures (Kentie *et al.* 2014), and due to the high mobility of Godwit families, they often end up moving through areas that will diminish their breeding success (Kruk *et al.* 1997, Schekkerman & Beintema 2007, Kentie *et al.* 2014). However, both AES and intensive agriculture sites keep reporting the largest breeding populations for the species (Roodbergen & Teunissen 2014). In more low-intensity semi-natural habitats found in eastern Europe, those ideal conditions continue to be well preserved by a mixture of extensive agricultural practices and natural flooding (Kose *et al.* 2004, Ławicki & Kruszyk 2011), but used by smaller, dispersed populations. In natural mires, the Sphagnum vegetation that covers most bogs and the tall grasses that grow on fens seem to be ideal for Godwits to build their nests, however, even lower breeding numbers are reported there (Leivits & Leivits 2016).

It is, therefore, surprising that the species is not able to sustain similar large breeding population numbers in low land-use intensity and natural habitats compared to more productive and intensified ones, considering that openness, wetness and vegetation structure heterogeneity are well maintained without the surrounding intensified farmland that diminishes the reproductive success of the AES and protected sites in the Netherlands (Kentie *et al.* 2015). Research focusing on those environmental conditions is mostly limited towards north-western European countries, with little exploration of the impacts of agricultural extensification on Godwit populations in eastern European populations. What makes a natural undisturbed site attractive for Godwit couples remains even less explored, and it is suggested that couples breeding there might not be remnants of old populations but birds that are now moving from nearby agricultural areas that became unsuitable (Popov & Starikov 2015). Potential trade-offs are occurring in these low land-use intensity and natural habitats. To our human perception, they seem perfectly suitable for Godwits, but the populations breeding there are unable to increase to numbers observed in more intensive agricultural farmland. Possibly higher nest and chick predation pressures or lower food supply for both adults and chicks are occurring, but these remain unexplored. A broader understanding of how structural and functional habitat characteristics affect Godwits is necessary, especially for the protection of those already smaller populations.

Presence of Other Birds & Required Space

As a semi-colonial species, Godwits are able to breed in locations where dense populations of conspecifics nest, forming small colonies (van den Brink *et al.* 2010). This was commonly observed in naturally flooded areas alongside large river systems in the past, such as the Matsalu delta in Estonia before the construction of a water canal (Kose *et al.* 2004). As present Godwit populations continue to decline, Godwit breeding colonies are now rare and currently couples breed in smaller groups. However, younger inexperienced birds might still prefer to nest in denser Godwit sites, as they perceive better quality areas by the presence of other conspecific couples (Kentie *et al.* 2014). Thus, this variance observed in breeding population densities across its breeding range points out that area size might not be a key habitat requirement, as long as the habitat remains within the suitable conditions previously mentioned. However, this is yet to be tested on a larger scale, with the compared breeding populations in similar area sizes and habitats slightly varying in land-use intensity (Kentie *et al.* 2014).

Little research has been published exploring whether Godwits benefit or actively select their breeding sites according to the overall number of breeding pairs within the wader community, or by the presence of other specific bird species. It is suggested that Godwits often prefer to breed nearby couples of the Northern Lapwing (*Vanellus vanellus*; Johansson, 2001), and wader species overall prefer larger, denser communities to benefit from predator avoidance (Møller *et al.* 2018). However, the opposite is more often reported, with smaller-bodied wader species known to use the Godwit as an umbrella species, often laying their clutches nearby their nests in order to gain from the collective mobbing behaviour the Godwit engages in when attacked by predators (Gochfeld 1984, Green *et al.* 1990). Furthermore, the Godwit seems to be part of a range of different bird communities, which may have been caused by its ability to breed in a variety of breeding habitats, where bird communities potentially differ greatly. This further demonstrates that the number and presence of specific species might not be a vital requirement for their habitat selection and breeding success.

Therefore, it seems that both the required area size and the intra- and interspecific interactions with other birds are more dependent on what the local habitat conditions enable than what the Godwit actively selects. Thus, we can delimit the main ultimate factors for habitat selection and requirements by the Godwit as food resources (prey availability and quality), predator pressure (nest and chick survival) and environmental conditions (vegetation characteristics and water table), with the presence or absence of intra- and interspecific interactions and breeding area size, potentially playing a secondary role.

GENERAL OBJECTIVES, STUDY SYSTEM AND OUTLINE OF THIS THESIS

As research on Godwit conservation and ecology starts to accumulate, little integration of the independent and geographically unbalanced results has been attempted. Comparisons between Godwit populations are often performed within countries and by sampling nearby locations, leaving much of the environmental differences that exist along the breeding range out of the analyses. In this thesis, I undertook the task of broadening those comparisons. With the help of a collaborative network of conservationists working on the Godwit, I conducted a cross-continental analysis to unveil global ecological patterns and highlight the species' most crucial breeding habitat requirements. This was performed by exploring how the identified three major factors influencing Godwit habitat selection (food resources, predation pressures, and habitat characteristics) differ across its breeding habitats and impact the breeding populations. As those three factors are intrinsically related, some thesis chapters tackle how they impact one another, or consequently how those relationships can affect Godwit breeding couples (Fig. 1.2). Additionally, this approach will allow us to fill some knowledge gaps in the ecology of the species, especially in eastern European populations and breeding habitats there located.

Cross-continental analyses offer the opportunity to unveil ecological patterns otherwise hidden from geographically more limited datasets. By compiling and comparing data from more diverse populations, broader ecological patterns can be established, while highlighting further under-researched topics or geographical regions. Cross-continental analyses have been used to unveil patterns in varying ornithological fields, such as anthropogenic effects on bird diversity (Clucas *et al.* 2015, Burns *et al.* 2021), environmental effects on migratory birds (Mandel *et al.* 2011, Schmaljohann 2019) or to help target and prioritize locations or endangered populations needing conservation (Powell *et al.* 2015, Koleček *et al.* 2016). As a widespread European breeding species (Keller *et al.* 2021), the Godwit provides the opportunity to perform such analysis. Therefore this thesis gathers data from a large part of its known breeding range, by collecting previously published peer-reviewed and grey-literature data but also through an empirical study that further investigates some missing ecological relationships.

In **Chapter 2** I explored and reviewed how wader populations differ in their breeding densities along their respective European breeding habitats. This was achieved by extracting and compiling data from previously published peer-reviewed and grey literature, which ended up gathering a high volume of varying information, including many species. I summarized the overall ecological and population dynamic mechanisms that are currently affecting wader communities in Europe. Furthermore, for species for which a relatively large amount of data was available (Godwit included), it was possible to test if breeding densities differ between land-use intensity classes. This study provided a good foundation for the rest of the thesis, which aimed to understand differences in the observed Godwit breeding densities along a land-use intensity gradient.

Next, I investigated more specific relationships between the habitat selection factors and how they influence the Godwit breeding populations. To accomplish this I introduced the original study system of this thesis: a cross-continental set of key Godwit breeding sites which more or less replicated the diversity and land-use intensity range observed in Chapter 2. Several biotic and abiotic variables were sampled throughout the Godwit breeding season in France, the Netherlands, Poland, Estonia and Finland. This provided me with an intricate dataset that included several variables depicting habitat characteristics, such as vegetation productivity or soil moisture content, the abundance of invertebrate food resources and some variables representative of predation pressures, that could be later related to the number of Godwit couples present in the same sites. This extensive dataset was used for Chapters 3, 4 and 5.

In **Chapter 3**, I investigated how the habitat characteristics as influenced by land-use intensity affect the abundance of the different Godwit food resources. By sampling the key invertebrate communities for the species (soil-dwelling, ground-active and flying) I compared sites and countries that have contrasting habitat conditions. I hypothesized that the invertebrate communities react differently in terms of their abundance, biomass and average individual size towards increasing land-use intensity, with some being more sensitive than others.

In **Chapter 4**, using the same set of sampled sites and variables, I investigated the relative importance of the two previously investigated habitat selection factors on the number of breeding pairs a site can support. As previously mentioned, the Godwit relies on early environmental cues that might indicate a site's suitability later in the season due to changes in the environment (e.g. vegetation growth; Klomp, 1954). Therefore, I used an approach where I test the relative importance of the habitat selection factors at two key moments in the species' phenology: the clutch laying time and the chick hatching time, which are on average 28 days apart (Verhoeven *et al.* 2020). Besides demonstrating which habitat selection factor plays a more dominant role in site selection, this also enabled us to disentangle whether earlier or later conditions are more crucial for Godwits to select breeding sites and influence breeding densities.

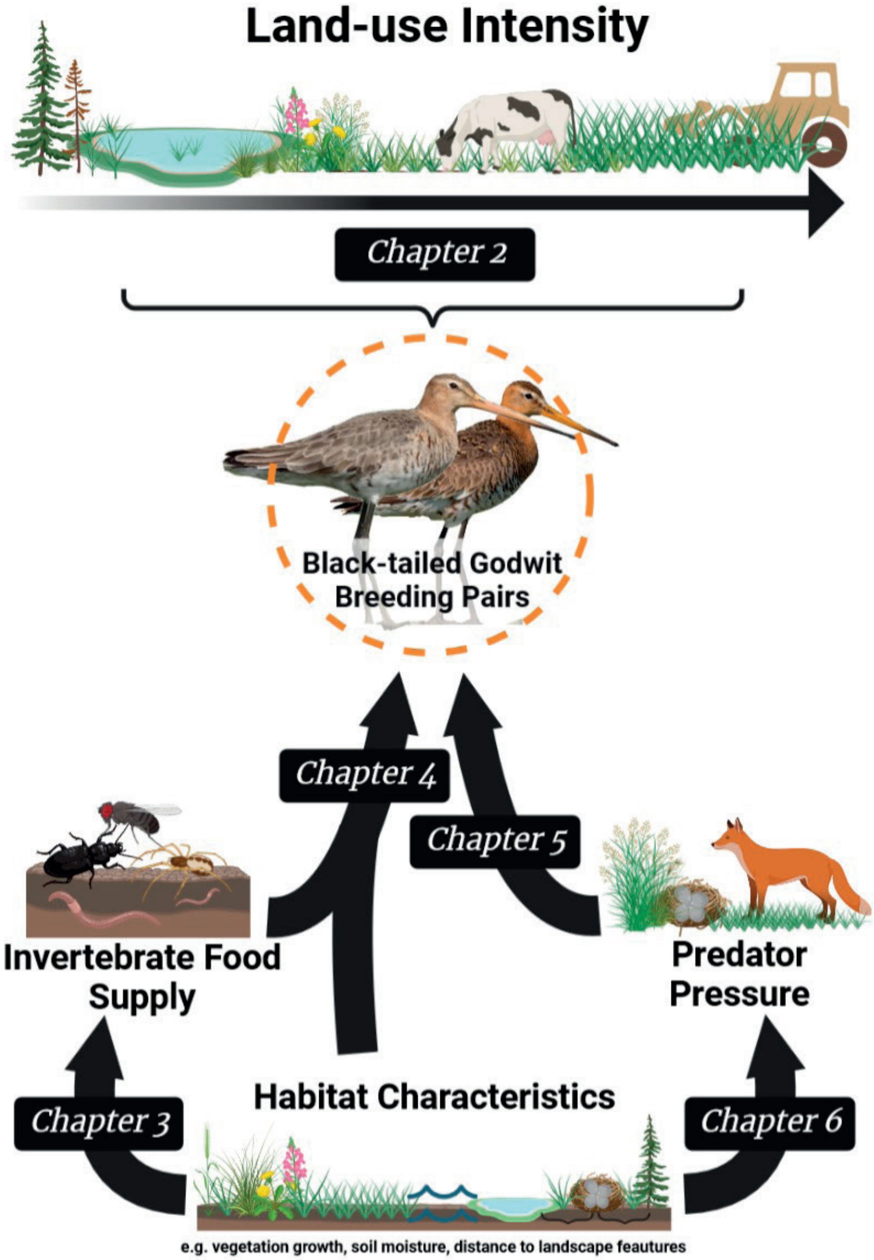


Figure 1.2. Conceptual overview of the chapters presented in this thesis. Understanding how Godwit population sizes and respective densities fluctuate along the land-use intensity gradient requires a broad collection of data coming from a multitude of breeding areas (Chapter 2). In Chapters 3-6, the interactions between the main Godwit habitat requirements are explored, either between themselves or directly with the Godwit populations sampled in the thesis study system.

In **Chapter 5** I focused on predator-evading behaviour during the incubation period across the sampled study sites. Because chick predation is logistically challenging and time-consuming to investigate (Mason *et al.* 2018), especially across an extensive number of sites and countries, I decided to focus solely on clutch predation. Taking advantage of the thermologger devices we deployed to study clutch survival rates and daily survival probabilities, I further extended the research and set up an alternative method that aims to infer predator pressure from the clutch incubation behaviour of Godwits. I examined whether areas with higher clutch mortality impact Godwit couples beyond directly reducing their breeding success, by indirectly creating a landscape of fear (Cervencl *et al.* 2011), that can further reduce breeding success through long incubation recesses.

Due to the continuously increasing wader nest predation rates observed in Europe, understanding the sources and mechanisms behind poor wader nest survival continues to be an extremely relevant conservation topic (Laidlaw *et al.* 2021). I additionally extended the research on the theme and experimentally applied a new methodological approach that tests the effects of some habitat characteristics on clutch survival probabilities. In **Chapter 6**, together with collaborators that surveyed landscape characteristics using unoccupied aerial vehicles (UAV), I test whether habitat conditions at the nest site and/or landscape level have a higher impact on nest site selection and survival probabilities in whole wader communities. This research was conducted in Baltic coastal grasslands, an under-investigated breeding habitat for many wader species including the Godwit, and assessed several habitat characteristics such as vegetation growth and heterogeneity.

Finally, in **Chapter 7**, I synthesized and discussed the results obtained in all the preceding chapters. I contextualize the major conclusions of this thesis within the current main challenges in the Godwit conservation field, in the hope of highlighting the next potential and most feasible steps in the protection of the species.

Chapter 2

Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: a review

Miguel Silva-Monteiro
Hannes Pehlak
Cornelis Fokker
David Kingma
David Kleijn

Published in Global Ecology and Conservation (2021),
Volume 28, August 2021, e01657

https://doi.org/10.1016/j.gecco.2021.e01657

ABSTRACT

Wading birds can be found breeding in a myriad of habitats and ecosystems across Europe that vary widely in their land-use intensity. Over the past few decades, wader breeding populations have declined steeply in habitats ranging from natural undisturbed ecosystems to intensively managed farmland. Most conservation science has focused on factors determining local population size and trends which leave cross-continental patterns and the associated consequences for large-scale conservation strategies unexplored. Here, we review the key factors underlying population decline. We find land-use intensification in western Europe and mostly agricultural extensification and abandonment in northern, central and eastern Europe to be important drivers. Additionally, predation seems to have increased throughout the breeding range and across all habitats. Using collected breeding density data from published and grey literature, we explore habitat specificity of wader species and, of the most widely distributed species, how breeding densities change across a land-use intensity gradient. We found that two-thirds of all examined wader species have relatively narrow breeding habitat preferences, mostly in natural and undisturbed ecosystems, while the remaining species occurred in most or all habitats. The most widespread generalist species (black-tailed godwit, northern lapwing, common redshank, Eurasian oystercatcher, common snipe and ruff) demonstrated peak breeding densities at different positions along the land-use intensity gradient. To conserve both diverse wader communities and viable meta-populations of species, a diversity of habitats should be targeted ranging in land-use intensity from natural ecosystems to medium intensity farmland. Alongside, strategies should be designed to moderate predation of wader clutches and chicks.

KEYWORDS

Wader; Breeding densities; Land-use intensity; Habitat selection; Agricultural activities; Nest predation

INTRODUCTION

Over the last century, the European agricultural landscape has expanded and intensified (Herzog *et al.* 2006). Large areas of natural habitats have been converted to anthropogenic habitats to better suit the needs of mankind; bogs, mires and marshes were drained and steppes were ploughed and fertilized to increase the productivity of cultivated crops (Dugan 1993, Hartig *et al.* 1997, Zedler & Kercher 2005, An & Verhoeven 2019, European Commission 2019). Within decades, Europe transformed from a continent consisting of ecosystems whose composition was predominantly controlled by natural dynamics into a continent with a mosaic of predominantly agricultural and urban habitats whose composition is primarily determined by human management (European Environment Agency 2017). The rate of habitat change increased continuously and was particularly high during the last few decades in which the last few remaining wildlife populations that relied on these habitats for food and shelter started showing dramatic population declines (Duncan *et al.* 1999, Donald *et al.* 2001, 2006, Benton *et al.* 2002, Flade *et al.* 2006).

For a long time, birds were a successful species group in adapting to anthropogenic changes in their habitat. A wide range of passerines and waders that originally bred in bogs, mires, swamps and alluvial grasslands co-evolved with early human agricultural developments and were able to successfully reproduce on land used for farmland practices (Pain & Pienkowski 1997, Donald *et al.* 2002). Improved habitat conditions such as increased openness of the landscape and shorter and more accessible vegetation types caused by cattle grazing or mowing were, and still are, beneficial for many ground-nesting birds (Milsom *et al.* 2000, Durant *et al.* 2008a). They became so typical of agricultural landscapes that they became known as farmland or meadow birds. It is theorized that the peak of many wader populations on farmland occurred right before the modernization of European agriculture in the late 1960's, in the so called "meadow bird golden era" (Cramp & Perrins 1983). However, with the start of the agricultural industrialization, their population numbers started declining and in many places even these species disappeared (Siriwardena *et al.* 1998, Donald *et al.* 2001, Pearce-Higgins *et al.* 2017). It is estimated that in the last two decades, 30% of all farmland birds have disappeared from their European breeding grounds (OECD & BirdLife 2019) and their numbers are predicted to continue declining in future years if no additional conservation measures and policies are implemented (Gamero *et al.* 2017).

Socio-economic developments have resulted in different patterns of agricultural land-use change across Europe. On more fertile and accessible land, particularly in northwestern European countries like the United Kingdom and the Netherlands, farming has almost exclusively intensified (Sutcliffe *et al.* 2015). However, in other parts of Europe, marginal lands and remote areas have been abandoned (Lebedeva 1998, Leito *et al.* 2014).

Ironically, both processes reduce the habitat quality of farmland and grassland nesting birds that depend on low-input grasslands in open landscapes (Olsen & Schmidt 2004, Durant *et al.* 2008a). However, while we have a detailed understanding of the status of the farmland bird communities of northwestern European intensive farmlands and the causes of their declines (e.g. Newton, 2004; Vickery et al., 2001), we know much less about the farmland bird communities that are found on the more extensively farmed lands and natural habitats have remained in central and northeastern Europe (Tryjanowski *et al.* 2011). For lack of better information, conservation management of low intensity habitats may therefore be partly based on insights obtained by research in intensively managed habitats even though they are likely to differ in key aspects such as the bird community composition.

Here we review how farmland wader communities differ between the main habitats in which they breed in Europe. We focus on Charadriiformes wader species as they represent a group of birds with overlapping breeding habitat requirements. We specifically ask whether population trends differ between high and low land-use intensity habitats and whether this can be related to differences in key population dynamical processes such as nest or chick survival. Using a quasi-quantitative approach based on data collected from previous published and unpublished studies, we ask how wader communities differ between the range of habitat types they occupy in Europe. Furthermore, for a number of the most widespread wader species, we test whether different habitat types support different breeding densities.

KEY FACTORS DETERMINING WADER COMMUNITY POPULATION SIZE IN RELATION TO LAND USE INTENSITY

Effects of agricultural intensification

The effects of agricultural intensification on wader populations have received a lot of attention. Although agricultural intensification occurs in various regions throughout Europe, most of the information on the effects of intensification comes from northwestern European countries, where agricultural intensification is the dominant form of land-use change and abandonment of farmland is relatively rare (Tryjanowski *et al.* 2011). In countries such as the Netherlands and Denmark, most remaining waders therefore breed in intensively managed agricultural grasslands (Thorup 2018, Roodbergen & Teunissen 2019). For the most widely distributed species of breeding waders (northern lapwing (*Vanellus vanellus*), common redshank (*Tringa totanus*), black-tailed godwit (*Limosa limosa*), Eurasian oystercatcher (*Haematopus ostralegus*) and Eurasian curlew (*Numenius arquata*)) a vast body of research exists linking their decline to a range of nonexclusive causes associated with the intensification of farming (Roodbergen *et al.* 2012). Drainage and grassland improvement transformed many structurally open wet grasslands into taller and denser vegetation swards, making many sites unsuitable for nesting (Chamberlain *et al.* 2000, Donald *et al.* 2001, Gregory *et al.* 2004, Wilson *et al.* 2004). Agricultural activities such as mowing or reseeding may destroy clutches or kill chicks (Baines 1990, Kruk *et al.* 1997, Schekkerman *et al.* 2009, Kleijn *et al.* 2010, Kentie *et al.* 2013, Santangeli *et al.* 2018) but may also have indirect negative effects by reducing food availability or accessibility (Mccracken & Tallowin 2004, Kleijn *et al.* 2010). For example, accessibility of invertebrate prey of wader chicks is very low in heavily fertilized dense swards (Kleijn *et al.* 2010), while mowing swards during the chick stage reduces invertebrate prey availability and removes cover against predators (Schekkerman & Beintema 2007). Agricultural drainage results in a more rapid drying out of the topsoil layer, which makes it harder, or impossible altogether, for birds to probe the soil for earthworm prey (Green 1988, Struwe-Juhl 1995a, Smart *et al.* 2006, Onrust *et al.* 2019). In several countries there is evidence that losses due to nest predation have increased as well (Newton 2004, Roodbergen *et al.* 2012) and that chick predation is enhanced by intensive farming practices because chicks in poor body condition are more susceptible to predators (Schekkerman *et al.* 2009). It is reported that, although numbers vary between years and sites, around 50% of studied wader clutches are lost to predators in most of the western European wet grasslands and farmland habitats (Macdonald & Bolton 2008, Roodbergen *et al.* 2012, Laidlaw *et al.* 2015). Effects of climate change have also been found to interact with effects of farming on waders, as farmers have advanced their activities in spring mainly because of higher spring temperatures, while some wader species, such as the black-tailed godwit, failed to advance their breeding phenology (Kleijn *et al.* 2010), which may have contributed to the observed increase in mortality caused by agricultural activities (Teunissen *et al.* 2008b). By means of a meta-analysis based on data from 1,323 site–year combinations, Roodbergen et al. (2012), established that adult survival is high and has remained stable over the past few decades, indicating that the low reproductive success caused by agricultural intensification is the main driver of the continuing steep decline of waders breeding in northwestern Europe. The few studies examining the impact of agricultural intensification on waders in central European countries such as the Czech Republic, Slovakia and Poland find similar results with extremely high clutch mortality caused by agriculture activities (e.g. early mowing, conversion of grasslands to arable land) and increased nest predation together with a reduction of the total breeding area (Wylegala *et al.* 2004, Ławicki & Bull 2011, Kubelka *et al.* 2018).

Conservation measures that have been introduced to counteract the effects of agricultural intensification on wader populations primarily aim to reduce farming intensity. In many northwestern European countries, low-intensity farming practices are implemented or maintained in protected areas to conserve wader communities and other farmland fauna

(Bignal & McCracken 1996, Doxa *et al.* 2010). On farmland, agri-environmental schemes have been introduced aiming to promote wader populations by delaying early-seasonal grazing or mowing, and restricting use of fertilizer and pesticides (Donald *et al.* 2002, Kleijn & Sutherland 2003, Durant *et al.* 2008a, Verhulst *et al.* 2011, Sharps *et al.* 2016). In some countries additional measures are being taken to reduce predation rates by fencing and culling of both native and invasive predators (Bolton *et al.* 2007, Fletcher *et al.* 2010b, Smith *et al.* 2011, Malpas *et al.* 2013). However, because reserves are often just small refugia in the middle of intensively managed farmland (Kentie *et al.* 2014) and conservation measures on farmland are generally too scattered or ineffective (Kleijn *et al.* 2001), they do not achieve the required environmental modifications. As a result, conservation efforts have not been successful in reversing the overall decline in breeding wader populations observed in Europe (Verhulst *et al.* 2006, Ohl *et al.* 2008, Schekkerman *et al.* 2008, Pe'er *et al.* 2014, Gamero *et al.* 2017). Yet intensive farmland areas remain the most important breeding habitats for a number of wader species in northwestern Europe (Roodbergen & Teunissen 2019). For example, Dutch agricultural landscapes are amongst the most intensively farmed landscapes in Europe, but nevertheless support an estimated 40% and 25% of the world breeding populations of respectively black-tailed godwits and Eurasian oystercatchers, even though the populations of both species are continuously declining (Roodbergen & Teunissen 2014).

Effects of agricultural extensification

The impact of agricultural extensification or farmland abandonment on wader communities is relatively poorly known. Abandonment of agriculturally marginal or remote areas occurs throughout Europe, but is considered to be the main driver of wader decline in central and eastern European countries such as Estonia and Russia (Leito *et al.* 2014, Kamp *et al.* 2018, Lesiv *et al.* 2018, Mischenko *et al.* 2019). Mischenko and Sukhanova (2016) for example, link drastic declines in local populations of ruff (*Calidris pugnax*), Terek sandpiper (*Xenus cinereus*), black-tailed godwit and northern lapwing in Russian floodplain meadows to the cessation of traditional extensive farming practices. In Poland, abandonment of grassland use is also listed as one of the main reasons for the 74-84% decline of species such as the black-tailed godwit and Eurasian curlew over the last 30 years (Ławicki & Kruszyk 2011). Land abandonment results in shrub and tree encroachment which slowly transforms open landscapes of hay meadows and pastures into wooded landscapes that are unsuitable breeding areas for most ground-nesting meadow birds (Verhulst *et al.* 2004, Sanderson *et al.* 2013, Leito *et al.* 2014, Kamp *et al.* 2018). Similar patterns can be observed in moorland and heathland habitats with most information coming from the United Kingdom and Ireland (Thompson *et al.* 1995, Tryjanowski *et al.* 2011). Waders breeding in moorland habitats, such as northern lapwing and Eurasian curlew, have declined by 50% between 1985 and 2005 (Sim *et al.* 2005). Extensification of management, and subsequent woodland encroachment, has been identified as a key driver because most waders avoid nesting near shrubs and trees (Amar et al., 2011; Douglas et al., 2014; Pearce-Higgins et al., 2009). Increased nest and chick predation is also mentioned frequently as a key factor underlying wader decline in these low land-use intensity habitats. Besides the nest and chick predation by native predators (Ławicki & Kruszyk 2011), invasive species such as the American mink (*Neovison vison*) and raccoon dog (*Nyctereutes procyonoides*) make up an increasing proportion of the predator community that preys on waders (Krüger *et al.* 2018, Brzeziński *et al.* 2019). Culling invasive predator populations has been shown to increase wader breeding success and sometimes doubling breeding densities in the following years (Nordström *et al.* 2003, Niemczynowicz *et al.* 2017). It has been speculated that land abandonment could promote an abundance increase of predators (Ejsmond, 2008; Tryjanowski et al., 2002, 2011) but data is lacking to confirm whether predation is influenced by land use. The few studies that have examined nest losses caused by predation find no differences in survival probability between managed and natural habitats (Rönkä *et al.* 2006, Pehlak & Lõhmus 2008). Nest losses caused by predation do seem to have increased between the late 1980's and the late 1990's in both natural and intensively managed habitats (Teunissen *et al.* 2005, Rönkä *et al.* 2006).

Whether overall nest losses in extensively managed or natural habitats are structurally different from those in intensively farmed habitats is likewise unclear. Few studies have been done in low-intensity habitats in Eastern Europe and these show nest losses ranging from 45 - 73 % (Ławicki & Kruszyk 2011, Mägi 2017, Zámečník *et al.* 2017). A meta-analysis of western European studies showed mean nest losses of 53 - 71% for a number of the most common waders in the same general period (Roodbergen et al. 2012). It is noteworthy that nest survival is the only demographic rate variable from low-intensity habitats for which some quantitative information is available for waders. We were able to find only a single article focusing on chick survival, where Pearce-Higgins and Yalden (2004) find that early chick survival is enhanced by the abundance of invertebrate prey. Next to habitat loss caused by farmland abandonment and predation, climate change has also been implicated in the decline in wader populations in low intensity systems. Climate change may alter the quantity and phenology in wader chick insect food resources, which may create mismatches between hatching and peak food abundance (Pearce-higgins *et al.* 2010) and may affect natural flooding processes with increasing consequent droughts and thus reducing habitat quality for wet grassland nesting and foraging of many species (Mischenko & Sukhanova 2016).

Waders in natural habitats

Interestingly, recent studies suggest that abandonment of farmland may actually drive waders back towards nearby unmanaged habitats such as bogs, fens, other open peatlands (Popov & Starikov 2015). These are the natural habitats which waders used before they started colonizing farmland (Järvinen *et al.* 1978, Bostrom & Nilsson 1983, Tomkovich 1992). In Russia, in the beginning of the 20th century, the northern lapwing was numerous on bogs but occurred only sporadically on farmland (Lebedeva 1998). The colonization of farmland allowed waders such as northern lapwing, black-tailed godwit and common redshank to follow the agricultural expansion to the north and expand their geographic distribution until the 1980's (Lebedeva 1998). A similar switch from natural to anthropogenic breeding habitats has occurred earlier in northwestern Europe where most natural wetlands and peatlands have been used for peat extraction or drained for agricultural purposes mostly before the second world-war (Beintema *et al.* 1995, Vasander *et al.* 2003). With the exception of some bogs and blanket bogs that can be found in northern United Kingdom and Ireland (Wilson *et al.* 2014) large expanses of bogs and fens are now restricted to northeastern European countries (Fraixedas *et al.* 2017). Here they are still inhabited by wader communities that are regulated entirely by natural processes such as annual fluctuations in hydrological conditions, limitations in available food resources (Bostrom & Nilsson 1983) and predation (Berg *et al.* 1992). Research into the ecology of waders in these habitats as well as long-term censuses are rare probably due to the difficulty of accessing these habitats. Recently, Fraixedas et al. (2017) found that most waders species breeding in these habitats in Scandinavian countries have been declining during the last 30 years. Standardized surveys indicated that, for some species, declines in breeding population have been as strong as in intensively managed grasslands: ruff declined by 87%, broad billed sandpiper (*Calidris falcinellus*) by 85% and spotted redshank (*Tringa erythropus*) by 61%. However, in Estonia and Latvia some wader populations actually increased with northern lapwing and wood sandpiper (*Tringa glareola*) both increasing 56%, while Eurasian curlew and whimbrel (*Numenius phaeopus*) declined 44 and 17% respectively (Fraixedas *et al.* 2017). These contrasting population trends between Scandinavia and Baltic countries is possibly explained by the majority of these peatlands habitats being protected in the Baltic countries (around 75%), while in Scandinavia this is the case for only a small fraction (14%), with the majority of peatlands being at continuing risk of further degradation. Fraixedas et al. (2017) suggest peatland drainage and consequent woodland expansion to be the main driver of wader decline in these habitats. However, there is very little empirical research that links wader breeding success or adult mortality to peatland habitat quality or area reduction (Hancock *et al.* 2009). Additionally, there is no evidence that the wader species with increasing populations do so because of high breeding success or because they relocate from nearby abandoned farmland habitats. Studies from western Europe suggest that many wader species show high philopatry, returning every year to the same locations to breed (Groen 1993, Thompson *et al.* 1994, Thompson & Hale 1998). However, in natural habitat in Eastern Europe, philopatry may not be as strong as black-tailed godwits were rarely observed in the same site in the year after color ringing (M. Silva-Monteiro, pers. observations). Likewise there are very few empirical studies focusing on wader nest and chick predation or survival in these natural habitats, with most studies using artificial nests to obtain predation estimations (Berg *et al.* 1992, Pehlak & Lõhmus 2008), which potentially bias true predation rates compared to real nests (Berg 1996, Valkama *et al.* 1999, Batáry & Báldi 2004).

During the last two decades research linking climate change and wader breeding success in natural peatland habitats continued to grow, but mostly in areas above the arctic circle, exploring arthropod phenology trends, snowmelt timings and their impacts on chick food abundance and growth (Meltofte *et al.* 2007, Tulp & Schekkerman 2008, McKinnon *et al.* 2012). In European sub-arctic natural habitats similar research has started only very recently. Machín et al. (2017) found that Eurasian golden plover (*Pluvialis apricaria*) chicks depend on late emerging arthropods which have extreme annual abundance variations in Swedish tundra. Furthermore, in an eight-year study in the same area, Machín et al. (2019) found that in years with late snowmelt had around two times higher predation rates because the scarcely available nest sites at the starting of the egg laying were more conspicuous for predators. To our knowledge no similar research has been conducted in other natural systems such as bogs or fens throughout Europe.

STUDIES EXAMINING WADER BREEDING DENSITIES IN EUROPE

To examine which habitats waders use for breeding in their main distributional range in Europe, how this differs between species and whether different habitats support different population densities, we searched published papers for quantitative data that could be used to calculate breeding densities. Initially we performed searches of peer-reviewed scientific articles reporting densities of breeding waders published between 1945 and 2018 using ISI Web of Science Core Collection (WoS) and Elsevier Scopus databases by using a specific combination of related keywords (see Supplementary Information' S2.1 for more detailed information). We only used studies that met the following requirements: (1) the study reported breeding pair density data or gave a number of breeding pairs for a certain specified area from which a breeding density estimation could be calculated; (2) the study described which methodology was used for surveying breeding birds; (3) the study specified the habitat type or vegetation composition of the surveyed area; (4) the study mentioned the year(s) of survey. We focused on continental Europe, including United Kingdom and Ireland but excluding Iceland. Although southern Europe has some locations supporting breeding waders (e.g. Tinarelli and Bacetti, 1989; Valle and Scarton, 1996) we were not able to find breeding density information in any country located in the Mediterranean area.

In total we found 32 scientific articles containing 984 breeding densities that included 26 wader species and 5 countries in the period 1967-2015. In line with previous observations (Tryjanowski *et al.* 2011), we found most studies originated from the United Kingdom (65% of all data). The other represented countries were Poland (10%), Finland (11%), Sweden (10%), European Russia (3%) and France (1%). Surprisingly, hardly any studies were found from countries such as the Netherlands, a renowned stronghold of wader species such as black-tailed godwit, northern lapwing and Eurasian oystercatcher (Roodbergen & Teunissen 2019) with various scientific groups working on meadow bird ecology. In most countries, it is common practice to report results of breeding wader surveys in local reports or journals in the national language. We therefore decided to include grey literature in our review, acknowledging that this biases our findings somewhat to languages that are accessible to the authors (Dutch), mostly from northwestern Europe. Data from non-peer reviewed conferences papers and government reports were searched on common search engines such as google scholar database using the same combination of keyword as was used for peer-reviewed papers. Our final dataset contained 87 studies, 29 species, 8 countries with a total of 2744 breeding density observations (see Supplementary Information S2.2). There was considerable variation in the way birds had been surveyed, how breeding density data had been reported and whether size of the surveyed area was listed (Table 2.1). Because sample size for a number of habitat types was too low to perform reliable analyses on, we grouped the different types of habitats or ecosystems into a smaller number of broader habitat classes (Table 2.2). We excluded fens and sandy habitats (beach and dunes) from our analyses due the low number of studies compared to other habitats and ecosystems.

Most breeding density data (i.e. a breeding density estimate for a specific wader species in a specific area in a specific year or period) were obtained from the Netherlands and the United Kingdom (Fig. 2.1a). Other important breeding sites are located in, for instance, Denmark or Germany but published data matching our requirements could not be found online.

Studies reporting densities of breeding waders were primarily done in the 1980’s and 90’s with much smaller numbers before and after this period. This trend was apparent in peer-reviewed papers as well as in grey literature (Fig. 2.1b). This data peak during that window of time might come from the adoption of the EU Birds directive in 1979, which promoted and inspired much conservation research in many European countries. By the 1980’s many farmland birds species were already in decline (Donald *et al.* 2001) and studies focusing on those species were considered timely and relevant. As scientific insights in ornithology advanced, publishing this type of descriptive data may not have been considered interesting enough anymore to merit publication in peer-review journals or even reports which could explain the decline in data after the year 2000. Consequently, our results mostly reflect densities as they were in the period 1980-2000 and because species have continued to decline in most places (OECD & BirdLife 2019), probably overestimate actual breeding densities. Absolute breeding densities should therefore be interpreted with care.

Table 2.1. Characteristics of the variation in the data that were used to calculate breeding density estimates. S: number of different source articles where data was extracted. N: number of observations (breeding density for a single species in a time period and habitat)

Variable	Categories	S	N (%)
Source type	Articles published in peer-reviewed journals	32	984 (36%)
	Grey literature (e.g. reports, non peer-reviewed conference papers)	55	1760 (64%)
Breeding density estimation	Territory mapping based on multiple surveys	69	2147 (78%)
	Average number of counted pairs in surveys	4	188 (7%)
	Highest number of counted pairs in surveys	5	150 (6%)
	Mix of above methods	9	259 (9%)
Breeding survey type	Transect line with varying number of visits	63	2053 (75%)
	Constant search effort with varying number of visits	18	465 (17%)
	Mix of above methods	6	226 (8%)
Breeding density units reported	Density of breeding pairs expressed by ha, km^2 or tetrad ($4km^2$)	78	2250 (82%)
	Local population size and surveyed area reported (breeding density calculated)	13	494 (18%)
Year interval	Single year breeding density estimate	74	2241 (82%)
	Multiple year breeding density estimate (average per year used in analyses)	16	503 (18%)
Area sampled	Size of surveyed area given	73	2222 (81%)
	Size of surveyed area not given	19	522 (19%)

Table 2.2. Distribution of wader species over the main ecosystems and habitat types in which they can be found breeding in Europe. Habitat classification generally follows terminology used in source papers (see also Table 2.3). Grey highlighting indicates presence with numbers showing the number of breeding density observations as an indication of the reliability of the occurrence (note that this depends on the total number of observations per habitat). Numbers between brackets indicate the number of papers on which the observations per habitat type were based out of the total of 96 papers.

Wader Species		**Tundra (1)**	**Bog (6)**	**Moorland (8)**	**Saltmarsh (3)**	**Floodplain Meadow (2)**	**Coastal Meadow (5)**	**Extensive Grasslands (29)**	**Intensive Grasslands (42)**	**Total Habitats per Species**
Little Stint	*Calidris minuta*	2								**1**
Purple Sandpiper	*Calidris maritima*	8								**1**
Temminck's Stint	*Calidris temminckii*	10								**1**
Eurasian Dotterel	*Charadrius morinellus*	10	1							**2**
Jack Snipe	*Lymnocryptes minimus*	2	5							**2**
Spotted Redshank	*Tringa erythropus*	6	5							**2**
Red-necked Phalarope	*Phalaropus lobatus*	10	4							**2**
Wood Sandpiper	*Tringa glareola*	9	17							**2**
Eurasian Golden Plover	*Pluvialis apricaria*		18	11				1		**3**
Whimbrel	*Numenius phaeopus*		8							**1**
Ruddy Turnstone	*Arenaria interpres*		1							**1**
Broad-billed Sandpiper	*Calidris falcinellus*		4							**1**
Common Greenshank	*Tringa nebularia*		12							**1**
Green Sandpiper	*Tringa ochropus*		5							**1**
Marsh Sandpiper	*Tringa stagnatilis*							2		**1**
Terek Sandpiper	*Xenus cinereus*							3		**1**
Great Snipe	*Gallinago media*						1			**1**
Pied Avocet	*Recurvirostra avosetta*						3			**1**
Little Ringed Plover	*Charadrius dubius*		2							**1**
Common Sandpiper	*Actitis hypoleucos*	1	1	9			1			**4**
Dunlin	*Calidris alpina*	10	3	38		4	27			**5**
Common Ringed Plover	*Charadrius hiaticula*	10	1	23	6		6	1		**6**
Eurasian Curlew	*Numenius arquata*		17	13	8	23	11	43		**6**
Ruff	*Calidris pugnax*	10	10			5	6	13	27	**6**
Black-tailed Godwit	*Limosa limosa*		3			27	9	66	310	**5**
Eurasian Oystercatcher	*Haematopus ostralegus*		1	40	7		8	83	309	**6**
Northern Lapwing	*Vanellus vanellus*		19	57	14	25	20	122	315	**7**
Common Redshank	*Tringa totanus*	5	9	41	19	24	29	115	259	**8**
Common Snipe	*Gallinago gallinago*	6	20	50	9	25	17	85	84	**8**
Total Species per Habitat		**14**	**22**	**9**	**6**	**7**	**12**	**11**	**6**	

Our review revealed that breeding densities were estimated using different area metrics and using different surveying methodologies (Table 2.1). For around 19% of the observations information on the size of the surveyed area was unavailable. The most frequently used method, representing 78% of the data, was territory mapping, where observations of breeding couples seen and/or heard of multiple surveys are clustered into territories to provide an estimate of the breeding pairs (Bibby *et al.* 1992). The number of surveys differed substantially between locations. Studies in bogs, tundra and moorland generally estimated densities of breeding birds by means of a single survey (e.g. Lehikoinen et al., 2016, Pienkowski et al., 1986). This is probably related to the difficult logistics of reaching and exploring these extensive and inaccessible areas. In other breeding habitats, densities were estimated based on two to six surveys which inevitably gives more reliable results. Such more detailed, labor intensive methods were generally used which in more easily accessible sites, often with the help of citizen scientists (e.g. Altenburg and Jalving, 1998). However, the other 22% of the data calculated breeding densities using either the maximum number of breeding pairs observed, the average of all surveys performed or both techniques depending on the species or location. Interestingly we found that mostly Eastern European countries used those techniques (e.g. Mischenko and Sukhanova, 2016), with some studies in Scotland, United Kingdom, being the exception (e.g. Sim et al., 2005).

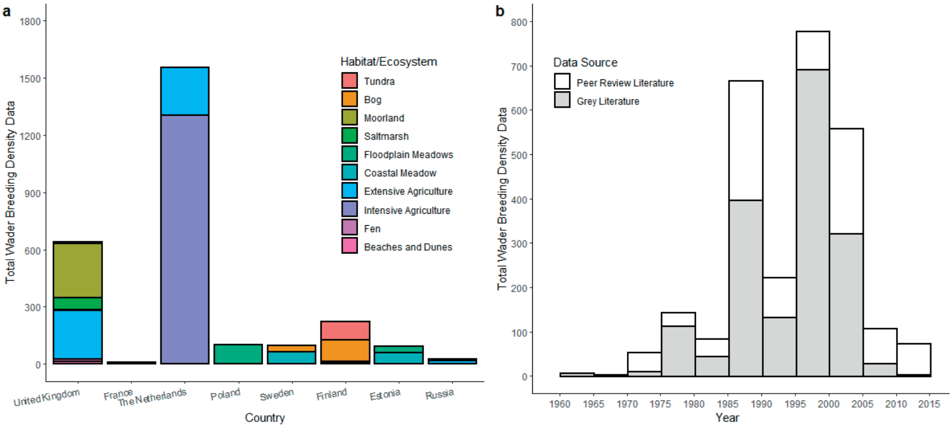


Figure. 2.1. Wader breeding density data frequency according to (**a**) country and habitat/ecosystem type and (**b**) year or average of year interval and data source type.

Comparing densities between areas that have been surveyed using different methods is tricky, especially when methods and countries/ecosystems/habitats are confounded. Brown and Shepherd (1993) found comparable results between two-survey territory mapping and intensive nest search surveys. As far as we know, no other study systematically compared breeding density estimates produced by different surveying methods. Results should therefore be interpreted with care as it is unknown whether one method systematically produces higher or lower estimates compared to another method. Likewise, variation in how breeding density data had been obtained and what area had been surveyed relative to the distribution of the birds may influence the outcome of analyses. However, we assume that the way in which birds had been surveyed did not differed systematically between the land-use intensity classes that were the main topic of interest of this part of the study. The main consequence of this variation will be that our data contains much environmental noise, making it more difficult to find significant differences between land-use intensity classes. It also makes it impossible to examine processes underlying any observed differences.

WADER COMMUNITIES OCCUPYING DIFFERENT HABITATS

Waders breed in a wide range of habitats and ecosystems including tundra, fens, bogs, moorland, saltmarshes, dunes and different types of grasslands (Fig. 2.1a). This essentially suggests that any type of terrestrial habitat that is open and wet can be used by some wader species. Inevitably, some habitats only occur in some countries which could influence the overall species community observed in that habitat or ecosystem. This is partly caused by the fact that in some countries certain habitat types do not occur (anymore). For example, eastern European countries have data mostly from natural habitats while the Netherlands only has data from intensively and extensively used grasslands (Fig. 2.1a). The United Kingdom has data from the widest range of breeding habitats (Fig. 2.1a) removing some of the regional bias from the dataset.

Table 2.2 suggests that most waders are able to breed in multiple habitats. Loose groups can be distinguished with specific habitat preferences. For example, Temminck’s stint, purple sandpiper (*Calidris maritima*), Eurasian dotterel (*Charadrius morinellus*), spotted redshank and jack snipe (*Lymnocryptes minimus*) show preference for high latitude habitats such as tundra and bogs and are mainly observed in northernmost Europe. Another prominent group with green sandpiper (*Tringa ochropus*), common greenshank (*Tringa nebularia*), golden plover or whimbrel shows preferences towards peatlands such as bogs and to a lesser extent moorland. Marsh sandpiper (*Tringa stagnatilis*) and Terek sandpiper together with the great snipe (*Gallinago media*) are mainly observed on the extensively managed marshes and wet grasslands along rivers and other water bodies. Nevertheless, one third of the species can be considered habitat generalist, having been observed breeding in at least five of the eight habitat types that are distinguished in table 2.1 with many of them occurring throughout Europe. This group includes both species that seem to thrive in many anthropogenic areas such as intensive grasslands, arable fields (Eurasian oystercatcher, northern lapwing or black-tailed godwit) and species that are more often observed in more undisturbed habitats (dunlin (*Calidris alpina*), common ringed plover (*Charadrius hiaticula*) or ruff).

Three-quarters of all wader species have been observed breeding in bogs, by far the highest proportion of the different habitats. A possible explanation for this may be that before the large-scale modifications of mankind to the European landscapes, bogs, mires and fens used to be the most widespread habitat providing open and wet conditions in the distributional range of most wader species and occupied far larger areas than floodplain grasslands, saltmarshes or coastal grasslands (Tanneberger *et al.* 2017). Bogs can therefore be considered the core primary breeding habitat for most waders in Europe. This is supported by the aforementioned observations of Lebedeva (1998) that Russian northern lapwings and ruff colonized agricultural grasslands from bogs. Furthermore, large parts of the wet grassland areas that currently hold the majority of the Dutch northern lapwing and black-tailed godwit populations consist of extensive peat bog formations that, over the past centuries, have been gradually transformed into grasslands by drainage and fertilization (Dugan 1993). This suggests that here (some) waders have not colonized new habitats but adapted to new conditions as their habitat changed. The relatively large number of species observed on extensively managed grasslands may reflect the fact that this is the habitat type that people created from most natural wet and open habitats. If management is extensive enough such grasslands may still share many traits and characteristics with the natural habitats from which they were derived and may therefore support species originally breeding in habitats such as river floodplains, saltmarshes and bogs. With increasing intensity of management, the environmental conditions that make these habitats suitable for waders, such as high soil moisture during the breeding season, will increasingly disappear. Together with saltmarshes, another habitat in which waders are exposed to relatively high levels of disturbance, intensively managed grasslands support the lowest number of different wader species and it is doubtful whether the populations that can still be found in this habitat type are viable in the long run given their negative populations trends (Roodbergen & Teunissen 2019).

DO WADER BREEDING DENSITIES DIFFER ACROSS LAND USE INTENSITY GRADIENT?

Because a number of species occur in most or all wader habitats and ecosystems present in Europe, we could explore how breeding densities of waders compare between different habitats. In some habitats, the number of observations were rather low for most species. For the purpose of analysis, we therefore grouped habitats in four contrasting land-use intensity classes (no management and low, medium and high land-use intensity; Table 2.3). This allowed us to explore general patterns in breeding population density across a land-use intensity gradient from natural and undisturbed to intensively managed habitats. We expected species to differ in their breeding density patterns along the gradient of land-use intensity classes, since some are known to be more strongly associated with farmland than others. We restricted this analysis to six species that were present in all land-use intensity classes. For each species independently, we used generalized linear mixed models with the number of breeding pairs per ha as our response variable and land-use intensity class as a fixed factor. A potential pitfall of using breeding densities is that very different population sizes can have the same densities (e.g. 2 pairs in 1 ha is the same as 50 pairs in 25 ha) which could make variation between land-use classes difficult to interpret. However, we found no relationship between the surveyed area size and the number of breeding pairs (in the different land-use classes) for the studies where both information was available (see Supplementary Information Fig. S2.1 for more information). The number of observations per species varied from 71 to 577, came from 25 to 80 studies and spanned the period 1960-2015. We included sampling year and study ID as random factors. We would have preferred to include country as a random factor but because most countries only had data of some land-use intensity classes this would produce unrealistic results since this would lead to unlikely high estimates for missing habitats in countries with overall high breeding densities and unlikely low estimates for missing habitats in countries with overall low breeding densities. For the same reason we decided not include sampling method as a random factor in our analysis. Our current analysis thus assumes that the effect of geographic location on wader densities is relatively small compared to that of land-use intensity. Given the exploratory nature of the study, we considered this acceptable. All analyses were performed using the “lme4” package (Bates *et al.* 2015) in R programming environment (R Core Team 2020). Data were log10 or square root transformed whichever gave the best fit. If land-use intensity demonstrated a significant effect, we used the function “emmeans” in the “emmeans” package (Lenth *et al.* 2018) to test land-use intensity classes differed significantly with a post hoc contrast analysis.

Patterns in wader breeding densities over the land-use intensity classes differed between the examined species with significant differences between classes for five of the six species (Fig. 2.2). The northern lapwing and the black-tailed godwit breeding densities’ increase from natural habitats to medium-intensity habitats after which the black-tailed godwit decreases sharply while the lapwing remains around the same value. Post hoc analysis reveal significance differences between no land-use and medium land-use intensity classes for both species (black-tailed godwit: Tukey’s test, p-value<0.01, df=95, t-ratio=-3.9; northern lapwing: Tukey’s test, p-value<0.01, df=461, t-ratio=3.5). Furthermore black-tailed godwit breeding densities differed significantly between no land-use and high land-use intensity and between medium and high land-use intensity classes (Tukey’s t-test p-value=0.01, df=94, t-ratio=-3.0; Tukey’s t-test p-value<0.01, df=313, t-ratio=3.7 respectively). Breeding densities of the northern lapwing differed significantly only between low and medium land use intensity classes (Tukey's t-test p-value<0.01, df=232, t-ratio=-3.7). Of all six widespread species, northern lapwing and black-tailed godwit showed the most pronounced differences between land-use intensity classes, suggesting that they are particularly sensitive to management. Although the mechanisms of why black-tailed godwit' breeding densities decrease at high land-use intensities are well understood (e.g. lower nest and chick survival resulting in lower recruitment (Kentie *et al.* 2018)), little is known about why breeding densities for both the black-tailed godwit and northern lapwing increase when natural and low intensity habitats are managed a bit more intensively. Populations in habitats belonging to low, medium and high land-use intensity classes mostly show the same, negative trend (Ławicki & Kruszyk 2011, Roodbergen *et al.* 2012) which are thought to be linked mainly to low reproductive success but this does not explain why breeding densities supported by one habitat are higher than those supported by another. Ecological theory predicts that population size is constrained by resources such as food, habitat and other essential resources (Hockey *et al.* 1992, Santisteban *et al.* 2012). Which resource is the main factor limiting the number of breeding pairs of waders in a habitat, and whether these are resources for the adults or for the chicks, has yet to be determined. Yet, this is important information if we want to design effective strategies for the sustainable conservation of waders. Differences in surveying methods between land-use intensity classes may have influenced the observed patterns. However, it is unlikely that they are at the basis of the approximately 11-fold increase in black-tailed godwit breeding densities from unmanaged to medium intensity management habitats. Furthermore, common snipe (*Gallinago gallinago*) breeding densities were determined with the same mix of surveying methods and shows almost the opposite pattern of northern lapwing and black-tailed godwit suggesting that differences primarily originate from habitat characteristics rather than methods of surveying.

The common snipe and ruff have their breeding density peak in unmanaged or low-intensity habitats. However, their breeding density patterns among land-use intensity classes differ. Breeding densities of the common snipe tend to decrease consistently along the land-use gradient with significant differences between medium and high land-use intensity classes (Tukey's test, p-value=0.02, df=133, t-ratio=2.8). The species is known to prefer breeding areas with prolonged high soil moisture and tall vegetation swards, and is able to lengthen the nesting period if those ideal conditions are met (Green 1988). Such characteristics are most frequently found in undisturbed habitats. Improving drainage is amongst the very first steps to improve the usefulness of natural wetlands for farming which immediately lowers habitat quality for this species and may explain why even low-intensity land-use tends to result in lower breeding densities.

The ruff shows high breeding densities in low land-use intensity habitats, that contrast markedly with low breeding densities in all other land-use intensity classes. Population declines in response to increasing land use intensity are well-known (Zöckler 2002). However, our results suggest that breeding densities in natural habitats are also significantly lower than those in low land-use habitats (Tukey's test, p-value=0.01, df=19, t-ratio=-3.6). This could indicate that, for ruff, anthropogenic habitats such as unimproved coastal meadows, floodplain meadows and saltmarshes have higher carrying capacity than natural habitats such as bogs and fens. It could explain the move of ruff into Russian agricultural grasslands starting in the 1960's (Lebedeva 1998). In the last 30 years, however, even in natural habitats the remaining populations have experienced 75-97% decreases (Fraixedas *et al.* 2017, Mischenko 2020), with the main causes unknown.

Table 2.3. A classification of different ecosystems and habitat types in different land-use intensity classes. The ecosystem or habitat types follow the terminology of the papers from which the breeding density data were obtained.

Land-use intensity class	**Characteristics**	**Ecosystem/habitat types**	**Countries**
None	Natural habitats. Habitat composition determined by natural processes (undisturbed). Not used by humans (unmanaged).	Tundra, bogs, fens, shorelines, some types of moorland.	United Kingdom, Ireland, Russia, Estonia, Finland, Sweden
Low	Semi-natural habitats. Habitat composition determined by a combination of natural processes and human use. Mostly grazed. No external inputs and no drainage.	Unimproved coastal meadows, floodplain meadows, saltmarshes, most moorland.	United Kingdom, Russia, Estonia, Sweden
Medium	Extensively managed semi-natural habitats and fields. Vegetation not improved but human use has significant effects on habitat composition. Low fertilizer inputs, moderate drainage. Extensively grazed or cut once and then grazed.	Traditionally managed, low-input grasslands, some nature reserves specifically managed for breeding waders (e.g. in north western Europe).	United Kingdom, Russia, The Netherlands
High	Agricultural fields, both grasslands and arable. Vegetation seeded. Moderate-high fertilizer inputs. Heavily drained.	Improved grasslands (e.g. *Lolium perenne*), arable fields.	United Kingdom, Russia, The Netherlands

Interestingly, the common redshank and the Eurasian oystercatcher show only modest differences in breeding densities between land-use intensities classes, with the latter demonstrating significant differences between no land-use and low land-use intensity classes (Tukey's test, p-value=0.03, df=435, t-ratio=-2.7). This suggests that these species are relatively insensitive to changes in agricultural management intensity. This is in line with the observation that, compared to other waders breeding in the same locations (e.g. black-tailed godwit, northern lapwing, Eurasian curlew), the common redshank usually demonstrates the lowest populations decline rates of the local breeding wader communities (Ławicki & Kruszyk 2011, Roodbergen & Teunissen 2019) and that in their

European breeding range common redshank demonstrated no overall major decline due to poor breeding success from 1992 until 2006 (Roodbergen *et al.* 2012). What makes the common redshank and the Eurasian oystercatcher more resilient towards management is again mostly unknown. One could hypothesize that the unique behavior among waders to feed their young during rearing period (Ens *et al.* 1992) makes Eurasian oystercatchers a bit more resilient to habitat changes that result in worsened foraging conditions for chicks, although the species has suffered significant population declines (Roodbergen *et al.* 2012, Pol *et al.* 2014, Roodbergen & Teunissen 2019).

The high breeding densities of the northern lapwing in the highest land-use intensity classes confirms the reputation of this species as the wader that is best adapted to intensive farming practices. However, most of the breeding density data originated from the period 1985-2005. Since then, the species has demonstrated drastic declines, especially on intensive farmland (Bell & Calladine 2017, Plard *et al.* 2019).

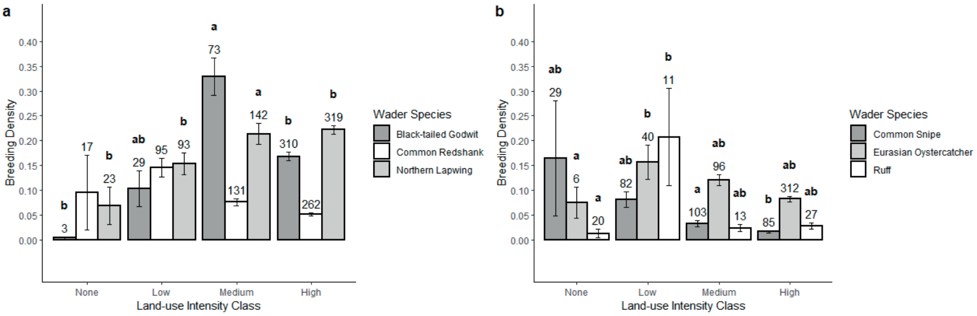


Figure 2.2. Breeding densities (the number of observed pairs per hectare) of widely distributed wader species in different land-use intensity classes. Error bars represent standard error interval and numbers above the sample size. Different letters indicate significant differences within species between land-use intensity classes. Absence of letters indicate no statistical significance.

CONSERVATION IMPLICATIONS

Our review demonstrates that European waders can be classified into loose groups of species with distinct distributions over the available breeding habitats. Approximately two thirds of the waders species have relatively specific and narrow habitat preferences, and are mostly restricted to natural and/or high-latitude areas. However, the remaining species breed in a wide range of habitats, including various forms of agricultural land-use habitats. Our exploratory analysis of breeding densities of the six most widely distributed species suggests that they are differently affected by changes in management intensity resulting in a different optimum at different land-use intensities.

Figure 2.3 summarizes these results in a conceptual model to emphasize the implications for wader conservation. This model suggests that, rather than one optimal level of management intensity, there is an intensity range in which diverse communities can be maintained with shifts in intensity benefitting some species but adversely affecting other species. With only northern lapwing able to sustain high breeding densities in high land use intensity habitats, a large number of species seem to actually benefit from farming practices that increase the productivity of natural habitats (Fig. 2.3, blue line). Especially in low-intensity traditional farming systems, reducing management intensity will therefore result in local population declines of these species (Leito *et al.* 2014, Kamp *et al.* 2018, Lesiv *et al.* 2018, Mischenko *et al.* 2019). Contrary to the main paradigm in northwestern Europe, conservation practices targeting these species need to focus on maintaining or even slightly intensifying low-input mowing or grazing regimes.

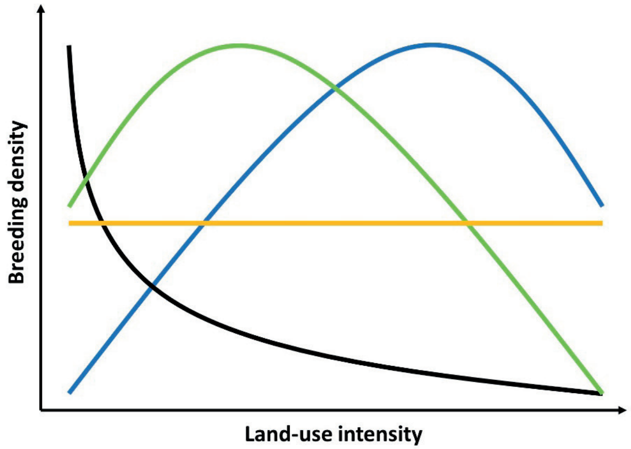


Figure 2.3. Conceptual model demonstrating the relationships between breeding density and land-use intensity for different wader species with different sensitivity for changes in land-use intensity (different colors). Modified after Beintema, 1983.

Figure 2.3 also suggests there are widely distributed species that show no clear relationships between breeding densities and land-use intensity (yellow line), such as common redshank and Eurasian oystercatcher in this study. Based on current knowledge, it is difficult to understand why this is the case. This highlights the fact that, despite waders being a relatively well-examined species group, we lack a basic understanding of the main factors that determine local population size, especially in low-intensity and natural habitats. Whether resources limit breeding densities or other mechanisms are at play, such as intra-specific competition for nesting sites, is unclear. Insight in these processes would greatly help with the design of conservation strategies. If population size cannot be easily manipulated through management of habitat quality, focus needs to shift towards habitat quantity.

Because evidence suggests that predation pressure has increased throughout the distribution range of waders, it is furthermore important to study how current land management practices and future management modifications moderate predation (Laidlaw *et al.* 2017). This not only requires insights into the size and composition of the predator community but also into mobility and behavior of individual predators. Until recently, it was virtually impossible to investigate this but with the development of advanced tracking devices this now moves into the realm of possibilities (Mason *et al.* 2018, Parra-Torres *et al.* 2020).

Natural undisturbed habitats are vital in sustaining breeding population for a large number of species that cannot be found elsewhere due to their sensitivity to landscape intensification (Fig. 2.3, black line). They also represent refugia for more flexible species by sustaining small breeding populations. Natural habitats, such as bogs and other peatlands, currently lack proper protection in several countries (Fraixedas *et al.* 2017). Research into key population dynamical aspects, such as survival of chicks and adult birds as well as the main causes of mortality are urgently needed in these under-researched habitats. Such studies should preferably include climate change scenarios, such as rising annual temperatures or severe droughts, because climate change induced ecosystem changes such as tree encroachment in tundra and bogs systems (Forbes *et al.* 2010, Aune *et al.* 2011, Heijmans *et al.* 2013) or changes in the phenology of the invertebrate prey of chicks will most likely be an additional major factor affecting the quality of wader breeding habitat.

Chapter 3

Invertebrate abundance increases with vegetation productivity across natural and agricultural wader breeding habitats in Europe

Miguel Silva-Monteiro
Jeroen Scheper
Hannes Pehlak
Olavi Kurina
Sami Timonen
Jorma Pessa
Esko Pasanen
Mo Verhoeven
Jelle Loonstra
Theunis Piersma
Frederic Robin
Michał Korniluk
Piotr Świętochowski
Melissa Onwezen
Morten Bongers
Jaap Hamelink
Sander Bik
Frederik Lembreght
Audrey Dunn
David Kleijn

Published in Biological Conservation (2022) Volume 273, September 2022, 109670
https://doi.org/10.1016/j.biocon.2022.109670

ABSTRACT

Grassland breeding waders have been steadily declining across Europe. Recent studies indicating a dramatic decline in grassland invertebrates' abundance and biomass, the key food of most grassland wader chicks, suggest a likely driver of the demise of waders. While agricultural intensification is generally inferred as the main cause for arthropod decline there is surprisingly little information on the relationship between land use intensity and total arthropod abundance in grasslands. Here, we explored those relationships across several key wader breeding habitats by surveying ground-active, aerial and soil-dwelling invertebrate communities in five European countries that range from natural undisturbed bogs to intensively managed grasslands. Using maximum vegetation growth and soil moisture content we investigated how they shape the size of the invertebrate community within and across different countries. We found predominantly positive relationships between grassland invertebrate abundance, biomass and body weight with increasing vegetation growth and soil moisture. Maximum vegetation growth was strongly positively related to ground-active invertebrate abundance and biomass and abundance of soil dwelling invertebrates (mainly earthworms). Body weight of aerial invertebrates furthermore increased with increasing maximum vegetation growth. Our results provide little support for the hypothesis that agricultural practices associated with intensification of grassland management result in a abundance decline of invertebrate prey for wader chicks. Conservation practices aiming to enhance wader chick survival require a careful balancing act between maintaining habitat productivity to secure high prey abundance, and keeping productivity low enough to maintain open swards that do not need to be cut before chicks have fledged.

KEYWORDS

Agricultural land-use; Arthropod; Bogs; Farmland; Insect decline; Invertebrate; Wader chicks

INTRODUCTION

Farmland birds are amongst the most rapidly declining species groups in Europe, and conservation attempts have so far failed to halt the decline in population size and distribution (Kentie *et al.* 2016, Gamero *et al.* 2017). Changes in agricultural practices have been identified as the core driving factor of many species' demise with both agricultural intensification and farmland abandonment having adverse effects on farmland specialists (Benton *et al.* 2002, Donald *et al.* 2006, Durant *et al.* 2008a, Howison *et al.* 2018). Ground-nesting waders are affected in particular (Siriwardena et al., 1998; Van Turnhout et al., 2010), with populations declining around 30% solely in the last two decades (OECD & BirdLife 2019). Low survival of wader nests and especially chicks seems to be the main factor driving wader population decline (Roodbergen *et al.* 2012, Kentie *et al.* 2018). Wader chicks of most species are precocial and forage for arthropods and other invertebrates such earthworms or leatherjackets from the moment they hatch (Beintema *et al.* 1991), with particularly large arthropods being important because these are energetically the most rewarding (Schekkerman & Beintema 2007).

Recent studies suggest that arthropod' abundance and biomass in European grasslands have dramatically declined (Hallmann et al, 2017, 2019; Seibold et al, 2019) and that this may drive declines of higher taxa that depend on them (Lister & Garcia 2018, Goulson 2019). Some studies furthermore report that large species have become smaller over time (Oliveira et al, 2016). It is commonly accepted that arthropod declines are largely the result of changing, more intensive agricultural practices (Møller 2019, Sánchez-Bayo & Wyckhuys 2019, Seibold *et al.* 2019, Raven & Wagner 2021), and interactions with future climate scenarios may potentially exacerbate abundance declines (Sohlström *et al.* 2022). However, the negative effect of farming is often implied from a lack of a relationship with other explanatory variables (Hallmann *et al.* 2017, Seibold *et al.* 2019).

While there is convincing evidence that farming practices can negatively affect specific species groups such as bees, carabids or spiders (Blake et al, 1994; Bell, Philip Wheater and Rod Cullen, 2001; Ekroos et al, 2020) there is surprisingly little information on the relationship between land use intensity and total arthropod abundance, arguably the most relevant variable for arthropod-feeding farmland birds. A notable exception is Benton *et al.*, (2002) who found, in a mixed farming system, a decline in invertebrate abundance with increasing farming intensity over time, which was correlated to a decline in farmland birds. However, not all agricultural practices are expected to adversely affect arthropod abundance. Grassland intensification typically involves increasing the vegetation quality and productivity through improving drainage, application of fertilizers or correcting soil properties that impede plant growth. Experimental fertilization studies often show an increase in arthropod abundance caused by increased quantity and/or quality of the vegetation (Vince *et al.* 1981, Siemann 1998, Haddad *et al.* 2000). Empirical studies that examine arthropod communities under different regimes of agricultural management indeed show varying results. For example, Dennis et al. (2007), finds that important bird arthropod prey abundances decreases with increasing grazing intensity in Scottish moorland. Simons et al. (2014) finds that the herbivore arthropod community' biomass and abundance in German semi-natural grasslands does not significantly differ in contrasting fertilizer application rates. Kleijn et al. (2010) finds positive relationships between total arthropod abundance and fertilizer input in Dutch meadow bird grasslands.

However, these studies only provide partial insight in the relationship between farming intensity and arthropod communities because they examine effects of manipulating the management of existing, often intensive, farming systems. In such studies, long-term and large-scale effects of, for example, past fertilizer applications, modifications in the regional hydrology or nitrogen deposition may partially mask relations between arthropod numbers and land-use intensity. This makes it difficult to assess whether, and under what conditions, arthropod availability is a key limiting factor for wader chick survival, or whether other processes play a more dominant role, such as mortality caused by mowing machinery (Schekkerman *et al.* 2009), too dense swards making the available arthropods inaccessible (Kleijn et al, 2010) or mowing-induced lack of cover leading to enhanced chick predation rates (Schekkerman & Beintema 2007).

Here we use an alternative approach to assess the relationship between land use intensity and arthropod abundance in wader habitats. We make use of the natural variation in land-use intensity that is still present in Europe and survey the range of key breeding wader habitats from no-input natural habitats such as mires and bogs to intensively managed high-input grasslands. We sampled aerial, ground-active and soil-dwelling invertebrates in 64 sites in five countries and related their abundance, biomass and average individual body weight to vegetation productivity (used as a proxy for land-use intensity) and soil moisture content as key variables affecting wader chick habitat quality. We test whether invertebrates decline with increasing land use intensity, which would support the hypothesis that intensive farming practices are a key driver of invertebrate prey. We also examine whether and how invertebrates are affected by soil moisture content, a key variable for many wader species as it affects the ability of adult birds to probe the soil for invertebrate prey (Struwe-Juhl 1995b, Smart *et al.* 2006, Korniluk *et al.* 2021) and known to influence vegetation productivity (Heisler-White *et al.* 2009).

METHODOLOGY

Study sites and design

Data was collected in 64 sites in five countries across mainland Europe: France, the Netherlands, Poland, Estonia and Finland. To standardize habitat types and to make sure that results would be relevant for wader conservation, all sites had been hosting breeding waders (particularly the near-threatened black-tailed godwit *Limosa l. limosa*; BirdLife International, 2017) in the years before sampling, as indicated by local experts. Eighty-one per cent of the sites hosted black-tailed godwit territories in the year we surveyed these sites, all contained contained at least one territory of a wader species and breeding densities varied substantially (Table 3.1). The relationship between environmental variables, invertebrate abundance and black-tailed godwit breeding densities is topic of another paper (Silva-Monteiro et al. in prep.) and will not be addressed here. We aimed to include sites that varied as much as possible in land-use intensity both within countries and between countries, and sampled bogs and fens (natural habitats with no agricultural use), coastal and floodplain grasslands (semi-natural habitats that are grazed or mown but do not receive any inputs) and improved grasslands varying in management intensity (none to high fertilizer input; see supplementary information' table S3.1 for more detailed information). Each site was sampled in a single season which was timed to start approximately three weeks prior to the estimated mean hatching date of black-tailed godwit chicks (roughly between April and June) and the sampling period covering 48 and 72 days, depending on country. Logistical constraints forced us to sample different countries in different years with sites in Finland being sampled in 2017, sites in Estonia both in 2017 and 2018, France and the Netherlands being sampled in 2018 and the Polish sites being sampled in 2019. Sites were located a minimum of 0.5 km apart ensuring they represented independent observations.

Invertebrate sampling

In each site, we surveyed aerial, ground-active and soil-dwelling invertebrates, sampled vegetation biomass and measured soil moisture content at twelve-day intervals throughout the local wader' breeding season (see supplementary information' Fig. S3.1 for a visual concept of the sampling methods). Each site had a total of four to six sampling rounds. Four rounds only occurred when individual sites were inaccessible due to flooding in the first sampling round. Only the French sites were sampled six times by extending the sampling period with one more survey round. Because black-tailed godwit, and other wader species' chicks are considered opportunistic feeders, foraging all available arthropod orders (Beintema *et al.* 1991, Johansson & Blomqvist 1996, Schekkerman & Beintema 2007), we considered all sampled arthropods as relevant prey items.

Arthropods (insects and spiders) were sampled using a combination of pitfall traps and sticky traps (Eglington et al., 2010). Aerial insects were surveyed using three yellow sticky boards (10 x 25 cm, adhesive on two sides; brand Koppert, type Horiver) per site and survey round, placed vertically in the vegetation with the bottom end approximately 10 cm above ground surface and spaced 10 meters apart. After four days, the traps were removed and individual arthropods counted. The abundance of the ground-active arthropods was estimated by means of three pitfall traps (plastic yoghurt cups, height 125 mm and diameter 85 mm) spaced 10 m apart, that were filled with water and cooling fluid to act as a preservative. A cover raised 60 mm above the pitfall traps protected them from flooding during rainfall. Pitfall traps were open for four days per sampling period and closed with a lid for the remaining eight days of the twelve-day period. Both ground and aerial arthropods were identified to order and categorized in four size classes according to their body length : 0-2, 2-4, 4-10 and ≥10mm. Arthropod biomass (mg) was estimated for each order and size class by means of length-weight formulas available in Rogers et al. (1976, 1977). We used 1mm for the “0-2mm” size class, 3mm for the “2-4mm”, 7mm for the “4-9mm” and 10mm for the “≥10mm” class. Average individual body weight (mg/individual) was calculated by dividing the sum of all size classes’ biomasses with the total abundance of arthropods.

Soil-dwelling invertebrates, primarily earthworms and leatherjackets (Tipulidae larvae) were surveyed by extracting 20 cm wide by 20 cm long by 15 cm deep soil samples from each site using a spade (Kleijn *et al.* 2011a). Because soil macro-fauna is not expected to change much over the season, sampling was done only twice during the breeding season, simultaneously with the first and last arthropod samples. In each field, five samples were taken randomly located in the same general location of the arthropod samples. Per site and sampling round, the pooled number of earthworms and leatherjackets were counted on site by manually inspecting the extracted soil sample and expressed in number of individuals per m^2. Soil-dwelling invertebrate abundance was expressed as the average of the two sampled rounds.

Surveying environmental variables

Vegetation biomass (dry weight in g/m^2) was estimated by clipping the vegetation in three 30 x 30 cm vegetation plots randomly located within 10 m of the arthropod sampling sites and weighing them after drying for two days in an oven at 70°C. To determine soil moisture content (%), five 15 cm deep soil samples located randomly in the same general vicinity as the biomass samples were taken using an auger (or soil corer). Subsamples were pooled and mixed and fresh weight was determined after which samples were dried at 105°C for 12 hours in order to determine their dry weight. Soil moisture content in percentage was calculated as (([soil fresh weight – soil dry weight]/soil fresh weight)*100).

We used temperature sums (Tsum; Prins et al., 1988) to correct for the unavoidable differences in phenology of the vegetation and arthropod communities caused by sampling sites with different management (see analysis framework below). Arthropod development, like vegetation growth, is strongly influenced by temperature (Ratte 1984, Logan *et al.* 2006). If sites were grazed or mown before maximum vegetation growth could occur, estimates would be expected to occur at a lower Tsum than undisturbed sites in the same country. Including Tsum in the analyses could therefore account for part of the environmental noise caused by management differences. Tsums were calculated by summing the daily average temperatures above 0°C starting on January 1st until the maximum vegetation growth day. Daily average temperatures were extracted from the Global Historical Climatology Network (Menne et al., 2012) using a nearby meteorological station where complete datasets were available.

Analytical framework

Our study included sites that did not receive external inputs or were even entirely unmanaged by people making it difficult to use commonly input-based indicators of land-use intensity such as nitrogen input or grazing intensity (Herzog et al., 2006; Kleijn et al., 2009). We therefore used maximum vegetation biomass growth as an indicator of land-use intensity as this reflects the outcome of all management practices implemented by farmers to enhance productivity. This has the added benefit that it also incorporates natural variation in productivity that may affect arthropod communities. In each site, maximum vegetation biomass growth was estimated as the largest increase between two successive biomass samples and dividing the difference by the number of days in between (daily g/m^2; Fig. 3.1a). Because the vegetation in bogs (surveyed only in Estonia) did not demonstrate any clear peaks in biomass production, for bog sites we used the average growth rate across the entire sampling period as maximum growth rate. We subsequently used the median day of the sampling interval with maximum vegetation growth to standardize our estimates of the other environmental variables and the arthropods (Fig. 3.1). For soil moisture content, we fitted linear relationships with time and used the model predicted value at the median day of maximum vegetation growth as our estimate of soil moisture content (Fig. 3.1b). The advantage of using this approach is it uses data from all our samples, thus reducing the impact of outliers. We followed the same approach for the arthropod sampling but here we used a linear or quadratic regression (best fit visually selected) from the sampled replicas (Fig. 3.1c). For the bog sites in Estonia, for which maximum vegetation growth estimates were based on the entire sampling period rather than an individual sampling interval (see above), we used the average date of maximum vegetation growth in coastal and floodplain meadows that were sampled in the same year to extract corresponding arthropod, soil moisture and temperature sum data.

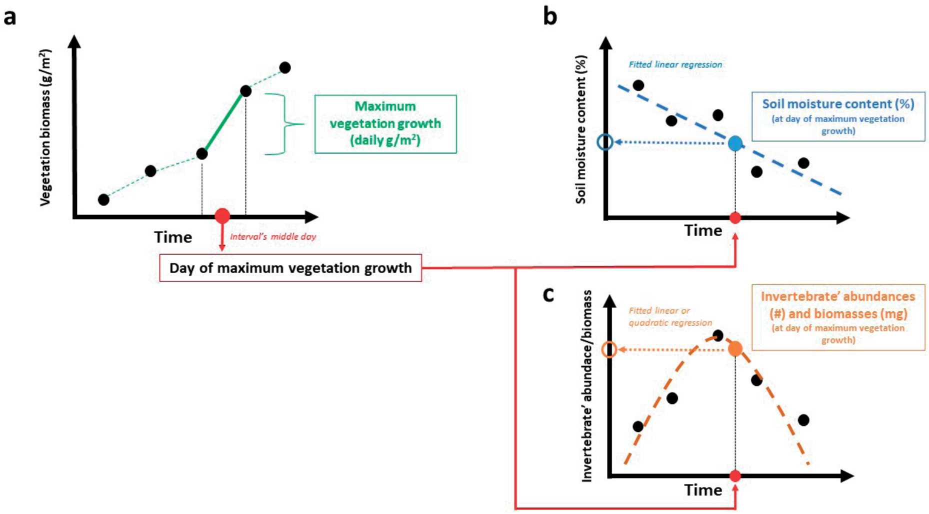


Figure 3.1. Methodological process for obtaining each sites' representative environmental explanatory variables (maximum vegetation growth in green, soil moisture content in blue) and respective invertebrate community response variables (in orange).

Statistical analyses

We employed generalized linear mixed models and an information theoretic approach to investigate to which extent the selected environmental explanatory variables drive the arthropod community's abundances, biomass and average individual body weight. We used country as a random variable and applied the "within-subject centering" procedure (van de Pol & Wright 2009) in order to disentangle effects of the explanatory variables within and between countries. To do this, we first scaled and centered the explanatory variables (maximum vegetation growth, soil moisture content and Tsum) through the whole dataset in order to observe potential within country relations (referred to as 'explanatory variable – within'). We then scaled and centered the country's averages of maximum vegetation growth and soil moisture content in order to observe potential relations across countries ('explanatory variable – across'). In our model selection approach, we forced the predictor Tsum-within to be included in all models to account for effects of local differences in mowing and grazing practices that were outside the scope of the study. Interactions between explanatory variables in the models were not considered due small sample sizes among countries as the analyses across countries are being done on the basis of a single mean value per country. Negative binomial and gamma distributions (with log-link) had the best data fitting and were thus used for abundance and biomass/average individual body weight respectively. Careful inspection of residuals, suggested none of the models was zero-inflated or suffered from over- or under-dispersion. We used an all-subsets approach to build a model set containing all possible combinations of the different explanatory variables. Individual models were restricted to have a maximum of three explanatory terms, in addition to Tsum-within, to avoid overfitting in view of sample size (Babyak 2004). We used the Akaike information criterion corrected for small sample size (AICc) to select models that had a ΔAICc<2 (Burnham *et al.* 2011). Full-model averaged parameter estimates (comprising zeroes when the predictors were not present in certain models) were calculated for each predictor in the model set (Symonds & Moussalli 2011). This approach allowed us to compare the relative importance of different predictor variables because standardized effect sizes of different predictor variables can directly be compared and the 95% confidence intervals of effect sizes can be used to assess their reliability. All analyses were performed in R (R Core Team 2017), using packages glmmTMB (Brooks et al., 2017) and Mu-MIn (Barton 2020).

RESULTS

Differences between habitat types and countries

A number of variables indicated the expected patterns (Table 3.1). For example, bogs and fens had the highest mean soil mositure content and agricultural grasslands had the lowest. Soil dwelling invertebrates only occured in considerable numbers in the relatively intensively managed Dutch sites and to a lesser extent in the Polish floodplain meadows. In a number of other habitat types they were completely absent. However, for the other variables there was considerable variation in the response and explanatory variables both between the habitat types, within countries and within habitat types between countries with no obvious patterns. Across all investigated habitats and countries, the variables showed four- to 13-fold increases from lowest to highest values (Table 3.1), indicating that sufficient variation was present for doing meaningful analyses on the relationship between response and explanatory variables.

Table 3.1. A summary of the observed invertebrate numbers and the main explanatory variables (maximum vegetation growth rate and soil moisture) per broad habitat type and country (mean±s.e.). Habitat types are ordered from low- to high-intensity. Observed settlement densities of black-tailed godwits and the wader community at large are also given for reference. See for survey methodology of waders Silva-Monteiro et al. (in prep.).

Habitat Type - Country	Maximum Vegetation growth ($g.m^{-2}.day^{-1}$)	Soil Moisture (%)	Invertebrate abundance			Black-tailed Godwits territories ($100ha^{-1}$)	Total wader territories ($100ha^{-1}$)
			Ground-active	**Aerial**	**Soil-dwelling**		
Bogs and fens							
Estonia (n=7)	3.8 ± 1.3	99.1 ± 0.9	32.3 ± 5.1	1103.1 ± 271.6	0.0 ± 0.0	1.8 ± 0.5	4.1 ± 1.1
Floodplain meadows							
Estonia (n=2)	15.5 ± 4.0	53.5 ± 12.3	93.5 ± 7.5	1187.0 ± 433.0	0.0 ± 0.0	0.7 ± 0.7	1.4 ± 1.4
Poland (n=5)	8.0 ± 2.0	50.5 ± 4.3	193.0 ± 29.6	1191.0 ± 116.6	3.0 ± 1.0	4.0 ± 4.0	18.6 ± 11.2
Coastal meadows							
Estonia (n=7)	13.2 ± 2.9	38.2 ± 1.8	99.4 ± 15.0	810.6 ± 81.9	0.1 ± 0.1	8.9 ± 2.6	19.6 ± 4.1
Finland (n=6)	4.0 ± 0.9	58.0 ± 5.6	39.3 ± 6.9	1459.2 ± 473.2	0.3 ± 0.3	16.8 ± 5.8	38.6 ± 11.5
Extensive Meadows							
Poland (n=6)	6.3 ± 0.9	67.0 ± 1.8	95.3 ± 9.1	1339.0 ± 276.8	1.2 ± 0.7	18.2 ± 9.4	32.7 ± 8.2
France (n=12)	14.9 ± 2.1	22.7 ± 0.8	222.6 ± 26.5	445.4 ± 38.5	1.8 ± 0.2	5.7 ± 1.6	17.5 ± 3.2
Netherlands (n=4)	10.4 ± 3.2	34.6 ± 4.7	328.8 ± 51.8	2083.3 ± 122.8	20.3 ± 2.5	145.9 ± 42.5	252.1 ± 60.4
Intensive Meadows							
Finland (n=7)	7.2 ± 1.9	30.1 ± 2.9	34.4 ± 8.3	377.6 ± 167.2	0.0 ± 0.0	18.2 ± 5.6	40.2 ± 17.0
Netherlands (n=8)	16.4 ± 2.5	39.4 ± 3.5	442.9 ± 83.8	1511.9 ± 174.3	11.3 ± 2.0	62.5 ± 11.3	115.2 ± 21.6

Factors related to ground-active invertebrates

In total, we counted 42,968 ground-active invertebrates. The model averaged estimates of the variables included in the candidate model set (ΔAICc<2) suggest that maximum vegetation growth across countries was most strongly related to the abundance of ground-active invertebrates (Table 3.2). This relationship shows a nearly fourfold increase in abundance between the near-natural sites with the lowest maximum vegetation growth in Finland and Poland and sites with the highest productivity in the Netherlands and France (Fig. 3.2a). There were only two models in the candidate set of best models, both featuring positive relations with vegetation growth within and/or across countries (supplementary information' table S3.2). Maximum vegetation growth across countries also had the highest averaged estimate (β = 0.43) for ground-active invertebrate biomass. However, the 95% confidence interval of the estimate overlapped zero indicating more uncertainty for biomass than for abundance. All other examined explanatory variables also featured in the candidate model set, but in contrast to maximum vegetation growth, estimates were close to zero, indicating low relative importance (Table 3.2). The correcting variable Tsum-within was however consistently positively related to ground active invertebrates (β = 0.18, 95% CI not overlapping zero). Average body weight of invertebrates was most strongly related to soil moisture within countries (Table 3.2, Fig. 3.2b) with positive relations across a wide range of soil moisture content (Fig. 3.2b).

Table 3.2. Model-averaging results of the candidate model sets explaining abundance, biomasses and average individual body weight (AIBW) of ground-active, aerial and soil-dwelling invertebrates. For each predictor, the model-averaged parameter estimate (**β**) is given, followed by its 95% confidence interval (CI), indicated in bold when not overlapping zero.

	Vegetation Growth within	**Vegetation Growth across**	**Soil Moisture Content within**	**Soil Moisture Content across**	**Temperature Sums within**
Ground-active					
Abundance	0.04 (-0.09 – 0.18)	**0.71** **(0.30 – 1.12)**			0.10 (-0.04 – 0.24)
Biomass	0.01 (-0.07 – 0.09)	0.43 (-0.35 – 1.21)	0.02 (-0.08 – 0.11)	0.03 (-0.29 – 0.34)	**0.18** **(0.02 – 0.34)**
AIBW	0.00 (-0.04 – 0.04)	-0.02 (-0.14 – 0.10)	**0.11** **(0.03 – 0.19)**	0.06 (-0.14 – 0.26)	0.08 (0.00 – 0.16)
Aerial					
Abundance	-0.10 (-0.26 – 0.06)		0.05 (-0.09 – 0.19)	0.03 (-0.17 – 0.23)	0.14 (-0.02 – 0.30)
Biomass		0.13 (-0.36 – 0.62)	0.02 (-0.10 – 0.14)	0.07 (-0.10 – 0.14)	**0.34** **(0.14 – 0.54)**
AIBW	**0.21** **(0.05 – 0.37)**	**0.29** **(0.11 – 0.47)**	-0.02 (-0.14 – 0.10)		0.10 (-0.07 – 0.28)
Soil-dwelling					
Abundance		0.47 (-0.94 – 1.88)		-0.23 (-1.37 – 0.91)	0.0 (-0.23 – 0.24)

Factors related to aerial invertebrates

We counted a total of 264,565 aerial invertebrates. The abundance of aerial invertebrates was not well explained in our study with none of the variables having high effect sizes and all 95% confidence intervals overlapping zero. Similarly, aerial invertebrate biomass was not strongly related to productivity indicators or soil moisture with the correcting variable Tsum-within having the highest averaged estimate (β = 0.34; 95% CI not overlapping zero). However, the best candidate model set for aerial invertebrate average body weight consisted of a single model (supplementary information' Table S3.2) that indicated consistent and pronounced positive relationships with both vegetation growth across and within countries (Table 3.2). Both across and within countries aerial invertebrate body weight increases almost threefold from low to high maximum vegetation growth (Fig. 3.3a and 3.3b respectively).

Factors related to soil dwelling invertebrates

In total 478 soil-dwelling invertebrates were observed. The abundance of soil dwelling invertebrates such as earthworms was positively related with maximum vegetation growth across countries. Effect size was relatively high (β = 0.47; second highest of all effect sizes) with a predicted increase from 0.05 to 0.73 individuals per square meters across the observed range of maximum vegetation growth rate (Fig. 3.4). However, many soil samples did not contain any earthworms and the large number of zeros may explain why the 95% confidence interval was so large and included zero. The negative effect size of soil moisture content across countries may have been relatively unreliable for similar reasons.

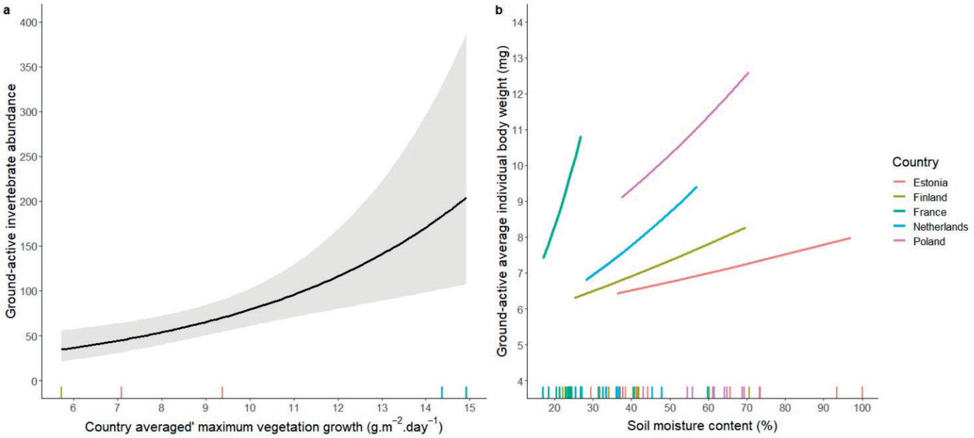


Figure 3.2. The relationships of ground-active invertebrate abundance with vegetation growth across countries (**a**) and ground-active invertebrate average individual body weight with soil-moisture content within countries (**b**). Regression plots are based on models with all explanatory variables present in the averaged model from the candidate model set. Light grey band in Fig. 3.2a displays 95% confidence interval for the shown across-country country relationship. Confidence bands are not presented in Fig. 3.2b to avoid unnecessary visual overlapping. Rugs at the bottom of the figure indicate the x-value for the partial residuals.

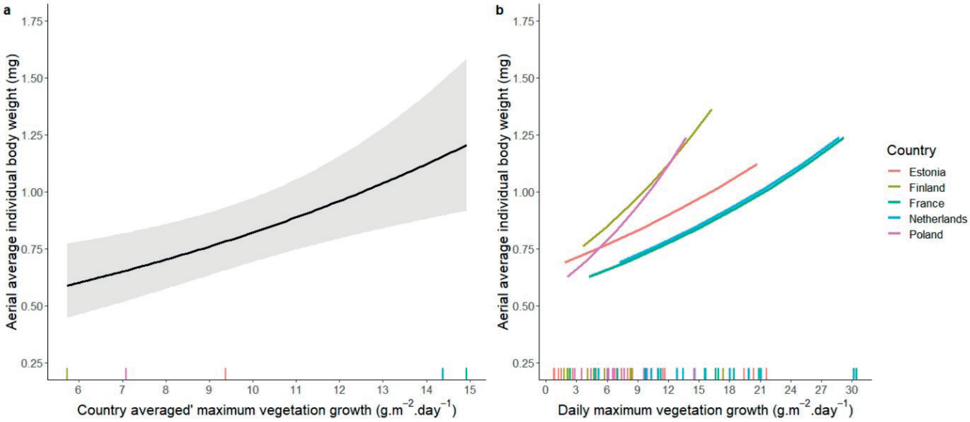


Figure 3.3. The relationships of aerial invertebrate average individual body weight with vegetation growth across (**a**) and within countries (**b**). Regression plots based on models with all explanatory variables present in the averaged model from the candidate model set. Light grey band in Fig. 3.3a displays 95% confidence interval for the shown across-country country relationship. Confidence bands are not presented in Fig. 3.3b to avoid unnecessary visual overlapping. Rugs at the bottom of the figure indicate the x-value for the partial residuals.

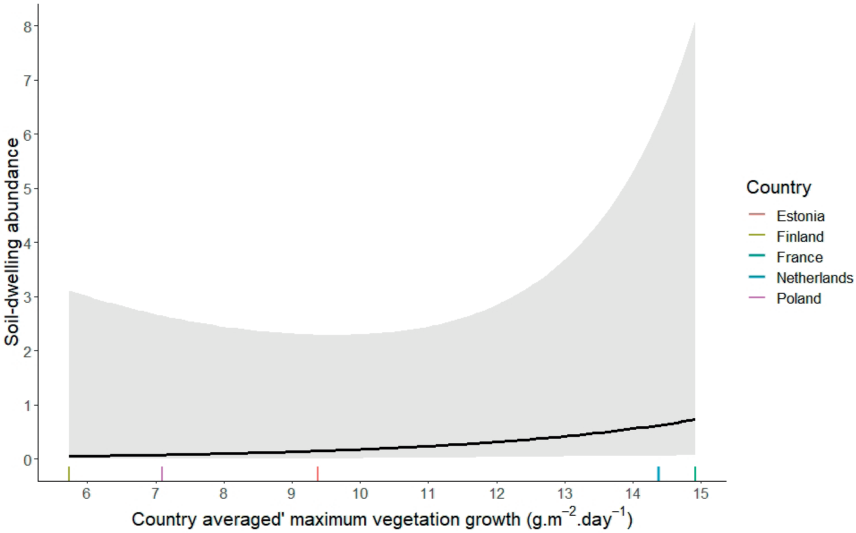


Figure 3.4. Soil-dwelling invertebrate abundance relationship with vegetation growth across countries. Regression plots based on model with all explanatory variables present in the averaged model from the candidate model set. Light grey band displays 95% confidence interval for the shown across-country country relationship. Rugs at the bottom of the figure indicate the x-value for the partial residuals.

DISCUSSION

Across a wide range of wader habitats that spans from waterlogged natural low-productive bogs and fens all the way to heavily drained high-input agricultural grasslands, our results show predominantly positive relationships between grassland invertebrate abundance, biomass and body weight on one hand and maximum vegetation growth and soil moisture on the other hand. This implies that drainage of (semi-)natural wader habitats may result in a decline in the size of ground-active invertebrates but at the same time the much larger effect sizes of maximum vegetation growth on a number of different invertebrate parameters suggests that practices aimed to increase vegetation productivity will enhance grassland invertebrates overall. Our results therefore provide little support for the hypothesis that agricultural practices associated with intensification of grasslands by definition result in a decline in the abundance of arthropods and therefore in the potential availability of invertebrate prey for wader chicks.

The observed predominantly positive relationships between invertebrates and vegetation growth is in line with the theory of cascading effects of nutrient availability on arthropods through plant biomass and quality (Siemann 1998, Haddad *et al.* 2000, Andrey *et al.* 2014). Living and dead plant tissue is, either directly or indirectly through consumption of other invertebrates, the primary food source for most invertebrates. It is therefore perhaps not surprising that the size of the invertebrate communities increases with habitat productivity because more productive habitats simply provide more resources to sustain invertebrates. Andrey et al. (2014), observed a marked increase in arthropod abundance after experimentally increasing the productivity of nutrient-poor grasslands. Our study observes a similar trend using a correlative approach that examines invertebrates in habitats with contrasting productivity. The disadvantage of our approach is that we did not study the impact of vegetation productivity under standardized biotic and abiotic conditions. This was inevitable, because a key objective of our study was to better understand how land-use intensity affects the abundance of invertebrate prey for wader chicks, and natural and intensively farmed wader habitats generally do not occur within close proximity of one another. The fact that our study found relatively clear patterns for ground-active invertebrates despite the environmental differences between habitats suggests a robust relationship between habitat productivity and population size of ground-active invertebrates such as beetles, spiders and ants that are generally caught with pitfall traps. The much wider range in observed maximum vegetation growth across countries than within countries, could explain why relationships across countries were generally more pronounced than relationships within countries (Table 3.2).

Soil moisture did not show clear relationships with invertebrate abundance or biomass. Only body weight of ground-active invertebrates was clearly positively related to soil moisture within countries (Fig. 3.1b). Little is known about how soil-moisture conditions influence invertebrate size (Smith *et al.* 2009) but the few available studies suggest that smaller body size does correlate with drier soils in some species of invertebrates (Huk & Kühne 1999, Vessby 2001). Invertebrate abundance and biomass has been found to be positively related to soil moisture and presence of wet features, such as footdrains or pools (Eglington *et al.* 2010, De Felici *et al.* 2019). Invertebrates generally prefer to oviposit in moist locations where larval development is often more successful (Huk & Kühne 1999, Knisley *et al.* 2018). Our study was done in wader habitats, which are generally rather wet, particularly in the (near-)natural sites. A possible explanation for the absence of a relationship with soil moisture in our study, could be that this was only a limiting factor for invertebrate abundance and biomass in the driest sites in France, the Netherlands and Finland (Fig. 3.2b). Because our sampling size did not allow for a reliable analysis of the interaction between maximum vegetation growth and soil moistures we could not actually test this. However, a clear conclusion is that, within wader habitats, productivity is a stronger driver of invertebrates than soil moisture.

The lack of an association of aerial invertebrate abundance or biomass with any predictor might originate from the sampling method that we used. Unlike pitfall traps, that generally sample specimens from the same area where vegetation growth and soil moisture were sampled (Elek *et al.* 2014), sticky traps sample invertebrates that may have come from much farther distances (Taylor *et al.* 2010). The larvae of many aerial insects, particularly of the Diptera that are often well-represented on sticky traps (Whitaker *et al.* 2000), develop in water bodies (Thorp & Rogers 2011), which are unrelated to the site characteristics as measured in our study. Yellow sticky traps furthermore sample pollinators (Wheelock & O'Neal 2016) that are related to landscape-level factors as well as local factors (Steffan-Dewenter *et al.* 2002). In our study, the characteristics of the landscapes surrounding the sampled sites may therefore have been more important than the local site conditions for aerial invertebrate abundance and biomass. Nevertheless, body weight of aerial invertebrates showed clear and consistent positive relations with both vegetation growth within and across countries (Table 3.2, Fig. 3.3), which is in line with previous findings in Dutch wader grasslands (Kleijn et al., 2009). Body size increases of important grassland invertebrates such as crane flies have been linked to increases in habitat productivity before (Jourdan *et al.* 2019). However, why we found clear relationships between local productivity indicators and body weight but not with invertebrate abundance and biomass remains puzzling.

Soil-dwelling invertebrates are occasional prey for precocial wader chicks (Beintema et al., 1991; Schekkerman and Beintema, 2007) but are the main food source of many adult breeding waders (Buchanan *et al.* 2006). Our results indicate that soil-dwelling invertebrates tend to increase primarily with increasing productivity of sites. Uncertainty of the relationship was large, probably because of a complete lack of soil-dwelling invertebrates, mainly earthworms, in most sites in Finland and Poland (Fig. 3.4). The increase in earthworm abundance in more productive sites is most likely linked to fertilizer application as earthworm densities generally increase with pH and fertilizer application (Atkinson *et al.* 2005). This result suggests that productive habitats provide food for both adults and chicks (Beintema & Visser 1989, Ewing *et al.* 2018). Unproductive habitats, on the other hand, only provide food for chicks so that adult birds have to forage on neighboring sites that are more productive (Struwe-Juhl, 1995).

Our study sheds more light on the current debate on the causes of insect decline. There is convincing evidence that agricultural intensification has negative effects on a wide range of invertebrate groups (Benton *et al.* 2002, Ekroos *et al.* 2020). However, our results indicate that generalist invertebrates that make up the bulk of insect biomass may actually benefit from agricultural practices aimed to enhance the productivity of grasslands. This is in line with a recent study showing that abundance of aquatic invertebrates in the Netherlands has declined over the past three decades because of reduced nitrogen and phosphorus concentrations in surface water while taxonomic diversity increased over the same period (Hallmann & Jongejans 2021). Unlike arable crops, even improved grasslands are only rarely treated with insecticides, which may allow saprophytic and herbivorous insects to build up substantial populations. Although our study did not determine whether peaks in invertebrate availability match the main chick foraging period or whether invertebrate availability was enough to meet wader chick energy demands (Meltofte *et al.* 2007, Tulp & Schekkerman 2008), these results suggest that lack of invertebrate prey is probably not the main driver of the high grassland wader chick mortality observed on intensively managed grasslands. This is further supported by findings that the growth rate of black-tailed godwit chicks does not differ between medium and high-intensity grasslands (i.e. herb-rich grasslands with foot drains vs. monocultures; Loonstra, Verhoeven and Piersma 2017).

Our results indicate that the abundance of invertebrate prey of wader chicks increases with increasing land-use intensity. We do, however, not recommend unconstrained intensification of management of wader habitats to enhance chick prey availability. Studies from Northwestern Europe show clear negative effects of agricultural intensification on both wader breeding population densities (Jóhannesdóttir *et al.* 2019, Douglas *et al.* 2021, Silva-Monteiro *et al.* 2021) and wader chick survival (Roodbergen *et al.* 2012) through mechanisms other than food abundance, such as more difficult access to invertebrate prey in dense, heavily fertilized swards (Kleijn *et al.* 2010), higher mortality rates due to more frequent agricultural activities or higher exposure to predators in recently cut vegetation (Schekkerman & Beintema 2007, Kentie *et al.* 2015, Loonstra *et al.* 2019). Conservation practices aiming to enhance wader chick survival therefore requires a careful balancing act of maintaining habitat productivity to provide enough prey for chicks, and possibly adult birds, while keeping productivity low enough to maintain open swards that do not need to be cut before chicks have fledged.

ACKNOWLEDGEMENTS

MSM was funded by a grant from Wageningen University & Research to DK (proj. nr. 5160957485). JL and MV and the research infrastructure in NL was supported by the Province of Fryslân and the NWO-Spinoza Premium 2014 to TP. Thanks to Kim Peterse and Ilona Lepik for the support in the fieldwork conducted in Finland and Estonia respectively. Thanks to Tomasz Tumiel, Paweł Białomyzy and Grzegorz Grygoruk from Nature Association Dubelt for the support in the fieldwork conducted in Poland. Thanks to Jean-Guy Robin for the support in the fieldwork conducted in France. Thanks to Thijs Fijen for the support in the statistical analysis.

Chapter 4

Cross-continental differences in Black-tailed godwit breeding densities are best explained by arthropod abundance in the chick-hatching period

Miguel Silva-Monteiro
Hannes Pehlak
Sami Timonen
Jorma Pessa
Esko Pasanen
Mo Verhoeven
A.H. Jelle Loonstra
Theunis Piersma
Frederic Robin
Michał Korniluk
Melissa Onwezen
Morten Bongers
Jaap Hamelink
Frederik Lembreght
Audrey Dunn
David Kleijn

Publish in Journal of Ornithology (2022), December 10th 2022
https://doi.org/10.1007/s10336-022-02041-9

ABSTRACT

The endangered continental Black-tailed Godwit (*Limosa limosa limosa*) is a migratory ground-nesting wader breeding in a wide variety of open, wet habitats across Europe. Conservation research has concentrated on the causes of population decline but we know surprisingly little about whether any resources limit local breeding populations and if so, whether these are resources for the adults or the chicks. We collected data from 63 key breeding sites in five countries across Europe to test whether, after correcting for differences in surveyed areas, the size of Godwit breeding populations was related to environmental variables (vegetation biomass, soil moisture) or food resources for adult birds (soil invertebrates) or chicks (vegetation dwelling arthropods) measured during different times of the reproductive cycle. We found the number of Godwit territories to be positively related to arthropod abundance during the chick-hatching period. We found additional, weaker support for a positive relation between Godwit territory numbers and the abundance of soil-dwelling invertebrates (mostly earthworms) at clutch laying, but not at chick-hatching. These relationships were observed across countries, while we found little support for relationships within countries, possibly due to the smaller range in conditions that exist within countries. Both vegetation growth and soil moisture weren't related to Godwit territory numbers. Our results suggest that food abundance for chicks, and to a lesser extent adult birds, are key factors determining the size of local Godwit breeding populations. Conservation management aiming to enhance local Godwit populations should therefore consider the impacts of management strategies on the arthropod prey of chicks.

KEYWORDS

Agricultural land-use; Black-tailed Godwit; Arthropods; Habitat selection; Invertebrate availability

INTRODUCTION

The continental Black-tailed Godwit (*Limosa limosa limosa;* Godwit hereafter), is a generalist migratory ground-nesting wader species, that breeds in a wide variety of open, wet habitats in Europe (Silva-Monteiro *et al.* 2021a). The largest populations are currently located in intensive agricultural grasslands in northwestern European countries such as the Netherlands and Germany (Thorup 2006, Keller *et al.* 2021). Smaller and more isolated populations can be found in most European countries, not only in agricultural habitats but also in natural ecosystems such as bogs and fens (Jensen & Perennou 2007, Ławicki & Kruszyk 2011, Strus *et al.* 2018b). Despite the species ability to thrive under a wide range of environmental conditions, it has been declining throughout most of its range in the last half-century (Gill *et al.* 2007). In the intensive grasslands of the Netherlands, population size decreased by 30% between 2007-2015 (from an estimated 47 to 33 thousand breeding pairs; (Kentie *et al.* 2016)). Similar trends have been observed in less intensively managed, semi-natural grasslands. For example, in the last three decades, Godwits declined by 38% and 85% in Ukraine and Poland respectively (Ławicki & Kruszyk 2011, Strus *et al.* 2018b). Little is known about population trends in natural habitats (Silva-Monteiro *et al.* 2021a). However, studies that examined other wader species that frequently share breeding areas with Godwits also report sharp declines during the last three decades (Fraixedas *et al.* 2017).

Conservation research has focused on understanding the causes for local Godwit declines, which, in northwestern Europe, have been linked to the direct and indirect impacts of increasing agricultural intensity (Beintema *et al.* 1995, Roodbergen *et al.* 2012). Here, high nest and chick mortality due to ever-advancing mowing and grazing dates (Schekkerman *et al.* 2009, Kentie *et al.* 2013), dense monocultural vegetation swards disabling Godwit chicks to forage or hide effectively from predators (Schekkerman & Beintema 2007, Kleijn *et al.* 2010), low water table potentially reducing invertebrate availability for both chicks and adults (De Felici *et al.* 2019, Onrust *et al.* 2019), all reduce the reproductive success of breeding pairs (Kentie *et al.* 2018). In eastern Europe, population decline is predominantly driven by agricultural land abandonment resulting in shrub and tree encroachment that makes many locations unsuitable for Godwits (Leito *et al.* 2014, Kamp *et al.* 2018, Żmihorski *et al.* 2018). Moreover, the predation pressure of both nest and chicks has been increasing across all breeding habitats in Europe, seemingly independent of the intensity of land-use (Silva-Monteiro *et al.* 2021a).

Surprisingly little is known about whether any resources limit the number of breeding pairs of waders in a habitat and if so, whether these are resources for the adults or the chicks (Silva-Monteiro *et al.* 2021a). This is important information if we want to design effective strategies for the sustainable conservation of waders because population size is determined by the product of the habitat area and the breeding density. Godwit breeding densities differ markedly and predictably across habitats with a clear optimum at intermediate land-use intensities where semi-natural grasslands are being managed to enhance productivity somewhat but are not yet heavily drained, levelled, fertilized and reseeded (Silva-Monteiro *et al.* 2021a). Why breeding densities in natural or extensively managed areas such as mires and coastal and floodplain meadows are so much lower than in the more intensively managed grasslands remains unclear. The population size of waders has been found to be determined by essential resources such as food (Goss-Custard 1991, Zharikov & Skilleter 2003, Piersma 2012, Bakker *et al.* 2021) although this has almost exclusively been examined in the non-breeding season. Kleijn *et al.* (2009a) reviewed studies in the Netherlands and Germany examining the relationship between breeding densities on one hand and groundwater level and prey abundance for adult Godwits (e.g. earthworms) on the other and found that settlement densities were more consistently positively related to water level than to earthworm abundance. They speculated that Godwits use soil moisture to select sites that provide good chick-rearing habitat. Wet habitats generally support higher arthropod prey (Eglington *et al.* 2010, De Felici *et al.* 2019) and have vegetation structure that is often more open and accessible to chicks (Kleijn *et al.* 2009b). Identifying the key environmental factors that determine the number of breeding pairs in Godwit habitats can help develop management practices to support and strengthen local populations.

Here we examine which environmental variables are most strongly related to the number of Godwit breeding pairs across a European gradient in land-use intensity. In 63 known Godwit breeding sites located in five countries, we determined local population sizes by means of territory mapping of breeding birds. In each site, we furthermore sampled vegetation biomass, soil moisture content and assessed above- and belowground invertebrate abundances throughout the breeding season. We specifically asked to which environmental variables Godwit territory abundance were most strongly related and whether this differed between the establishment phase (clutch-laying) and the chick-hatching phase.

METHODOLOGY

Study sites and design

We collected data in 63 sites in France, the Netherlands, Poland, Estonia and Finland. All sites were areas potentially hosting breeding Godwits, as indicated by survey information from the years before this study was conducted. Site selection aimed to include locations varying widely in environmental conditions both within countries and between countries to incorporate as much variation as possible in variables potentially explaining Godwit breeding numbers and representing all habitat types used by Godwits for breeding (Silva-Monteiro *et al.* 2021a). This included bogs and fens (natural habitats with no agricultural use), coastal and floodplain grasslands (semi-natural habitats that are grazed or mown but do not receive any inputs) and improved grasslands varying in management intensity (no to high fertilizer input; see supplementary information' Table S4.1 for more detailed information). We thus used a space for time design that reflects the complete transition from a natural undisturbed Godwit breeding habitat to an intensively managed agricultural one (Silva-Monteiro *et al.* 2021a). Additionally, sites were located in countries that included both the extremes and average latitudes of the species' main breeding distribution (AEWA 2008, Keller *et al.* 2021). We surveyed and sampled each site in a single season starting approximately two weeks before the estimated mean laying date of Godwit clutches (roughly between March and May) with the sampling period covering 48-72 days, depending on the country. Logistical constraints forced us to sample different countries in different years with sites in Finland being sampled in 2017, sites in Estonia both in 2017 and 2018, France and the Netherlands being sampled in 2018 and the Polish sites being sampled in 2019. Sites were located a minimum of 0.5 km apart ensuring they represented independent observations and varied in size from 2 to 617 ha (mean: 38 ha). Western European countries (e.g. Netherlands) generally had smaller areas compared to Eastern European countries (notably Estonia). Twelve surveyed sites did not have any Godwit breeding pairs in the year of the survey, possibly due to early-season extreme weather events (e.g. drought). Because the sites' environmental variables still represent important data explaining Godwit site selection we nevertheless included the data from these sites into our analysis.

Surveying breeding populations and determining laying date of Godwit clutches

Godwit breeding populations were estimated by means of a territory mapping approach following Bibby et al. (1992), where observations of territory-indicative behaviour (e.g. pair bond, display, alarm, nests etc.) were recorded on field maps and observations from multiple rounds were clustered into territories. We aimed for five rounds per site, but the final number of rounds ranged between four and six. Eighteen sites were inaccessible in the first sampling round due to flooding and therefore had only four rounds. In the twelve French sites, we decided to extend the surveying and sampling period with one more round resulting in six rounds. Surveys were generally performed using a line transect of parallel lines 200m apart through the whole surveyed area. To determine the exact phenology of the Godwit breeding season we additionally tried to find as many nests as possible. Once a nest was found, we assessed the laying date following the floatation method of Paassen et al. (1984), for which we used the earliest date of three analyzed eggs. The hatching date was subsequently assessed by adding 28 days to the laying date because Godwits generally lay four eggs in four days and start the average 24.5 day incubation period (here rounded to 25 days) immediately after the last egg is laid (Haverschmidt 1963a, Verhoeven *et al.* 2020). To avoid the inclusion of replacement clutches, we excluded all clutches laid after a country-specific date after which we considered it unlikely that first clutches would still be laid. This date was estimated by adding 44 days to the date the first clutch was found in each country. The 44 day period was based on the period between the earliest clutch and May 1st, the known local date where first clutches are stopped being laid in the Netherlands (Verhoeven *et al.* 2020).

Surveying environmental conditions

In each site, we surveyed arthropods (aerial and ground-active) and soil-dwelling invertebrate abundance, sampled vegetation biomass and measured soil moisture content at twelve-day intervals throughout the local Godwit breeding season. In each site, the number of sampling rounds was the same as the number of bird survey rounds.

Arthropods (insects and spiders) were sampled using a combination of pitfall traps and sticky traps (Eglington et al., 2010). Aerial insects were surveyed using three yellow sticky boards (10 x 25 cm, adhesive on two sides; brand Koppert, type Horiver) per site and survey round. Sticky boards were placed vertically in the vegetation with the bottom end approximately 10 cm above the ground surface and spaced 10 meters apart. After four days, the traps were removed and individual arthropods counted. Ground-active arthropods were surveyed using three pitfall traps (plastic yoghurt cups, height 125 mm and diameter 85 mm) spaced 10 m apart, that were filled with water and cooling fluid to act as a preservative. A cover raised 60 mm above the pitfall traps protected them from flooding during rainfall. Pitfall traps were open for four days per sampling period and closed with a lid for the remaining eight of the twelve days. Total arthropod abundance (of aerial and ground-dwelling arthropods) per round was considered to be the sum of the three pitfalls and three sticky board traps.

Soil-dwelling invertebrates, primarily earthworms and leatherjackets (Tipulidae larvae) were surveyed by extracting 20 cm wide by 20 cm long by 15 cm deep soil samples from each site using a spade (Kleijn *et al.* 2011a). Because soil macro-fauna is not expected to change much over the season, sampling was done only twice during the breeding season, simultaneously with the first and last arthropod samples. In each field, five samples were taken randomly located in the same general location of the arthropod samples. Per site and sampling round, the pooled number of earthworms and leatherjackets were counted and expressed in number of individuals per m^2 and the average of the two sampling rounds was used in the analyses.

Vegetation biomass (dry weight in g/m^2) was estimated by clipping the vegetation in three 30 x 30 cm vegetation plots randomly located within 10 m of the arthropod sampling sites and weighing them after drying for two days in an oven at 70°C. To determine soil moisture content (%), five 15 cm deep soil samples located randomly in the same general vicinity as the biomass samples were taken using an auger. Subsamples were pooled and mixed and fresh weight was determined after which samples were dried at 105°C for one night to determine their dry weight. Soil moisture content in percentage was calculated as (([soil fresh weight – soil dry weight]/soil fresh weight)*100).

Analytical framework

We investigated how the total arthropod and soil-dwelling invertebrate abundance, vegetation biomass and soil moisture in two separate periods were related to the number of Godwit territories per site. As this gave a better model fit than directly using territory densities, we used as the main response variable the number of territories while statistically accounting for differences between sites in the area surveyed. Additionally, it allowed us to examine whether area-territory number relationships differed between countries. Because it is unknown if adult Godwits select a breeding area because it confers benefits to themselves or to their chicks during the rearing period we ran analyses with variable estimates at the estimated clutch-laying and chick-hatching dates (Fig. 4.1a). For this, we extracted for each environmental variable an estimate at each site's average clutch-laying date and chick-hatching date. For sites where we did not find any nest, we used the country-averaged clutch-laying date and associated chick-hatching date. For soil moisture content we fitted linear relationships with time and used the model predicted values (Fig. 4.1b). The advantage of using this approach is that it uses data from all our samples, thus reducing the impact of outliers. We followed the same approach for the arthropod abundance and vegetation biomass sampling but here we used either a linear or quadratic regression (best fit visually selected) from the sampled replicas (Fig. 4.1c and 4.1d). We used the averaged value of the two soil-dwelling invertebrate abundance samples in the models for both periods since soil-dwelling abundance is expected to only slightly vary during the breeding season. The different sites varied in size and we included site area in our analyses to correct for this.

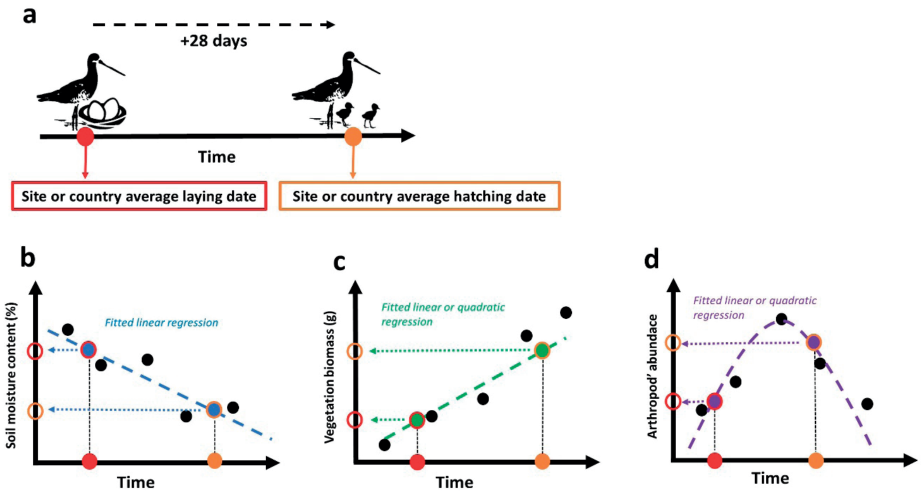


Figure 4.1. (**a**) Methodological process for obtaining estimates of environmental variables at clutch laying and hatching date: (**b**) soil moisture content, (**c**) vegetation biomass and (**d**) arthropod abundance. Country average laying dates were only used in sites without nests.

STATISTICAL ANALYSIS

To investigate to which extent the set of environmental variables were related to the number of Godwit territories, we employed generalized linear mixed models and an information-theoretic approach. We chose this approach because we were specifically interested in the relative importance of the different variables and we had no prior expectations about the outcome. In contrast to the more traditional hypothesis testing approaches, information-theoretic approaches present likelihoods that a model or variable is the best model or variable rather than tests of significance. We analyzed two sets of models using the same set of environmental variables: the first with the estimates obtained at the site or country averaged laying dates and the second with estimates obtained at the associated hatching dates. We used country as a random variable and applied the "within-subject centring" procedure (van de Pol & Wright 2009) to disentangle the effects of the explanatory variables within and between countries. Some environmental variables, while not being relevant due to lack of variation within countries, can become relevant when analysed across a wider geographical range. For this, we first scaled and centred the explanatory variables through the whole dataset to observe potential within-country relations (referred to as 'explanatory variable – within'). We also scaled and centred the country's averages of the environmental conditions to observe potential relations across countries ('explanatory variable – across'). We removed variables that were demonstrating multicollinearity by examining the variance inflation factors (VIF; Quinn & Keough 2002, Graham 2003). "Area size - across" was excluded from both sets of analyses and "soil moisture content -

across” and “vegetation biomass - within” from the analyses at laying and hatching dates respectively. The remaining explanatory variables all had VIFs lower than 2.5. Interactions between explanatory variables in the models were not considered due to small sample sizes among countries as the analyses across countries are being done based on a single mean value per country. Poisson distribution gave the best fit for both sets of analyses and inspection of residuals suggested none of the models was zero-inflated or suffered from over- or under-dispersion.

We used an all-subsets approach to build a model set containing all possible combinations of the different explanatory variables. Given the sample size, individual models were restricted to have a maximum of four explanatory terms, to avoid overfitting (Babyak 2004). We used the Akaike information criterion corrected for small sample size (AICc) to select a candidate set of best models (ΔAICc<2; Burnham *et al.* 2011). Full-model averaged parameter estimates (comprising zeroes when the predictors were not present in certain models) were calculated for each predictor in the model set (Symonds & Moussalli 2011). This approach allowed us to compare the relative importance of different predictor variables because standardized effect sizes of different predictor variables can directly be compared and the 95% confidence intervals of effect sizes can be used to assess their reliability. All analyses were performed in R (R Core Team 2017), using packages glmmTMB (Brooks et al., 2017) and Mu-MIn (Barton 2020).

RESULTS

The results of the analyses at clutch-laying date only provided support for a positive relationship with soil-dwelling invertebrates, such as earthworms and leatherjackets, across countries with a parameter weight of 0.56 and a model-averaged estimate of 0.20 (Table 4.1). The best model containing soil-dwelling invertebrates indicates an approximately two-fold increase in Godwit territory numbers from sites with the lowest earthworm densities in Finland and Estonia to sites with the highest earthworm densities in the Netherlands (Fig. 4.2). The 95% confidence intervals of the model-averaged estimate overlapped zero indicating some uncertainty in the support for this variable, but this is perhaps not surprising given that no invertebrates had been observed in near 50% of the sites (n=31) and the many zero values making the analyses less powerful. We additionally found support for the obvious positive relationship between breeding pairs and area size within countries. There was little or no support that godwit territory numbers at clutch laying were related to vegetation biomass, soil moisture or arthropod abundance.

Table 4.1. Model selection and model averaging results for candidate models explaining Godwit breeding population size at the site and country averaged laying date. Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (ΔAICc). Akaike model weights (ωm) indicate the probability that a model is the best-approximating model given the set of models considered. For each predictor, the parameter estimate for each candidate model is given, along with its model-averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ωp). Confidence intervals that do not overlap zero are indicated in bold.

			Clutch-Laying Period Model					
Predictor	#1	#2	#3	#4	#5	**β**	**95% CI**	**ωp**
Site Area Within	**0.20**	**0.20**	**0.18**	**0.18**	**0.19**	**0.19**	**0.03 – 0.36**	**1.00**
Soil Invertebrate Across	0.35		0.35		0.35	0.20	-0.25 – 0.65	0.56
Arthropod Within			0.09	0.09		0.03	-0.10 – 0.16	0.32
Vegetation Biomass Within					0.05	0.01	-0.06 – 0.07	0.07
ΔAICc	0.00	0.12	1.16	1.21	1.99			
ωm	0.29	0.28	0.16	0.16	0.11			

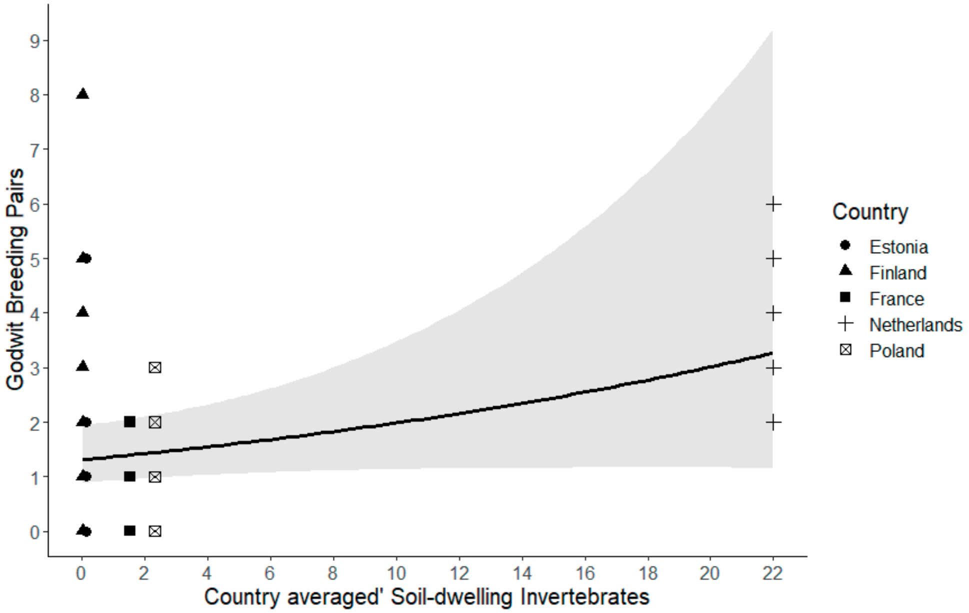


Figure 4.2. The relationships of the number of Godwit breeding pairs with the soil-dwelling invertebrate abundance across countries, based on the regression plots of the second model of table 4.1. The light grey band displays the 95% confidence interval for the shown across-country country relationship. Several site observations are overlapping due to many sites having identical breeding pair counts.

However, at chick-hatching, the arthropod abundance across countries was strongly related to the number of breeding pairs as indicated by the fact that the variable was included in all models in the set of best models (i.e. parameter weight of 1). Furthermore, the model-averaged estimate was 0.66 and its 95% confidence interval did not overlap zero (Table 4.2).

Table 4.2. Model selection and model averaging results for candidate models explaining Godwit breeding population size at the site and country averaged chick-hatching date. Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (ΔAICc). Akaike model weights (ωm) indicate the probability that a model is the best-approximating model given the set of models considered. For each predictor, the parameter estimate for each candidate model is given, along with its model-averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ωp). Confidence intervals that do not overlap zero are indicated in bold.

			Chick-Hatching Period Model				
Predictor	**#1**	**#2**	**#3**	**#4**	**β**	**95% CI**	**ωp**
Site Area Within	**0.20**	**0.20**	**0.20**	**0.22**	**0.20**	**0.03 – 0.36**	**1.00**
Arthropod Across	**0.70**	**0.70**	**0.51**	**0.70**	**0.66**	**0.35 – 0.97**	**1.00**
Moisture Across	-0.22				-0.08	-0.34 – 0.18	0.37
Moisture Within				-0.09	-0.01	-0.11 – 0.08	0.14
Soil Invertebrate Across	-0.28	-0.21		-0.21	-0.19	-0.48 – 0.10	0.78
ΔAICc	0.00	0.56	1.04	1.97			
ωm	0.37	0.28	0.22	0.14			

An illustration of this relationship based on the model with the lowest AICc suggests a nearly fourfold increase in abundance between sites with the lowest invertebrate abundance (e.g. France and Estonia) and sites with the highest abundance (e.g. Netherlands) (Fig. 4.3a). Again, results indicate the obvious positive relationship between Godwit breeding pairs and area size but it is noteworthy that its average estimate was three times lower than that of arthropod abundance across countries (Table 4.2). A graphical illustration of the relationship suggests that the number of Godwit pairs increase with 0.24-0.83 breeding pairs per 10 ha in all countries except for Estonia (Fig. 4.3b). In Estonia, which had most of the larger surveyed areas that were most often located in bogs and fens, the number of pairs increased only marginally with the increasing size of the surveyed area. Additionally, soil-dwelling invertebrate abundance demonstrated a negative relationship, contrasting with the earlier positive one during the clutch-laying period. However, its -0.19 model-average estimate also overlapped zero. Values for each site's vegetation biomass, soil moisture and invertebrate abundances at the two different explored dates are described in the supplementary tables S4.2 and S4.3.

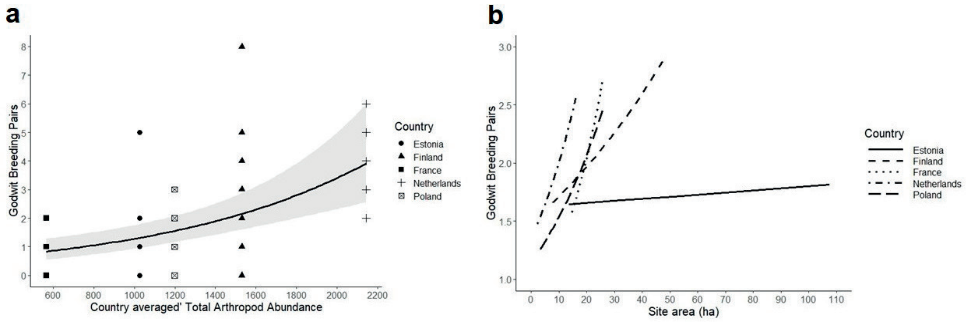


Figure 4.3. The relationships of the number of Godwit breeding pairs with total arthropod abundance across countries (**a**) and surveyed area size within countries (**b**). Regression plots are based on the third model on the candidate model list in table 4.2. The light grey band of (a) displays the 95% confidence interval for the shown across-country country relationship, while several site observations overlapping due to identical breeding pair counts. Confidence intervals and partial residuals are not presented in (b) as multiple overlapping confidence intervals would have made the graph difficult to read. For similar reasons of presentation the x-axis of the panel (b) was shortened and does include two Estonian sites with surveyed areas of 547 and 616 ha.

DISCUSSION

Our cross-continental analysis revealed that soil-dwelling invertebrates in the clutch-laying period and even more so, local arthropod abundance in the chick-hatching period are the best predictors for the number of Black-tailed Godwits breeding pairs. We only found support for relationships with environmental variables across countries with both variables describing food availability. Variables describing the physical conditions of the breeding habitat, vegetation biomass or soil moisture, were found to be far less important or not related to Godwit territory numbers at all.

The positive relationship between the number of Godwit territories and local arthropod abundance at chick-hatching may be explained through two mutually non-exclusive mechanisms. Firstly, breeding pairs may select nest sites that are perceived to be high-quality habitats for their chicks (Kleijn *et al.* 2009c). Godwit chicks are nidifugous and have to forage for themselves right after hatching. Grassland-dwelling arthropods are the main prey items of Godwit chicks (Beintema *et al.* 1991, Schekkerman & Beintema 2007) and chick survival immediately after hatching, when chicks are most vulnerable to limitations in food availability (Schekkerman *et al.* 2009), may be constrained by arthropod abundance. Nest site selection may therefore at least partially be determined by the parent bird's assessment of the abundance of food for their chicks when they hatch. Secondly, arthropod availability may be related, through its positive effect on chick survival, to reproductive success. As far as we know, chick survival is currently the key process driving determining reproductive output throughout the breeding range (Roodbergen *et al.*

2012, Loonstra *et al.* 2019). Breeding pairs in sites with more arthropods may be more successful and because Godwits demonstrate natal philopatry (Kruk *et al.* 1998, Kentie *et al.* 2014), this may result in higher recruitment rates and therefore larger population size, in sites with high arthropod abundance compared to sites with low arthropod abundance. These two potential mechanisms influencing the population size of breeding Godwits operate at different scales. Site selection will mainly be relevant at local scales as godwits predominantly remain in the region in which they bred before with Godwits in the Netherlands renesting an average of 564m away from previous years' nest sites (Verhoeven *et al.* 2020). The potential effect of arthropod abundance on reproductive output will most likely act at a larger, continental scale. Differences in arthropod abundance within habitats are relatively small because they are driven to a large extent by land-use intensity (Silva-Monteiro *et al.* 2022). The fact that we found support for a relationship with arthropod abundance across countries but not within countries could then suggest that the mechanism through reproductive output is the dominant factor explaining the patterns in our data (Fig. 4.3a).

The high relative importance of abundance of soil-dwelling invertebrates, such as earthworms and leather jackets, suggests that food for the adults may be an additional factor determining Godwit breeding densities although to a lower extent. In our study, the high abundance of soil-dwelling invertebrates was mainly restricted to intensively managed grasslands in the Netherlands. However, Leito *et al.,* 2014, observed that within Estonia, with a generally low abundance of soil-dwelling invertebrates, the species often select breeding locations with relatively high earthworm densities. The relationship of godwit territories with prey items for adults may be weaker than that with prey items for the chicks because adult birds are more flexible. For example, Godwits have been found nesting in long-term flooded meadows dominated by sedges that contained only very few prey items of adult birds (Struwe-Juhl 1995b). Between incubation bouts, birds were seen foraging up to 500m from the nest on agricultural lands with high densities of earthworms. The long-term flooding may clear the area of vertebrate prey of potential nest predators (Bellebaum & Bock 2008, Laidlaw *et al.* 2017) and the benefits of lower nest predation rates may outweigh the costs of larger foraging distances. After the chicks hatch, Godwit families often move to areas where the arthropod availability is higher or more accessible (Schekkerman & Beintema 2007), with adults frequently foraging in different areas when not on guard (Beintema & Visser 1989). The observed negative relationship with soil-dwelling invertebrate at chick-hatching may be the result of the intensive drainage of the most productive grasslands in the Netherlands. The top layer of such grasslands are known to dry out rapidly after which soil-dwelling invertebrates migrate to deeper soil layers where they become inaccessible to Godwits (Onrust *et al.* 2019). This suggests that sites that combine high soil-dwelling invertebrates at egg-laying with high arthropod abundance at hatching support the highest numbers of Godwit territories.

The somewhat surprising finding that in Estonia the number of Godwit territories was not related to the size of the surveyed area may also be explained by foraging ecology. In many parts of the very large bogs and mires that we surveyed, and that were completely devoid of soil-dwelling invertebrates, adult Godwits may have to fly too far to feed themselves. Here the benefits of safe nesting may no longer outweigh the foraging costs. We may therefore have surveyed areas that seemed suitable to the human eye, but could in fact not support large breeding Godwit populations.

In an earlier study, Silva-Monteiro *et al.* (2021a) found that, across Europe, Godwit breeding densities increase with increasing land-use intensity from natural to moderately intensively managed grasslands. In another study, Silva-Monteiro et al. (2022b) found that the abundance of vegetation-dwelling arthropods and soil-dwelling invertebrates was generally positively related to vegetation productivity, an indicator of land-use intensity. The high availability of vegetation biomass, mostly enhanced by fertilizer input, allows for a more abundant invertebrate community, as it is their primary food source (Haddad *et al.* 2000, Andrey *et al.* 2014). Our current study, therefore, suggests that agricultural improvement of (near-)natural habitats has improved the food availability for both adult Godwits and chicks and may thus have increased the carrying capacity of breeding sites. It could explain why Godwits, along with many other wader species, colonized Russian farmland and expanded their range during the course of the 20th century (Lebedeva 1998) and why Godwits are thought to have increased in population size in the first half of the 20th century in their current stronghold, the Netherlands (Mulder 1972, Bijlsma *et al.* 2001). Practices associated with the continued intensification of farming, such as increasingly frequent cutting regimes, the use of dense monocultural swards and removal of within- and between-field relief (Kleijn *et al.* 2010, Groen *et al.* 2012, Kentie *et al.* 2015), are now making modern farming landscapes more and more unsuitable for Godwits, even though they still support abundant arthropod communities (Silva-Monteiro et al. 2021b, in preparation). Our findings, therefore, suggest that moderately managed agricultural grasslands (relatively low fertilizer input, cattle grazing intensities, and extensive cutting regimes and high water tables) offer the ideal breeding habitat for Godwits, as they enhance food availability for both adults and chicks but do not yet have a negative impact on the environmental conditions that enhance chick survival such as proper vegetation cover and high arthropods abundance. Although the exact management practices with which this has to be achieved will have to be tailor-made to each breeding area to take into account inherent differences in, for example, soil type, local hydrology, farming system as well as the impact managment will have on other bird species that inhabit the site this means that the optimal conservation management to enhance local Godwit populations should aim for modest increases in land-use intensity at the extensive end of the habitat range, while it should aim for reducing land-use intensity at the intensive end of the range.

ACKNOWLEDGEMENTS

MSM was funded by a grant from Wageningen University & Research to DK (proj. nr. 5160957485). JL and MV and the research infrastructure in NL was supported by the Province of Fryslân and the NWO-Spinoza Premium 2014 to Theunis Piersma. Thanks to Kim Peterse, Ilona Lepik and Samuel Leeming for the support in the fieldwork conducted in Finland and Estonia. Thanks to Tomasz Tumiel, Paweł Białomyzy and Grzegorz Grygoruk from Nature Association Dubelt for the support in the fieldwork conducted in Poland. Thanks to Jean-Guy Robin for the support in the fieldwork conducted in France.

Chapter 5

Frequent and prolonged incubation recesses across European Black-tailed Godwit populations: a successful nest defence strategy?

Miguel Silva-Monteiro
Hannes Pehlak
Sami Timonen
Mo A. Verhoeven
A.H. Jelle Loonstra
Frederic Robin
Michał Korniluk
Paweł Białomyzy
Tomasz Tumiel
Samuel Leeming
Sander Bik
Melissa Onwezen
Frederik Lembreght
David Kleijn

This manuscript is in review at *Wader Study*.

ABSTRACT

Birds have evolved a wide range of behaviours to minimize the impact of predators on clutch survival. Here, we examine whether leaving the nest for prolonged periods of time during the incubation period is a potential nest defence strategy of continental Black-tailed Godwits (*Limosa limosa limosa*). The Black-tailed Godwit is a ground-nesting, grassland breeding wader that has sharply declined in its European breeding area, a decline which has been partly attributed to increased nest predation rates. We used iButton thermologgers placed in nests to determine the frequency and length of long incubation recesses (>20 minutes) and the daily amount of time breeding couples spent taking these recesses, in five European countries with contrasting predation levels (France, the Netherlands, Poland, Estonia and Finland). We test whether these incubation recess variables differ between daytime and nighttime and whether this type of behaviour is related to the nest survival rate. We found that long incubation recesses occurred in all examined populations and differed significantly between daytime and nighttime in some populations but not others, without any apparent relationship to local clutch predation rates. Furthermore, we found evidence for a positive trend between frequent and prolonged long incubation recesses and the daily clutch survival probabilities. Further study on the direct links between predator presence and other likely causes for long disruptions in the incubating behaviour is needed to confirm the role of incubation recesses in ground-nesting waders.

KEYWORDS

Nest defence; Predation pressure; Clutch incubation; Thermologger; iButton; Black-tailed godwit; Breeding habitat; *Limosa limosa*

INTRODUCTION

The continental Black-tailed Godwit (*Limosa limosa limosa,* Godwit from here on) is a wader species that breeds in a myriad of habitats, from intensive agricultural land and semi-natural ecosystems such as coastal and floodplain grasslands, to more natural undisturbed areas such as fens or bogs (Silva-Monteiro *et al.* 2021). For the last half-century, the population size has been declining throughout much of the European continent (Gill *et al.* 2007). Important drivers of the decline are loss of breeding habitat and diminished breeding habitat quality caused by agricultural intensification in western European countries (Beintema *et al.* 1995, Roodbergen *et al.* 2012) and agricultural abandonment in more eastern European countries (Kamp *et al.* 2018, Żmihorski *et al.* 2018). Additionally, high rates of nest and chick predation observed in most habitats may further contribute to the decline of this species (Ławicki & Kruszyk 2011, Roodbergen *et al.* 2012, Kentie *et al.* 2015, Silva-Monteiro *et al.* 2021). Agricultural land-use modifications potentially increased Godwit nest and chick predation rates; in intensified agricultural landscapes, the mowing regimes removed important tall, open patches of vegetation used by chicks to hide from predators (Schekkerman & Beintema 2007) and caused nesting sites to be more conspicuous to predators (Kentie *et al.* 2015), while in more extensive grasslands wader nest predation seem to have increased due to afforestation, which promotes predator presence in nearby grasslands (Kaasiku *et al.* 2022).

Ground-nesting bird species such as the Godwit are exposed to a wide range of potential nest predators that feed on their clutches (Macdonald & Bolton 2008). The Netherlands, which hosts the majority of the Godwit breeding population (Roodbergen & Teunissen 2014), reports average nest predation rates of around 30-50% of all clutches (Teunissen *et al.* 2008a, Kentie *et al.* 2015). In Poland, nest predation rates of 60-70% have been reported (Ławicki & Kruszyk 2011, Niemczynowicz *et al.* 2017). On the other hand, in northern Finland, home to one of the few growing European Godwit populations, nest predation is rare (Timonen et al. unpublished). Mammals are considered to be the main nest predators, with the Red Fox (*Vulpes vulpes*) usually causing the majority of nest losses, followed by mustelid species (e.g. Stoat, *Mustela erminea*; Teunissen *et al.* 2008, Ławicki & Kruszyk 2011, Salewski & Schmidt 2022). Moreover, invasive species are increasingly considered a problem for wader conservation, particularly in eastern European countries. In that region, attempts have been made both to control invasive predators such as the American Mink (*Neovison vison*) by culling (Niemczynowicz *et al.* 2017), and to protect ground-nesting bird species by fencing parts of important breeding areas against both invasive and natural predators (Korniluk M. data unpublished).

Waders species have a diverse set of nest defence strategies to counteract roaming predators (van de Kam *et al.* 2004). Godwits often use “predator-mobbing” behaviour, where birds from several breeding couples join forces, often along with breeding birds from other wader species, to simultaneously attack an intruder (Gochfeld 1984, Green *et al.* 1990). However, this strategy is effective only when breeding populations are large and many birds can share the burden of trying to chase nest predators away (Kirby 1984). Godwit breeding populations most likely have other, more passive, nest-defence strategies, similar to what has been observed for smaller wader species (Nethersole-Thompson & Nethersole-Thompson 1986, Larsen 1991), but these have so far not been described in detail for Godwits. A study on the Common Redshank (*Tringa totanus*) observed that birds breeding at a site in mainland Germany were absent from the nest for several hours every night, while on a nearby islet, the breeding birds remained on the nest throughout the night (Cervencl *et al.* 2011). The authors linked this difference in incubating behaviour to predation rates, which was much higher in the mainland breeding site than on the islet (87% compared to 2%). They suggested that these incubation recesses could potentially result in higher clutch and breeding bird survival but that the long absences from the nest might negatively impact chick development (Webb 1987). It is relatively unexplored whether such long incubation recesses also occur in other biparental wader species, such as the Godwit, and whether this is influenced by frequent exposure to predators.

Here we investigate the nesting success and predation rates of Godwit populations in five European countries and examine whether long incubation recesses occur, whether the amount of time spent daily in these recesses, along with their average daily frequency and length, differ between populations and between daytime and nighttime, and whether these variables are related to nest survival. In line with Cervencl *et al.* (2011), we hypothesize that (i) long incubation recesses are more frequent in Godwit populations experiencing higher predation rates and (ii) breeding couples that frequently deploy long incubation recesses have a higher nest survival rate than birds that rarely deploy them.

METHODS

Study sites and data collection

We collected data in five European countries: Finland, Estonia, Poland, the Netherlands and France. The selected Godwit breeding areas reflect both the diversity of habitats in which the species breeds and cover a significant part of the known European breeding range of the continental *limosa* subspecies (Silva-Monteiro *et al.* 2021). Sites were comprised of grasslands that differed in their land-use intensity (e.g. grazed semi-natural coastal grasslands, fertilized and mowed monocultures) but also included natural undisturbed habitats (e.g. fens; see supplementary information table S5.1 for more details). The sites represented key breeding areas for the species in the respective countries and were subject to the local predator fauna. The exception was Poland, where the sampled clutches were located inside a fence intended to counter the low breeding success of previous years by protecting ground-nesting birds against large mammalian predators (e.g. Red Fox and Raccoon Dog), but having little effect against smaller species (e.g. Stoat; Korniluk M. data unpublished). Due to the difficulty of finding enough Godwit clutches in nearby non-fenced sites, we had to resort to focusing only on the fenced breeding population. However, this allowed us to check whether the breeding behaviour of the birds in the fenced Polish sites was markedly different from that of birds in the other countries where birds were exposed to larger ground-active predators.

Godwit clutches were surveyed following the protocols and objectives of the fieldwork team in each country. In early 2018, each local team was provided with around 20 temperature sampling devices (thermologgers from here on). Thermologgers were deployed in the breeding seasons (between March-July, depending on the country) of 2018, 2019 and 2020 in Estonia and Poland and only in 2018 in France, the Netherlands and Finland.

Clutch fate and incubation pattern determination

We noted the geographical coordinates and estimated the laying date for each found Godwit nest. The laying date was estimated using the egg flotation method (van Paassen *et al.* 1984), assuming the date of the earliest laid egg of all measured eggs. A thermologger was placed under the clutch. Thermologgers were wrapped in a small plastic bag and were attached to a nail stuck in the ground to avoid it being thrown out of the nest by the incubating bird (see supplementary information Fig. S5.1 for more detailed information). We used iButton DS1921G thermologgers (Thermochron®, Australia), which are widely used in ornithological research to record incubation temperatures and infer ground-nesting species' nest fates (e.g. Ospina *et al.* 2018, Laidlaw *et al.* 2020). Thermologgers were programmed to take temperature data points in time intervals of 20 or 30 minutes, depending on the clutch's incubation stage, with the larger interval being used in early-stage incubation nests. These time intervals allowed us to collect data on the whole incubation period while avoiding additional visits to the nest to switch devices due to inadequate memory capacity. Thermologgers were retrieved 28 days after the estimated laying date of the nest, which corresponds to the average estimated hatching date (Haverschmidt 1963b, Verhoeven *et al.* 2020). If the clutch had not yet hatched by this point, the thermologger was retrieved on a later day after the nest had hatched.

Based on the patterns in the temperature data, we created an incubation presence or absence dataset for each sampled clutch. Temperature data between one hour after deployment of the thermologger and the end of incubation were used for this. The final moment of clutch incubation was determined by visually inspecting the temperature fluctuations and locating the last high-temperature point (indicating incubation) before the temperature dropped permanently (signalling its hatching or predation; Bolton *et al.* 2007). If a clutch successfully hatched, an erratic interval of temperatures (usually 12 hours in duration) could be observed before the nest cup temperature started following ambient temperatures. If the clutch was predated, a sharp decline in the incubation temperatures could be observed before logging ambient temperatures (see supplementary information Fig. S5.1 for more details). Nest success or failure was determined by this final temperature examination. Nests that had failed due to other reasons (e.g. abandonment, flooding) were excluded from our analyses.

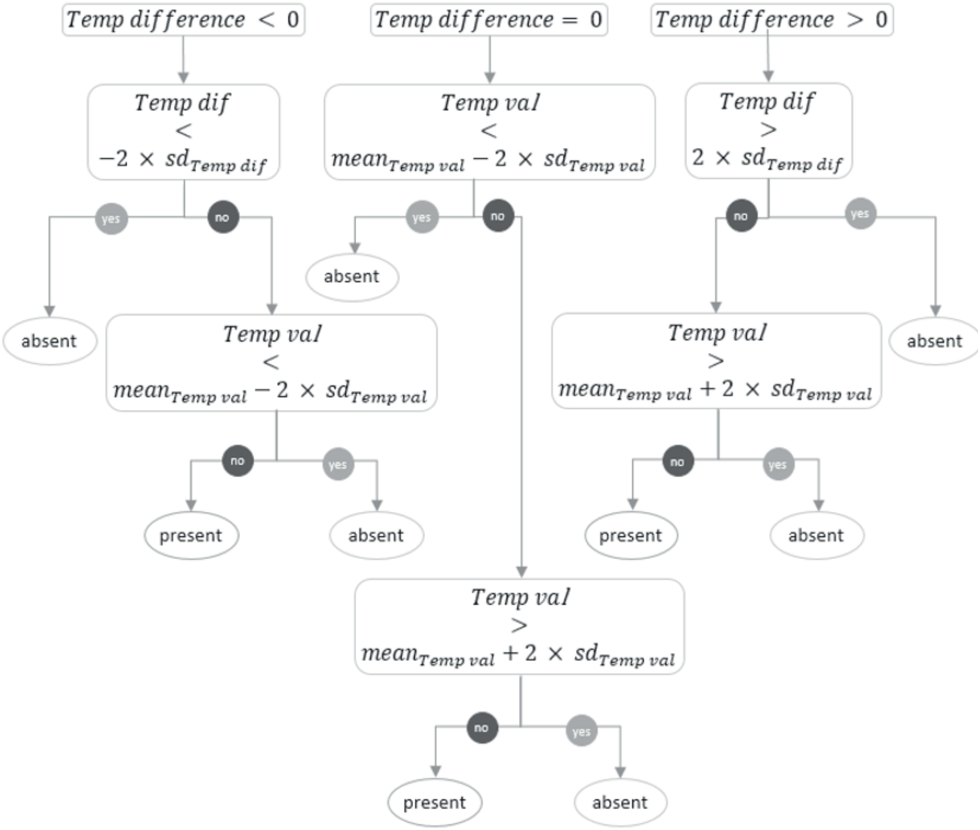


Figure 5.1. Decision tree for incubation presence or long incubation recess classification, starting with the temperature difference between two consecutive temperature points.

Previous studies that use thermologgers to investigate incubation recesses often use an additional thermologger located outside the nest cup to separate incubation-induced changes in temperature from environmental temperature fluctuations (Cervencl *et al.* 2011, Saalfeld *et al.* 2012), or follow incubation temperature fluctuations in more detail (every minute) in areas where environmental temperatures are strikingly different to the wader incubation temperatures (Meyer *et al.* 2021). Due to limitations in the number of thermologgers at our disposal and the data storage possible in them, we chose to monitor more nests rather than have such a control thermologger for each nest. We subsequently developed a protocol to evaluate if a parental bird was present or absent at the clutch incubation based on the possible temperature interval differences. Because the minimum interval between temperature recordings was 20 minutes, our study focused only on long incubation recesses (>20 minutes in length), which we think are also more indicative of interactions with predators because short incubation recesses can be the consequence of parent birds switching places or rolling eggs. Following a decision tree that takes into consideration the means and standard deviations of the temperature values and the temperature difference with the previous point, each temperature data point was classified as present or absent at clutch incubation (Fig. 5.1). A thorough check suggested that this automated procedure produced a classification that was ~99% in line with our own visual assessment. We manually corrected the ~1% of the classifications where we did not agree with the automated classification. For each temperature entry, we furthermore recorded whether it was made during the daytime or nighttime, with "nighttime" being considered all entries with a time falling between sunset and sunrise time, using the R package "suncalc" (Thieurmel & Elmarhraoui 2019).

Statistics

For each Godwit clutch, the following long incubation recess variables were calculated: (i) The daily average time (in hours) a breeding couple spent taking long incubation recesses; (ii) The daily average number of long incubation recesses performed and (iii) The average length (in hours) of a long incubation recess. Due to the low sample size, we pooled nests from the same country that were sampled in different years. We used program R version 4.0 (R Core Team 2021) to analyse if the three variables differed among sampled countries and within countries between day- and nighttime by standardizing according to each country's day and night duration and using the non-parametric unpaired or paired Wilcoxon rank-sum test, respectively.

Additionally, we investigated if any of the long incubation recess variables were associated with the daily survival rate of the nest (Mayfield 1975). The daily survival rate was estimated using survival models in MARK (White & Burnham 1999) and the R Package RMARK (Laake 2013). We standardized the breeding season date by starting to count in each country at the date of the first laid clutch (=1). Furthermore, we inspected if the three long incubation recess covariates demonstrated multicollinearity by examining variance inflation factors (Zuur *et al.* 2009). We had to remove the daily average time spent in a long incubation recess, due to its high variance inflation factors and correlation with the other two variables of interest (r>0.6). We also included country as a covariate to test for differences between countries and associated ecosystems, land use, and management (e.g. fenced vs. unfenced). As a first step, we analysed whether a linear, quadratic or third-degree equation best explained the decline in daily survival rate over time. Next, we ran models that included the best fitted temporal model, country and the two remaining long incubation recess variables to test whether they increased model fit, by assuming that those variables remained constant throughout the breeding season. Models were ranked using the corrected Akaike's Information Criterion (AICc) values and weights, and a subset of best candidate models that had ΔAICc<2 was selected (Burnham & Anderson 2001).

RESULTS

Thermologgers from 94 Godwit nests produced data that could be used for analyses. The hatching success varied highly across countries. All nests successfully hatched in Finland while the majority of the nests hatched in The Netherlands and (in the fenced area) in Poland. In France, about half of the nests hatched while the majority of nests were predated in Estonia (Table 5.1).

Table 5.1. The number of nests analysed by country, clutch fate, and average sampled incubation duration.

Country	Hatched	Predated	Average sampled incubation duration (days +/- se)
Estonia	10 (31%)	22 (69%)	8.9 +/- 1.1
Finland	19 (100%)	0 (0%)	12.1 +/- 1.3
France	6 (43%)	8 (57%)	13.7 +/- 1.8
The Netherlands	9 (75%)	3 (25%)	16.3 +/- 1.0
Poland	11 (65%)	6 (35%)	12.4 +/- 1.4

In Estonia and Poland, most nests were predated during the nighttime, while in France and the Netherlands they were mostly predated during the daytime period (Fig. 5.2). Across all countries, and disregarding short incubation recesses that arguably have little impact on chick development, Godwit clutches were incubated on average 94.6% of the time (22.7 hours per day).

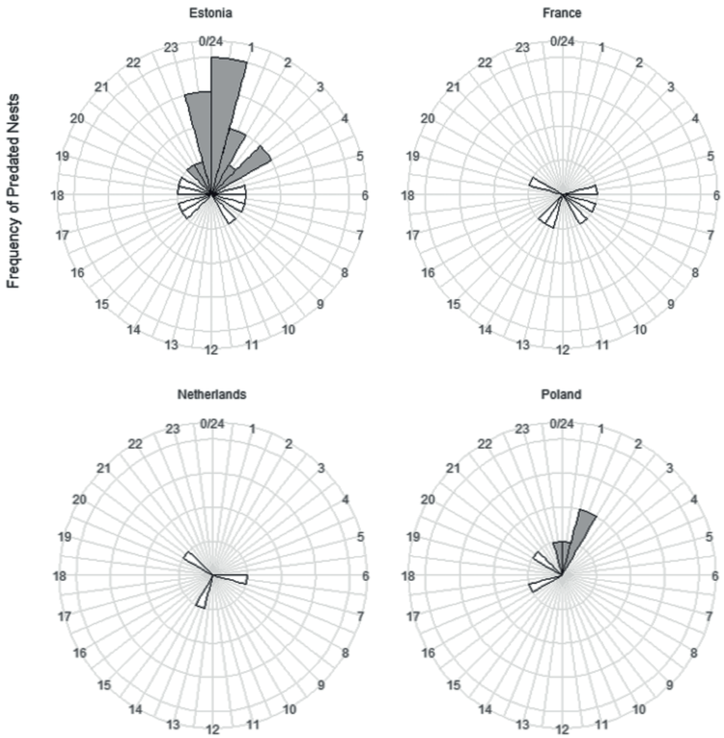


Figure 5.2. Radial graphs showing the frequency and time of occurrence of nest predation in four countries. White and grey bars represent day- and nighttime, respectively. No clutch was predated in Finland.

Godwits breeding in Estonia, Finland and France spent more time away from the nest in long incubation recesses than in the other two countries, although the difference was only statistically significant for Poland (Fig. 5.3A; all Wilcoxon test statistics available in supplementary information tables S5.2-4). Likewise, couples breeding in those three countries spent more time in long incubation recesses during the nighttime than during the daytime period compared to Poland and The Netherlands (Fig. 5.3B); again, this difference was only statistically significant for Poland where couples spent more time away from incubation during the daytime than during the nighttime period. The number of long incubation recesses performed per day was significantly higher in Finland than in all other countries, while in Poland it was significantly lower than in all other countries (Fig. 5.4A). Additionally, the frequency per hour of long incubation recesses was significantly higher during the daytime period compared to nighttime in France, The Netherlands and Poland (Fig. 5.4B). In all countries except for Estonia, more long incubation recesses occurred during the daytime than during the nighttime (Fig. 5.4B). The average incubation recess length was significantly higher in France compared to other countries (Fig. 5.5A), and tended to be longer during the night in most countries although those differences were not statistically significant (Fig. 5.5B).

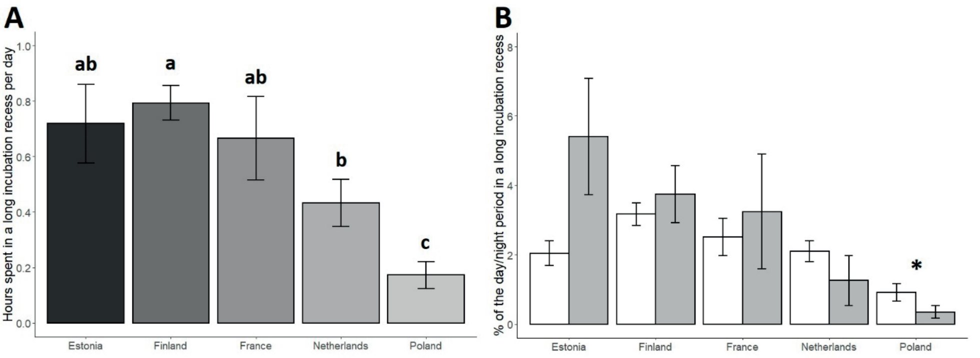


Figure 5.3. (**A**) Average daily hours (means ± standard error) a godwit breeding couple spent in a long incubation recess in the different sampled countries. (**B**) Average percentage of the day and night duration (means ± standard error) the breeding couple spent in a long incubation recess. White and grey bars in plot B represent day and night time, respectively. Different letters represent statistical significance between countries. Asterisk (*) represents statistical significance between the day and night period. Note that higher latitude countries have longer daytime.

The best daily survival model with only temporal relationships included time as a linear variable, although the model with time as a quadratic term performed only marginally worse (Table 5.2). When adding the other variables of interest, the country variable was present in all models with ΔAICc<2 (Table 5.2), not surprisingly indicating that the daily survival rate differed between the study areas in the different countries. The models that included the long incubation recess variables were also included among the three best models, suggesting that long incubation recesses explain part of the variation in daily survival rates (Table 5.2).

Table 5.2. Survival model selection results for (**A**) best temporal trend and (**B**) Long Incubation Recesses (LIR) variables of interest. The best model is highlighted in dark grey while other supported models (ΔAICc<2) are in light grey.

Model	**AICc**	**ΔAICc**	**weight**	**LogL**
Temporal relationship models				
Linear Date	327.31	0.00	0.53	-161.65
Quadratic Date	328.96	1.65	0.23	-161.47
Null Model	330.08	2.77	0.13	-164.04
Third-degree Date	330.39	3.08	0.11	-161.18
Best temporal relationship + Country + LIR Variables models				
Linear Date + Country + LIR Frequency per Day	306.88	0.00	0.45	-147.40
Linear Date + Country + LIR Average Duration	307.78	0.89	0.29	-147.85
Linear Date + Country	307.93	1.05	0.27	-148.94
Linear Date + LIR Frequency per Day	326.44	19.56	0.00	-160.54
Linear Date + LIR Average Duration	327.11	20.23	0.00	-160.21
Linear Date	327.31	20.43	0.00	-161.65
Null Model	330.08	23.20	0.00	-164.04

An illustration of the effect of long incubation recesses based on the best survival model indicates that in all countries except Finland, where no nest was predated, the daily survival rate decreased as the breeding season progressed and that a higher daily number of long incubation recesses increased the daily survival probabilities, especially in Estonia and France, the two countries with the lowest daily survival rates (Fig. 5.6).

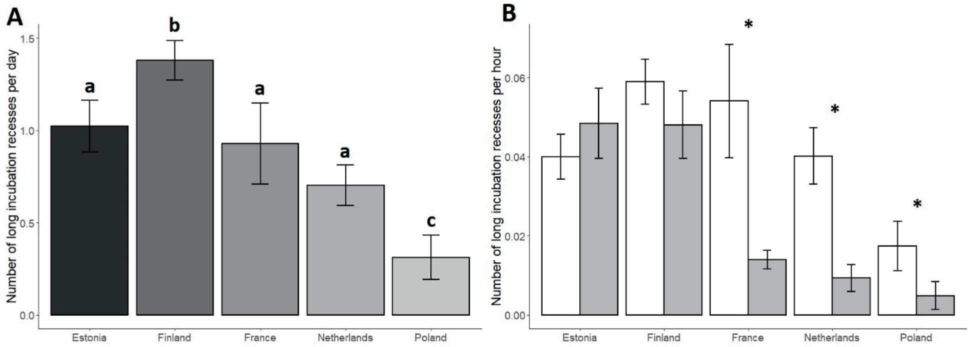


Figure 5.4. (**A**) The average number of long incubation recesses per day in the different sampled countries. (**B**) The average number of long incubation recesses per hour between day and nighttime. In both plots, the interval lines represent the standard error. White and grey bars represent day and nighttime respectively. Different letters represent statistical significance between countries. Asterisk (*) represents statistical significance between the day and nighttime period. Note that higher latitude countries have longer daytime.

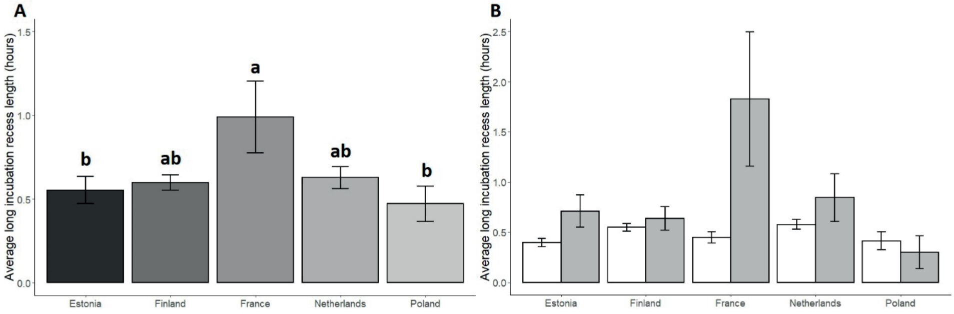


Figure 5.5. (**A**) The average length of a long incubation recess in the different sampled countries. (**B**) The average length of a long incubation recess during the day and nighttime. In both plots, the interval lines represent the standard error. White and grey bars represent day and nighttime respectively. Different letters represent statistical significance between countries. Asterisk (*) represents statistical significance between the day and nighttime period. Note that higher latitude countries have longer daytime.

DISCUSSION

Our results suggest that Godwit breeding couples that regularly leave the nest for longer periods of time have higher daily nest survival probabilities. Two of the best nest survival models included a long incubation recess variable. Couples displaying this type of behaviour may therefore be more successful in hatching their eggs than couples that spend a larger proportion of their time incubating. Furthermore, model outcomes suggest that the effects on daily nest survival rates of more or less frequent long incubation recesses can be as large as the differences in survival rates between study areas in the different countries (Fig. 5.5). The daily total time, frequency, and length of long incubation recesses differed significantly between countries, but we did not find any indications that they were higher in countries with high predation rates. Although such a country-level comparison is not very conclusive, the fact that none of the examined nests in Finland were predated but breeding couples still took long and frequent incubation recesses runs strongly counter to our first hypothesis.

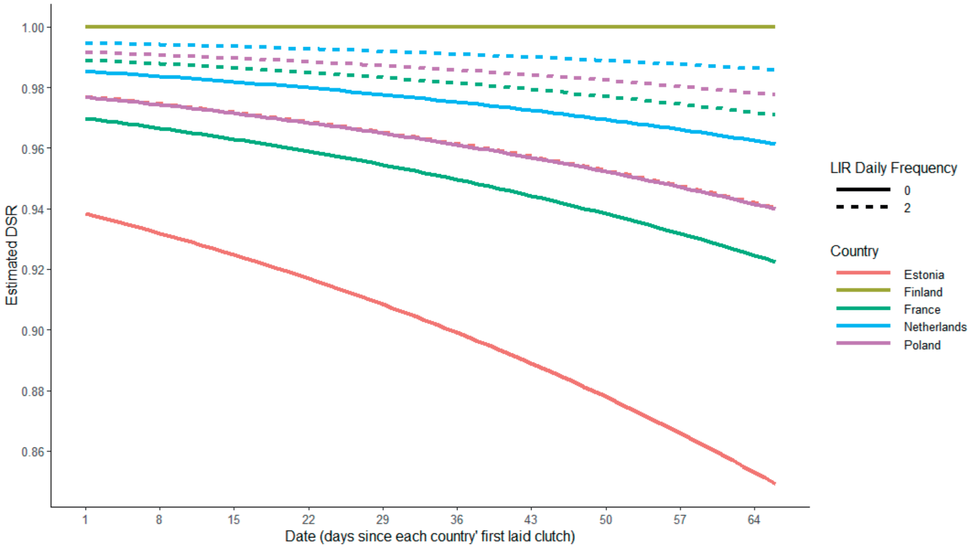


Figure 5.6. An illustration of the highest ranked nest survival model from the set of models in Table 5.2 section B. Relationships are estimated based on either zero or two long incubation recesses performed per day (continuous and dashed lines, respectively). Note that the dashed line for Estonia is covered by the continuous Polish line. Similarly, the dashed and continuous lines for Finland overlap each other, because nests in this country had 100% survival.

The predation rates observed in this study are in line with what has previously been reported: very high predation rates in Estonia (Kaasiku *et al.* 2022), very low predation rates in Finland (Pakanen *et al.* 2011), and about half of the clutches being predated in both France and Netherlands (Teunissen *et al.* 2008a, Kentie *et al.* 2015). For the fenced population in Poland, nest predation rates were about half of the rates recently reported for unfenced clutches in this country (35% compared to 70%; Ławicki & Kruszyk 2011, Niemczynowicz *et al.* 2017). Although we lack direct observations of Godwits leaving the nest due to an approaching predator, such apparent nest-defence behaviour has recently been documented in other wader species breeding in the same general areas as the Godwits in Estonia in this study (Kaasiku *et al.* 2022); camera traps employed to identify wader nest predators in the vicinity of the nest captured incubating Northern Lapwings (*Vanellus vanellus*) and Common Redshanks abandoning their nests for several hours when a Eurasian Fox or invasive Golden Jackal (*Canis aureus*) was roaming the area (Kaasiku T. pers. obs.). Leaving the nest generally increases clutch incubation time (Cervencl *et al.* 2011) and consequently clutch predation rates, which suggests that birds only leave the nest when they are forced to. This lends support to our hypothesis that the majority of our identified long incubation recesses might have been caused by roaming predators. However, our study does not examine direct links between predator presence or predation pressure and long incubation recesses, and care should be taken in interpreting these results. It is likely that birds might leave the nest unattended for longer periods for other reasons as well, such as foraging opportunities (Bulla *et al.* 2015), local cattle disturbance in grazing sites (Durant *et al.* 2008b), weather conditions (Smith *et al.* 2012), or the occasional human presence inside some farmland locations (Silva-Monteiro personal observations).

Nest survival probabilities decreased during the course of the breeding season, a finding consistent with previous studies on this species (Kentie *et al.* 2015, Niemczynowicz *et al.* 2017). Additionally, the patterns observed across and within countries elicit some speculation about which type of predator may have caused differences in long incubation recesses. For example, couples breeding in Estonia and Finland had longer incubation recesses during the nighttime period compared to the other countries, which all had significantly longer incubation recesses during the daytime period. Because mammals are known to roam breeding areas mainly during the nighttime (Laidlaw *et al.* 2019, Kaasiku *et al.* 2022), this could suggest that local predation pressure by mammals was higher in Estonia and Finland than in the other three countries. This aligns with our finding that couples breeding in the fenced Polish area (and thereby protected against large mammalian predators) all had incubation recess variables that were significantly lower compared to the other countries.

Our observation that clutches were incubated on average 95% of the time is slightly higher than previous reports for this species, with 89% observed in Hungary (Hegyi & Sasvári 1998) and 92% in a Dutch nature reserve (Kleijn & Bos 2010). The latter studies were done through direct observations during the daytime only, which in the Netherlands could have led to a slight underestimation of the proportion of time spent on the nest (Fig. 5.3B). The average length of long incubation recesses was 37 minutes and was very similar across countries. We believe this measurement was likely influenced by the 20-30 minute sampling interval of the thermologger, which did not record shorter recesses. Nonetheless, it does indicate that even though long incubation recesses of 40-60 minutes are rare in our sampled populations, they are still relatively common compared to studies of other wader species in which recesses were usually shorter than 10 minutes (Sládeček *et al.* 2019, Meyer *et al.* 2020). Only the clutches in France during nighttime are an exception, with on average almost two-hour-long incubation recesses. This was caused by some specific incubating couples performing exceptionally frequent and prolonged incubation recesses every night.

In principle, long incubation recesses could also have negative effects on the hatching rate of clutches because frequent absences from the nest may reduce embryo development and growth (Webb 1987, Olson *et al.* 2006) and thus extend the length of the incubation process. This in turn increases the vulnerability of the clutch to roaming predators (Cervencl *et al.* 2011). However, for the 57 clutches that successfully hatched, we found no significant relationship between the daily amount of time spent in long incubation recesses and the incubation duration (Generalized Linear Regression Model assuming a Poisson distribution, Z = 1.02, P = 0.31).

In sum, we find that Black-tailed Godwits display similar behaviour to what has previously been reported for Common Redshanks, regularly leaving the clutch for prolonged periods of time (Cervencl *et al.* 2011). Although it is likely that they do this to evade potential predators, we find little evidence to support the idea that in areas with high predation losses Godwits demonstrate this behaviour more frequently. Even in areas with high predation pressure, where two-thirds of the nests are predated, breeding birds remain incubating on the nest for roughly 92.5% of their time. Staying away from the nest likely has negative consequences for hatching success and chick development and we suggest further studies aim to link incubation patterns of wader species with nest and chick survival. It is worth exploring in more detail how the impact of predators modifies the behaviour of ground-nesting birds such as the Black-tailed Godwit.

ACKNOWLEDGEMENTS

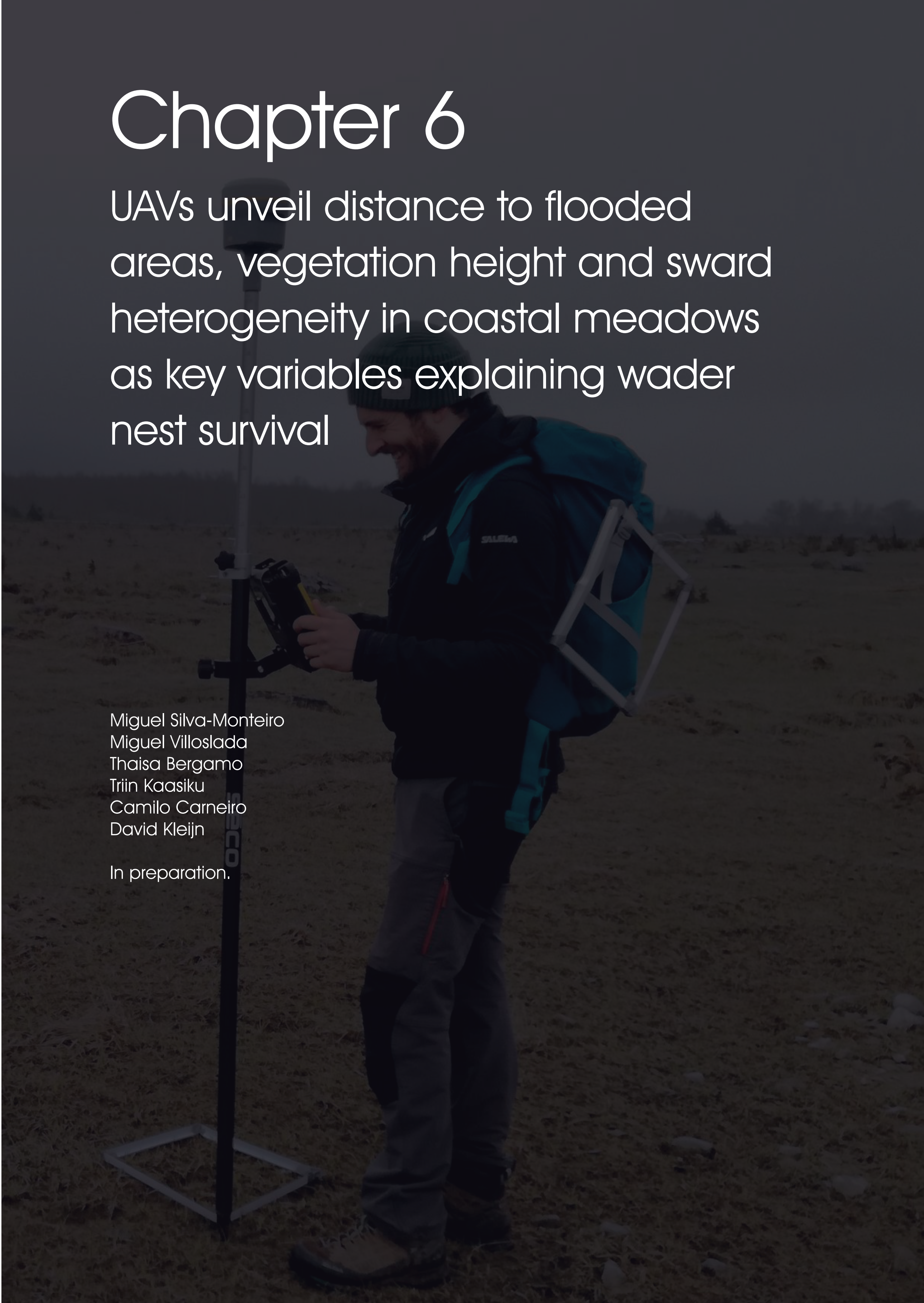
MSM was funded by a grant from Wageningen University & Research to DK (proj. nr. 5160957485). JL and MV and the research infrastructure in NL were supported by the Province of Fryslân and the NWO-Spinoza Premium 2014 to Theunis Piersma. Fieldwork in Poland was funded by the Polish Society for Bird Protection (PTOP) with a support from POIiŚ 2014-2020 grant nr OS.02.04.00-00-0031/16. Thanks to Triin Kaasiku and Ilona Lepik for the support in the fieldwork conducted in Estonia. Thanks to Jean-Guy Robin for the support in the fieldwork conducted in France. Thanks to Piotr Świętochowski and Grzegorz Grygoruk for the support in the fieldwork in Poland.

Chapter 6

UAVs unveil distance to flooded areas, vegetation height and sward heterogeneity in coastal meadows as key variables explaining wader nest survival

Miguel Silva-Monteiro
Miguel Villoslada
Thaisa Bergamo
Triin Kaasiku
Camilo Carneiro
David Kleijn

In preparation.



ABSTRACT

Several ground-nesting wader species rely on Boreal Baltic coastal meadows as their breeding areas. Due to a combination of habitat quality loss and an increase in clutch predation in recent decades, wader populations have sharply declined, with some becoming endangered. Therefore, identifying which grassland characteristics are essential for waders to select their nesting location and which ones enhance their clutch survival probability is vital to implement efficient conservation plans to halt many species' population declines. However, many vegetation variables, such as vegetation height or heterogeneity, can be logistically complex to measure using traditional methods in relatively large areas, especially considering the highly accurate resolution needed. Here, we assessed several sward vegetation characteristics together with other key landscape features by combining innovative UAV surveys with nest survival study, in five key Estonian coastal grasslands for waders. We found that the main four wader species found, Northern Lapwing (*Vanellus vanellus*), Common Redshank (*Tringa totanus*), Common Ringed Plover (*Charadrius hiaticula*) and the Baltic Dunlin (*Calidris alpina schinzii*), do not significantly differ in their nest site selection vegetation height, growth or heterogeneity. Yet, we found that vegetation sward height and heterogeneity surrounding the nest sites within a 2-meter buffer were positively related to nest survival probability. Additionally, the distance between the nest location towards large flooded area ($\geq 20m^2$) was negatively correlated, and all variables affected the species in the wader community similarly, with no variable interacting with a specific species. Our results signal the importance of diverse sward structures and the presence of constantly flooded areas in Estonian coastal meadows, which could be achieved through more diverse grazing management. Moreover, our study highlights the importance of integrating UAV technologies within the animal conservation research field, in order to unveil ecological patterns that could remain hidden using more traditional methods.

KEYWORDS

UAV; Shorebird; Nest site selection; Nest survival; Vegetation heterogeneity; Sward height

INTRODUCTION

Boreal Baltic coastal meadows are a key semi-natural habitat for ground-nesting birds, with many wader species relying on these wetlands as breeding grounds across northern European countries such as Sweden, Finland or Estonia (Ottvall & Smith 2006, Pakanen *et al.* 2011, Leito *et al.* 2014, Rannap *et al.* 2017). These areas have been maintained by traditional and extensive agricultural practices for decades, creating unique open landscapes characterized by very high plant species richness (Joyce & Wade 1998, Burnside *et al.* 2007). However, during the second half of the 20th century, many wader species' populations that rely on those habitats, such as the Northern Lapwing (*Vanellus vanellus*), Common-ringed Plover (*Charadrius hiaticula*) or the Baltic Dunlin (*Calidris alpina schinzii*), sharply declined (Kuresoo & Mägi 2004, Thorup 2006, Hellstrom & Berg 2014). Habitat loss and quality degradation are pointed as the main causes for such declines, with agricultural land abandonment or insufficient grazing pressures rendering most locations unsuitable for ground nesting birds due to shrub and tree encroachment (Amar *et al.* 2011, Douglas *et al.* 2014, Kaasiku *et al.* 2019). Additionally, an increase in nest predation by both native and invasive predators has further contributed to the negative population trends (Manton *et al.* 2016, Krüger *et al.* 2018, Kaasiku *et al.* 2019, Silva-Monteiro *et al.* 2021).

In Estonia, the remaining coastal grasslands for breeding waders are mainly preserved through agri-environmental schemes (AES). They now occur in small, fragmented patches of both original and previously abandoned, currently restored sites (Kose *et al.* 2021). AES compensate farmers for not intensifying local grazing regimes, while locations are kept with at least half their area with relatively short vegetation swards up to 10cm in height. However, sites under the current AES management still have up to one-third of the land with unsuitable quality for breeding waders (Kaasiku *et al.* 2021), with those AES sites often surrounded by fragmented patches of woodland, consequently increasing nest predator presence and enhancing clutch predation probability (Kaasiku *et al.* 2022). Additionally, it has previously been argued that sites continuously grazed with cattle may show declines in grassland structural diversity and heterogeneity (Villoslada *et al.* 2021). Those vegetation characteristics are essential for ground-nesting bird species for their nesting site selection (Verhulst *et al.* 2011) and as a refuge against predators (Schekkerman & Beintema 2007, Laidlaw *et al.* 2015). It is unclear whether the grazing regimes and the management practises that are currently being implemented in Estonia for wader conservation are effective, as continuous attempts to revert population declines have not succeeded for several species (Estonian Environmental Agency 2019). Better insights into which vegetation characteristics wader species select for their nest sites and how this and additional landscape characteristics influence clutch survival could help design more effective conservation practices targeted at grassland breeding waders.

Previous studies exploring the waders nest site selection and/or survival often define contrasting classes of vegetation structure or heterogeneity by surveying and mapping relatively small samples of breeding habitats or by visually inspecting aerial photography (Verhulst *et al.* 2011, Laidlaw *et al.* 2015, Bertholdt *et al.* 2016, Żmihorski *et al.* 2018, Kaasiku *et al.* 2022). Estimates of grassland structural heterogeneity and sward height are then inevitably restricted to the local scale that these methods can be used for. Such estimates may not fully account for the spatial nature and complexity of grassland habitats, therefore hindering the representativity of habitat quality estimates. Satellite data has partially overcome these obstacles, providing wall-to-wall estimates of grassland vegetation height (Kaasiku *et al.* 2021). Yet, the relatively coarse resolution of satellite images may not adequately capture the spatial scales relevant to the habitat vegetation preferences of wader species.

However, recent developments in Unnocupied Aerial Vehicles (UAVs) technologies have enabled wall-to-wall, rigorous assessments of coastal grasslands' vegetation composition, sward height, and heterogeneity, at highly detailed, centimetre-scale spatial resolutions (Villoslada *et al.* 2020, 2021, 2022). These small Ground Sampling Distances (GSD), coupled with the ability to capture multispectral images over relatively large areas, and the processing capabilities of machine learning algorithms, render UAVs highly efficient field tools to map and model habitat structure and quality (Librán-Embid *et al.* 2020, Adade *et al.* 2021). These improvements in data collection also overcome some of the logistical limitations associated with traditional field surveying techniques. Integrating these available technologies into avian conservation research is only a logical step to help create or update necessary conservation actions.

Here, we combine UAV-based assessments of grassland sward height, growth and heterogeneity with wader nest site selection and survival information in five Estonian coastal grasslands. We hypothesize that breeding wader species will have specific nest-site preferences, and we unveil those preferences by comparing the surrounding and landscape characteristics of their nest-site choices against randomly selected points. Additionally, we hypothesize that those nest-site characteristics will also affect their nest daily survival probabilities. Therefore, we employ nest survival models to investigate if the surrounding nest vegetation characteristics or selected landscape-level features, such as nearby forest cover or proximity to flooded areas, have a bigger influence on the survival probability.

METHODOLOGY

Study sites

We conducted our study in five semi-natural coastal grasslands located in western Estonia (Fig. 6.1) between April and June 2020. Sites ranged from 32.8 to 86.2 ha, all managed through AES requirements by cattle grazing (at least 50% of short swards) and known to be key wader breeding areas (Estonian Environmental Agency 2019).

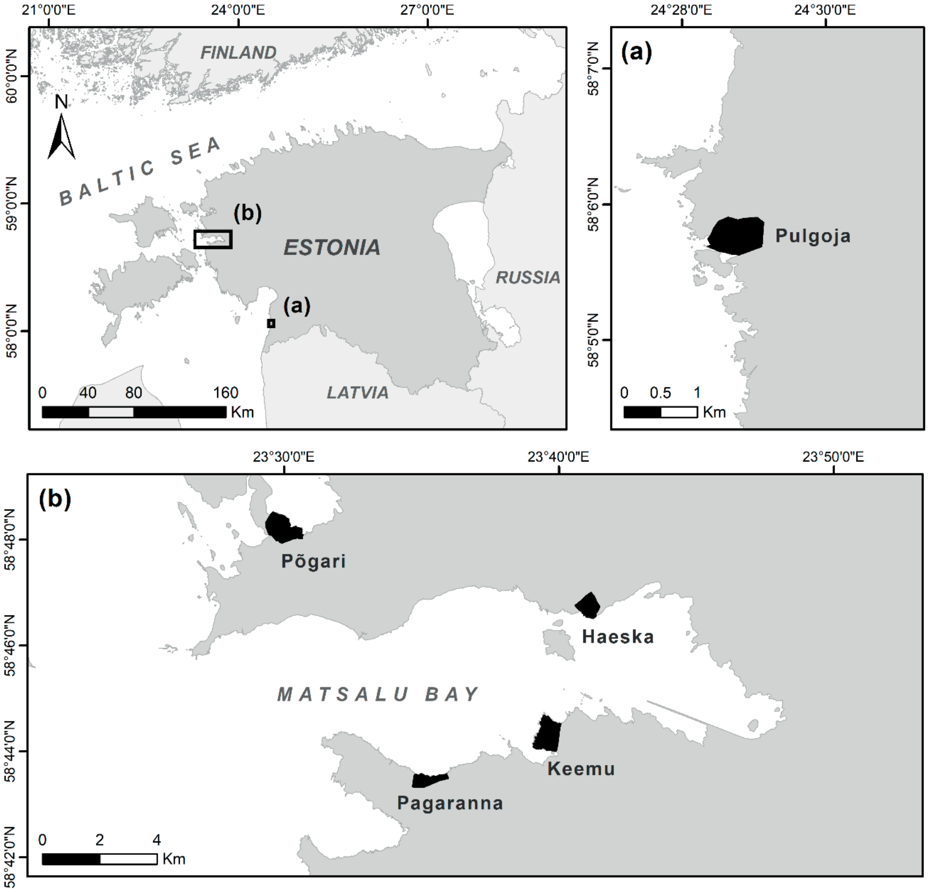


Figure 6.1. Geographical locations of the five sampled coastal grasslands along the western Estonian coastline.

We identified four plant communities commonly occurring in Estonian coastal meadows, which have been previously described in detail: Lower shore (LS), Upper shore (US), Open pioneer (OP) and Tallgrass (TG; Bergamo et al., 2022; Burnside et al., 2007; Villoslada et al., 2021). The composition and distribution of plant communities in Estonian coastal meadows are mainly driven by the brackish conditions in the Baltic Sea and seasonal flooding driven by storm surges (Ward *et al.* 2016). Regular management in the form of grazing or mowing halts succession and avoids reed or juniper encroachment. While LS, US and TG follow a salinity or moisture gradient from the coastline to the upper edge of the meadow, OP appears as low-lying depressions characterized by very high salinity and low vegetation cover.

To capture the full range of sward height and structure, we followed a stratified random sampling approach and in each study site we estimated vegetation height in 20 locations per plant community. For each estimate, we used a 30 x 30 cm plot and collected five random vegetation height measures within the plot using a ruler at a precision of 1 mm. Measurements were subsequently averaged per plot. The exact plot locations (x, y and z coordinates) were recorded with a Trimble R8s GNSS receiver.

Wader surveys, clutch laying date estimation and fate determination

Nests belonging to wader species (*Charadriiformes)* were thoroughly surveyed and monitored by scanning the landscape using binoculars and walking through the site to flush birds and detect their respective nests (Sutherland 2006). Surveys started at the onset of the local breeding season (April 5th) and were conducted 7 or 8 times per site in a 9-12 day interval. The geographical coordinates of each found nest were fixed using a Trimble R8s GNSS receiver. In each survey, previously found nests were revisited for incubation or fate update. Clutch's laying date estimation followed the egg floatation method (van Paassen *et al.* 1984, Liebezeit *et al.* 2007), where the earliest laying date of two or three measured eggs was considered. We considered the full laying period plus an incubation time of 25, 27, 27 and 28 days for the species Baltic Dunlin, Common-ringed Plover, Common Redshank (*Tringa totanus*) and Northern Lapwing respectively (Kaasiku *et al.* 2022). If a nest did not have a complete clutch (i.e., 4 eggs), and eggs were freshly laid, we would consider the start of the laying date as the current date minus the number of eggs present. Nest fate was considered by inspecting the remains of the nest cup, with a clutch being successful when small eggshell fragments were located inside the nest cup and predated when no eggs nor remains could be found inside the nest cup or egg remains were found in the vicinities of the nest cup before the predicted hatching date (Green *et al.* 1987). Clutches that failed to survive due to other reasons besides predation (e.g. abandoned, flooded) were excluded from our dataset. Because we were interested in testing differences between species we also excluded the four observed Black-tailed Godwit (*Limosa limosa lim*osa) nests from our dataset due to the small sample size.

UAV surveys and modelling of vegetation height and sward complexity

Each study site was surveyed twice using a Sensefly Ebee X equipped with a Parrot Sequoia 1.2 megapixel monochromatic multi-spectral sensor and a senseFly S.O.D.A camera. The first set of flights took place on May 2nd-5th whereas the second set was on June 4th-7th. We collected both multispectral and RGB images at a GSD of 10 and 3.5 cm per pixel respectively. Multispectral images were collected in four spectral bands: Green (530–570 nm), red (640–680 nm), red edge (730–740 nm) and near-infrared (770–810 nm). The multispectral sensor was radiometrically calibrated with an Airinov calibration panel before each flight. Once collected, we increased the positional accuracy of all images in eMotion 3® applying a post-processed kinematic (PPK) correction process, based on RINEX observation and navigation files from the ESTPOS Estonian GNSS-RTK permanent stations network. Finally, we built RGB and multispectral orthomosaics in Pix4D v.4.3.31®, totalling five orthomosaics per study site.

To predict vegetation height, we generated two distinct datasets from the UAV images: vegetation indices based on multispectral data and a digital surface model based on RGB data. We used the multispectral orthomosaics to compute 13 vegetation indices (VIs; Supplementary Information Table S6.1). VIs reflect spectral information related to essential ecosystem structures and functions such as vegetation fractional cover, gross primary productivity or water content (Camps-Valls *et al.* 2021). The choice of VIs in this study was based on their ability to accurately predict above-ground biomass in coastal meadows (Villoslada *et al.* 2021). To complement the spectral information conveyed by VIs, we also computed a digital elevation model (DEM) at each site. Microtopography in coastal meadows is closely related to soil moisture gradients, salinity, availability of nutrients and ultimately, vegetation productivity (Ward *et al.* 2016). We generated the DEMs using the Structure-from-Motion (SfM) and Multi-View stereo photogrammetry algorithms integrated into Pix4Dmapper (Smith *et al.* 2015). Within this step, the RGB images are transformed into photogrammetric 3D point clouds through common key points selection, point cloud extraction and point cloud densification. We imported the 3D point clouds into CloudCompare v2.11.3, where we used a Cloth Simulation Filtering (CSF) algorithm (Zhang *et al.* 2016) to sort points as “ground” or “outliers”. We deleted points classified as outliers and interpolated ground points to generate DEMs with a resolution of 10 cm/pixel, matching that of the multispectral orthomosaics.

Finally, we modelled vegetation height at both dates and each study site using a Random Forest regression algorithm (Breiman 2001) with the “randomForest” (Liaw & Wiener 2002) and “raster” packages in R v4.1.2 (Hijmans *et al.* 2015). The RF key parameters “Ntree” and “mtry” were set to 600 and 4 respectively, based on the good performances obtained in previous studies (Villoslada *et al.* 2021, 2022). We used the 13 vegetation indices and the DEMs as explanatory variables and 50% of the field samples as the training dataset. We tested the accuracy of results with the remaining 50% and used the explained variance (R^2) and Root Mean Squared Error (RMSE). We assessed the prediction performance of each explanatory variable using the per cent increase in Mean Squared Error (MSE; Breiman, 2001).

We adopted the methodology proposed by Villoslada et al. (2021) to estimate sward heterogeneity. Here, we refer to sward heterogeneity as changes in the distribution and arrangement of aboveground plant material (Laca & Lemaire 2000). We applied the Mean Shift clustering routine (Comaniciu & Meer 2002) to each of the vegetation height maps in QGIS v.3.16.0. The Mean-Shift segmentation algorithm groups together adjacent pixels with similar values by iteratively assigning each pixel with a peak of the image probability density (Zhou *et al.* 2011). The Mean-Shift clustering routine is an unsupervised segmentation technique and does not require a priori knowledge of the number of output clusters (Comaniciu & Meer 2002). The clustered above-ground biomass maps were further analysed using the Patch density index (Pd), calculated as the number of distinct vegetation patches per circular polygon area through the “landscapemetrics” package in R (Hesselbarth *et al.* 2019). In this study we use Pd as a proxy for the sward structural heterogeneity: larger variability in above-ground biomass within the sward corresponds to a higher Pd value.

Landscape Variables

Additionally, we calculated the percentage of forest area cover within a 1 Km radius and the distance towards large flooded areas of all nests. Forest patches were extracted from the Estonian Land Board (2020), whereas flooded areas and seawater were classified using the UAV imagery obtained in the surveys. We created a binary (water vs non-water surfaces) training/validation dataset of 50 samples with a split sample of 50%/50%. The samples consisted of 50x50cm polygons manually digitized using the RGB image of the first UAV survey as a basis. For the classification of the flooded surfaces, we used the 23 vegetation indices as co-predictors in a classification RF with “ntree” set to 600 and “mtry” set to 4. We then filtered out all flooded surfaces with an area of less than 20 m^2.

Statistical analyses

We used a set of habitat variables known to affect both nest site selection and respective clutch survival probabilities to explore potential differences between wader species and the whole breeding wader community. For each surveyed nest we extracted the following variables: (i) vegetation sward height detected during the first UAV survey; (ii) vegetation sward height growth, by subtracting the vegetation sward height of the first UAV survey from the second; (iii) patch heterogeneity index, the density of distinct vegetation microhabitats patches per area unit; (iv) distance to a large flooded area (≥20 m^2) and; (v) the percentage of forest cover in a one-kilometre buffer. Variables i-iii were calculated using the data gathered from the UAV surveys by estimating the average of all cells that fell inside a two-meter circular buffer around the geographical coordinates of each nest.

Other buffer areas (10cm and 50cm) were tested and we found no substantial differences between estimated averages of both vegetation height and growth (see Supplementary Information Fig. S6.1 for more details). Therefore, we decided to use the two-meter buffer as we believe it to be a more ecologically representative area that wader species inspect for the selection of their nest site (Cunningham *et al.* 2016).

Because vegetation sward height and growth depend on a multitude of environmental variables (e.g. rainfall, temperatures; Lieth, 1975), and can change within weeks, we only used clutches that were laid between two weeks prior and one week after the first UAV survey for each site in our analyses, as nests laid beyond those dates would probably select nest locations according to vegetation values and indices already not captured by our UAV surveys.

To unveil potential species-specific nest site preferences, we compared the average estimates of the selected nest-surrounding vegetation characteristic variables (i-iii) against random points. Random points were generated in QGIS v.3.16.0, equal to the number of wader clutches found in each site. We used generalized linear mixed models with the three variables of interest as our response variables and a control variable (real nest vs random point) with interaction with wader species (including random points) as a fixed factor to infer possible differences between species and/or random points. We additionally included the study site as a random factor. Models were created using the "lme4" package (Bates *et al.* 2015) in the R programming environment (R Core Team 2020). In case the control variable showed a significant effect, we searched for significant differences within the wader species variable with a post hoc contrast analysis using the "emmeans" package (Lenth *et al.* 2018).

Moreover, we explored if the three vegetation variables, together with the two landscape-level variables (distance to flooded area and percentage of tree cover) influenced daily nest survival probabilities (Mayfield 1975). Daily survival rates were estimated using survival models in MARK (White & Burnham 1999) and the R Package RMARK (Laake 2013). We additionally included wader species as a covariate to test if survival probabilities varied between species and also the interaction of species with the other five environmental variables to inspect if the survival of individual species is differently affected by them. Initially, we examined whether daily nest survival probabilities differed along the selected window of time by including a null model (no time influence) or time as a linear or quadratic equation. In the next step, survival models were used that included the best-fitted temporal trend model and the remaining habitat variables. We investigated all possible models with a maximum of two covariates to prevent overfitting and ranked according to the corrected Akaike's Information Criterion (AICc) values and weights. A subset of best candidate models was selected that had ΔAICc<2 (Burnham *et al.* 2011) for trend visualization.

RESULTS

We found and monitored a total of 194 wader nests during our surveys. A subset of 101 nests fitted the UAV survey window of time, which was used in further analyses. Nests had an overall 34% clutch hatching success, with the majority belonging to the Northern Lapwing (53%). Clutch hatching success was similar between species (29-40%; Table 6.1) but highly variable between sites (0-86%; Table 6.2). No statistically significant associations were found with the average initial sward height, vegetation growth and patch heterogeneity between the species' nest sites and random points (Fig. 6.2). However, we could still observe subtle non-significant differences between species, such as smaller-bodied species (Baltic Dunlin and Common Ringed Plover) having a narrower preference for lower patch heterogeneity index compared to large-bodied species (Common Redshank, Northern Lapwing; Fig. 6.2).

Table 6.1. Clutch hatching success and predation rates observed with respective sample sizes in surveyed wader species.

Species	Hatched	Predated
Baltic Dunlin	4 (40%)	6 (60%)
Common Redshank	8 (40%)	12 (60%)
Common Ringed Plover	5 (29%)	12 (71%)
Northern Lapwing	17 (31%)	37 (69%)

Table 6.2. Sampled site's clutch hatching success and predation rates observed with respective sample sizes and selected environmental variables' averages estimates (+/- standard error).

Site	Hatched	Predated	Veg. Height	Veg. Growth	Patch Dens. Index
Haeska	0 (0%)	8 (100%)	91.8 +/- 13.5	51.9 +/- 13.0	15.7 +/- 2.4
Keemu	8 (20%)	32 (80%)	44.0 +/-2.9	104.9 +/- 9.9	16.2 +/- 0.7
Pogari	12 (44%)	15 (56%)	35.9 +/- 1.2	52.7 +/- 4.5	26.1 +/- 2.0
Pagaranna	2 (29%)	5 (71%)	67.6 +/- 10.7	56.4 +/- 3.8	20.6 +/- 4.1
Pulgoja	12 (86%)	2 (14%)	133.1 +/- 11.8	107.3 +/- 17.8	44.1 +/- 3.6

The best nest survival model with only temporal trends revealed the time variable to not be critical to explain nest daily survival probabilities (Table 6.3, Section a), with the null model assuming that nest daily survival probabilities remain constant along the explored window of time. Therefore, we did not include the variable in the following nest survival analysis. When adding the other covariates of interest, the best two models (ΔAICc<2;

Table 6.3, Section b) included the covariates “distance to a large flooded area”, “patch heterogeneity index” and “initial vegetation height”. We found little evidence that the nest site vegetation growth and forest area cover influenced the daily nest survival probabilities. Likewise, we found no evidence that daily survival probabilities were different between the analysed species or that the environmental variables affected differently the wader species.

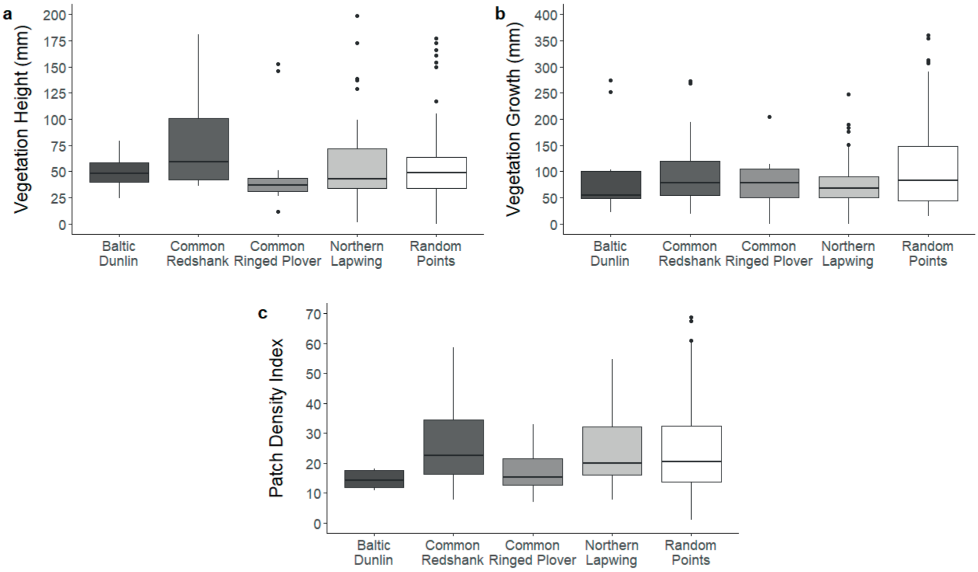


Figure 6.2. The average initial vegetation height (**a**), growth (**b**) and patch heterogeneity (**c**) of nest sites of the four found wader species and of randomly selected points.

An illustration of the effect of distance to a large flooded area at different levels of patch heterogeneity, based on the best survival model, indicates that the daily survival rate decreases with further distance to a flooded area and that a higher sward heterogeneity index at the nest site increased the daily survival probabilities substantially (Fig. 6.3a). Based on the second-best model we observe that a larger vegetation height also increases daily nest survival probabilities similarly (Fig. 6.3b).

Table 6.3. Survival model selection results for best temporal trend (**a**) and the top ten models with the selected environmental variables of interest (**b**). The best model is highlighted in dark grey while all suitable models (ΔAICc<2) are in light grey.

	Model	AICc	ΔAICc	weight	Deviance
a.	Temporal relationship models				
·	Null Model	236.4	0.0	0.4	234.3
·	Quadratic Date	236.6	0.3	0.4	230.6
·	Linear Date	238.3	1.9	0.2	234.3
b.	Environmental covariates models (top 10 models)				
·	Distance to Flooded Area + Patch Heterogeneity	224.7	0.0	0.5	218.6
·	Veg. Height + Distance to Flooded Area	225.7	1.0	0.3	219.7
·	Distance to Flooded Area	228.9	4.2	0.1	224.9
·	Veg. Growth + Distance to Flooded Area	230.2	5.5	0.0	224.2
·	Patch Heterogeneity	232.3	7.7	0.0	228.3
·	Distance to Flooded Area + Species	232.8	8.2	0.0	222.8
·	Veg. Height + Patch Heterogeneity	233.9	9.2	0.0	227.9
·	Patch Heterogeneity + Forest Area Cover	233.9	9.3	0.0	227.9
·	Veg. Growth + Patch Heterogeneity	234.0	9.3	0.0	227.9
·	Patch Heterogeneity + Species	235.3	10.7	0.0	225.3

DISCUSSION

Our findings demonstrate that integrating UAV-based vegetation models with traditional breeding bird surveys can help unveil hard-to-detect landscape characteristics that are related to the nest survival probabilities of wader species. Vegetation height and sward heterogeneity have been previously demonstrated to be important factors influencing wader nest site selection and survival (Groen et al., 2012; Laidlaw et al., 2015; Verhulst et al., 2011). However, most studies couldn't demonstrate clear relationships between nest survival and immediate surrounding vegetation characteristics, although this is usually examined at much larger scales such as 1 km radius buffers (Laidlaw et al., 2020, 2015). Here, due to our more finely detailed vegetation assessments, we present evidence for the characteristics of the vegetation within 2m of the nest site moderating its survival. Nests located in vegetation patches that had higher sward heights and patch heterogeneity levels at the beginning of the breeding season, when the first UAV survey was conducted, had higher chances of survival. The main nest predator in our sites, the Red Fox (*Vulpes vulpes*; Kaasiku et al., 2022), is a species known to forage in important wader breeding areas and opportunistically feeds on clutches that it may encounter (Seymour *et al.* 2010, Meisner *et al.* 2014). Nests in taller and more heterogeneous vegetation were possibly better-concealed and may have been less likely to be detected by predators. Because most nests were predated during night time (personal observations), this could indicate that nest predation in Estonian coastal meadows mainly functions by predators' scent detection, and nests within more heterogeneous vegetation might be better at concealing those scents. These findings contrast with Icelandic semi-natural grasslands that couldn't detect any vegetation characteristics affecting predation probabilities (Laidlaw *et al.* 2020).

Our finding that distance to large water bodies is a major variable for nest survival is in accordance with previous studies, that observed that species such as the Northern Lapwing or the Common Redshank benefit from nesting in proximity to wet features, as it makes it harder for predators to navigate and forage around (Smart *et al.* 2006, Laidlaw *et al.* 2017). However, we failed to find an effect of forest cover, despite forest cover and the distance to the forest edge having previously been identified as key factors related to wader nest survival (Kaasiku *et al.* 2022). This could indicate that the presence of constantly flooded areas is more important than previously assumed, even if observations of red foxes foraging in flooded areas are common within our study sites (Kaasiku personal observations). The lack of negative effect of the forest edge on nest survival could be explained by the relative lack of heterogeneity in this characteristic within our sample compared to Kaasiku *et al.* (2022).

The four main wader species breeding in our sites did not differ in their nesting site preferences and their nesting site characteristics did not deviate significantly from the vegetation characteristics of random points. On one hand, this could suggest that sites are sufficiently managed for their overall breeding habitat selection. On the other hand, this could also have been caused by overgrazing which would create homogenous vegetation in which it is impossible to adequately assess specific vegetation preferences. All species nested within buffers close to an initial vegetation height average of 5cm, with randomly selected points having a similar estimate and rarely above the 10cm threshold. Large-bodied waders (Common Redshank and Northern Lapwing) had a broader nest site use in terms of both vegetation height and heterogeneity. For those species, the optimization of grazing regimes toward larger sward heights (e.g. ≥10cm) in certain areas might be a possible tool to increase their nest survival. Using a more heterogeneous grazing regime (e.g. diverse grazer species with intercalating intensities) could also increase vegetation heterogeneity at the local scale (Tichit *et al.* 2005, Villoslada *et al.* 2021). However, at the beginning of their breeding season, swards of 10-20 cm consist mostly of dead grasses pushed down by the weight of snow, which are usually avoided by birds (personal observations). Thus, a trade-off is probably occurring through the current practised grazing regime: while aiming for shorter swards creates suitable nesting habitat for all species, this suitable habitat might decrease nest survival during the early stages of the breeding season, caused by the seemingly too high predator density (Kaasiku *et al.* 2022).

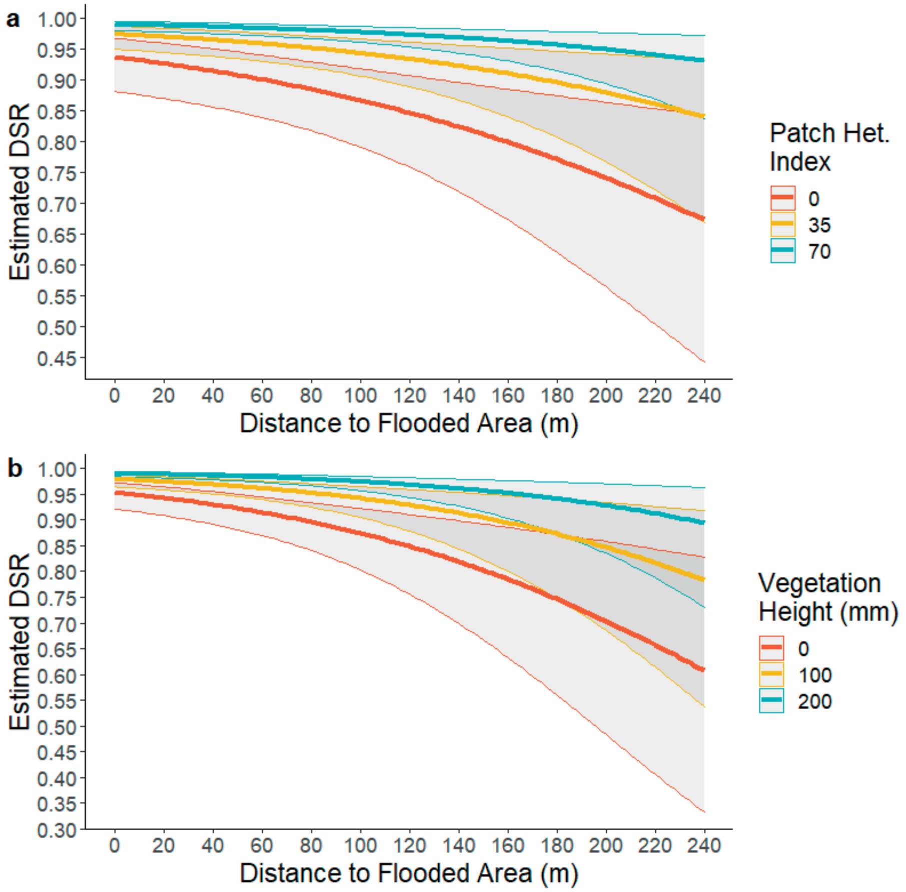


Figure 6.3. (**a**) An illustration of the highest-ranked nest survival model from the set of models in Table 2, Section: The estimated nest Daily Survival Rates (DSR) decrease with further distance to a large flooded area (≥20 m^2) and with lower surrounding patch heterogeneity index; (**b**) An illustration of the second-ranked nest survival model from the set of models in Table 2, Section b: The estimated nest DSR decrease with further distance to a large flooded area (≥20 m^2) and with lower initial vegetation sward heights.

Furthermore, the feasibility of modifications in grazing regimes needs to take into account all the local breeding bird species. Smaller-bodied waders (Common Ringed Plover and Baltic Dunlin) that share the same breeding sites, likely need patches that remain in the current sward structure and heights, as their narrow vegetation selection suggests. Considering that the current vegetation height and heterogeneity at our study sites seem to be suitable for the present local wader community, practices to potentially revert the observed wader population declines should be aimed towards predator control, such as fencing areas (Smith *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022b) or culling predator populations (Bolton *et al.* 2007, Fletcher *et al.* 2010a). This would be especially crucial in sites known to have a higher abundance of predators, as predation seems to be extremely site-specific (Table 6.2). At the same time, management practises aiming for higher vegetation heterogeneity, as shown in this study, could be a tool to support predator control approaches sustainably.

Our study shows the potential for interdisciplinary between UAV technologies and research in animal conservation, with results highlighting the benefits of more accurate data that traditional methods cannot achieve.

ACKNOWLEDGEMENTS

MSM was funded by a grant from Wageningen University & Research to DK (proj. nr. 5160957485). Thanks to Ilona Lepik for the support in the fieldwork. Thanks to Mariana Rodrigues-Morgado for the support in the map creation.

Chapter 7

General Discussion

Miguel Silva-Monteiro

WHY SUCH CONTRASTING GODWIT DENSITIES ACROSS HABITATS?

Data from a total of 415 Godwit breeding populations was collected in Chapter 2, allowing me to calculate and compare breeding density averages between distinct land-use intensity classes. As the widely varying population sizes found across Europe suggest, respective breeding densities also fluctuate immensely along the land-use intensity gradient (Fig. 7.1). Interestingly, the Godwit seems to be one of the habitat generalist waders investigated in detail in Chapter 2 that has more pronounced breeding density variations between land-use classes. Other species, that often share the same breeding areas, such as the Common Redshank or the Northern Lapwing, tend to have lower disparities. This already demonstrates that, although the Godwit can endure contrasting habitats, its breeding success and potential population growth might be exceptionally dependent on some requirements related to a specific land-use intensity.

The highest Godwit breeding densities can be found in medium land-use intensity habitats, which in Chapter 2 are described as extensively managed agricultural land that has low fertilizer input, but due to yearly systematical grazing or mowing regimes, the vegetation composition and structure are substantially modified. This type of landscape is mostly found in northwestern countries, such as the Netherlands, where it is paradoxically considered to be “low” land-use intensity compared to the surrounding, more intensive agricultural land (Groen *et al.* 2012, Howison *et al.* 2018). These sites are categorized as “meadow bird reserves”, as the land management used has the main goal of enhancing and protecting several endangered bird populations (Melman *et al.* 2008, Roodbergen & Teunissen 2014). Nonetheless, these habitats have considerably more human-induced modifications in their vegetation than the extensive farmland found in eastern Europe, most of them included in the low land-use intensity class described in Chapter 2. The reason medium land-use intensity habitats are the most suitable breeding habitats for the Godwit can be better understood when we contextualize the observed decreasing breeding densities in habitats included in other land-use intensity classes.

Godwit breeding densities unsurprisingly drop in half towards high land-use intensity farmland (Fig. 7.1). The main causes these habitats are not able to sustain larger, denser populations have been extensively researched in the past decades, all arising from grassland intensification management (Fig. 7.2, black arrow). Extremely low clutch and chick survival from either direct impacts, such as mortality caused by heavy machinery (Kruk *et al.* 1997, Schekkerman *et al.* 2009, Kentie *et al.* 2013) or indirect impacts, such as reduced accessibility to invertebrate prey food (Mccracken & Tallowin 2004, Kleijn *et al.* 2010) or lack of vegetation cover against predators (Schekkerman & Beintema 2007), turn these sites unattractive for unsuccessful breeding couples, which will disperse in following seasons, especially towards patches of lower land-use intensity (Kentie *et al.* 2014). Additionally, the recruitment of juvenile individuals into the area will also decrease, as insufficient fledglings are produced on-site, and the absence of more experienced couples, often used as a proxy to infer the breeding site quality, further contributes to larger natal dispersal distances (Kentie *et al.* 2014). However, these farmland habitats are still used by many couples, probably due to a lack of better alternatives or by their proximity to higher quality patches of lower land-use intensity, making it difficult for them to distinguish or avoid these areas during the whole breeding season (Groen *et al.* 2012, Kentie *et al.* 2015).

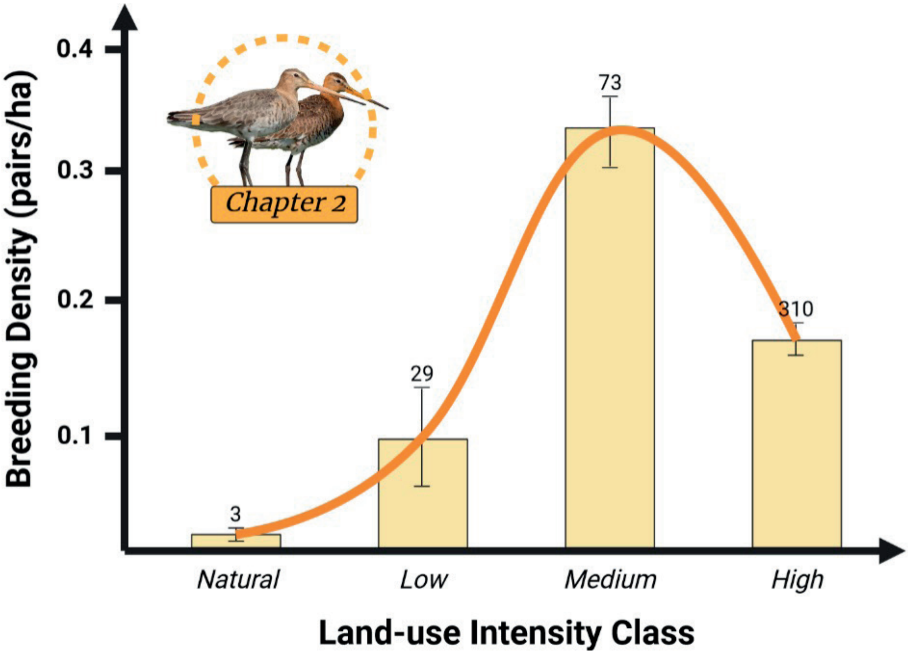


Figure 7.1. Average Godwit breeding densities along the land-use intensity gradient classes based on Chapter 2. The numbers above bars represent sample sizes while error bars represent standard error intervals. The orange bold line models the hypothetical breeding density fluctuation across the land-use intensity gradient.

Chapter 3 demonstrates that the abundance of important invertebrate food for chicks increases along the land-use intensity gradient, remaining high even in the most intensified agricultural sites sampled. This indicates that the primary problem of intensified agricultural sites lies in negative effects beyond invertebrate abundances, such as their poor accessibility, due to the difficulty of walking through dense vegetation swards (Kleijn et al., 2010). This is corroborated by the observed movements of GPS-tracked breeding individuals that, besides favouring the lower land-use intensity patches available at the country level, need larger areas to guide their foraging chicks in search of invertebrate food in patches of higher land-use intensity compared to the lower-end (Li *et al.* 2023).

Contrarily to the highest end of the land-use intensity gradient, the decreasing breeding densities towards low land-use intensity and natural habitats remain poorly understood. The lowest breeding densities observed are located in those habitats, with undisturbed bogs and other mires having 30 times fewer couples in an area of the same size compared to medium land-use class habitats (Fig. 7.1). These habitats are extremely under-researched in their importance for many wader species (Bostrom & Nilsson 1983, Fraixedas *et al.* 2017, Rannap *et al.* 2017), including the Godwit, as seen by the low number of breeding populations extracted in the literature review of Chapter 2. However, some variability might still exist that due to the lack of data couldn't be observed, such as potentially higher breeding densities in larger mires (Bostrom & Nilsson 1983) or in populations described in floodplain river islands that were more common in the European landscapes of a century ago (Magi *et al.* 2004). Nonetheless, from the available data, both the found reports and the sampled sites in our study system point to very low breeding densities in mires (Fig 7.1 and Fig 7.3a). The breeding densities increase substantially towards the low-land use intensity habitats, which are regulated by natural flooding processes but differ from the natural land-use class due to their minimal grazing regimes. Still, the breeding densities observed in those habitats, mostly flooded and coastal grasslands located in eastern European countries, remain three times lower than medium land-use intensity habitats, and slightly lower compared to the high land-use intensity farmland habitats.

We can observe a strikingly identical pattern in the breeding density fluctuations across our study system sites when grouping them following the same land-use intensity classification of Chapter 2: a clear peak in the medium class while decreasing towards intense, and the lower and natural classes (Fig. 7.3a). The data in our study system was collected in the period 2017-2019 while the data underlying the literature review from Chapter 2 mainly originated from 1980-2000. This suggests that the effects of land-use management on godwit breeding populations are relatively robust.

Chapters 3 and 4 contributed to understanding the main environmental variables that can explain differences in breeding densities of Godwit across the land-use intensity gradient (Fig. 7.2, green arrow). When exploring the relative importance of the main habitat requirements (Chapter 4), the invertebrate food supply for chicks at hatching time was the best variable to explain the variability observed in the number of breeding pairs a site was able to host. In Chapter 3 we observe that the overall abundance and individual body size of chick invertebrate food are positively correlated with the site's maximum vegetation growth, arguably the most representative variable of land-use intensity (Fig. 7.2, blue line). Thus, we can infer that the Godwit breeding population size and respective breeding density are mainly dependent on the relative abundance of food a site can generate and provide specifically for chicks, during hatching time. The abundance of those ground-active and flying arthropods is low in natural and low land-use intensity habitats, thus becoming poor-quality breeding sites for couples, by potentially conferring lower survival probability to their chicks, as they are especially vulnerable during the first days regarding necessary food as energy input (Beintema *et al.* 1991, Schekkerman & Beintema 2007). It is also plausible that Godwits can infer future invertebrate abundances using environmental cues of the breeding site, and select those which will grant higher probabilities of a larger food supply close to hatching time. However, within countries, we find no significant relationships with the investigated environmental variables, even for countries with contrasting land-use intensities. This provides more support to the first possibility, as the chick survival probability bears more impact on the site's carrying capacity through the species' high breeding site fidelity (Kruk *et al.* 1998).

Nevertheless, although not as central as chick invertebrate food, the abundance of adult invertebrate food during the clutch-laying period, mainly earthworms in our study system, also played a role in explaining the breeding populations of sites. In addition to enhancing reproductive success, areas that can sufficiently provide food for both chicks and adults might be an enticement for more Godwit couples to settle there, especially at the early stage of the breeding season when female Godwits might need a large energy supply to start egg formation (Musters *et al.* 2010). These sites would additionally enable shorter foraging trips for adults, possibly increasing their own fitness as well as increasing their ability to protect their clutches and chicks against predators. This seems to be the case in some countries, where Godwit territories are mostly found in areas with higher soil-dwelling invertebrate abundance, such as Estonian coastal meadows (Leito *et al.* 2014), while in other countries, such as the Netherlands, Godwit breeding densities do not seem to correlate with the abundance of soil-dwelling invertebrates (Verhoeven *et al.* 2022a). However, in the last case, the study analyses sites where the abundance is overall high compared to other countries where most sites are completely empty of soil-dwelling invertebrates (e.g. Finland, Poland, Estonia). This further demonstrates why cross-continental analyses can be appropriate for understanding whether certain variables are relevant outside certain geographically limited contexts.

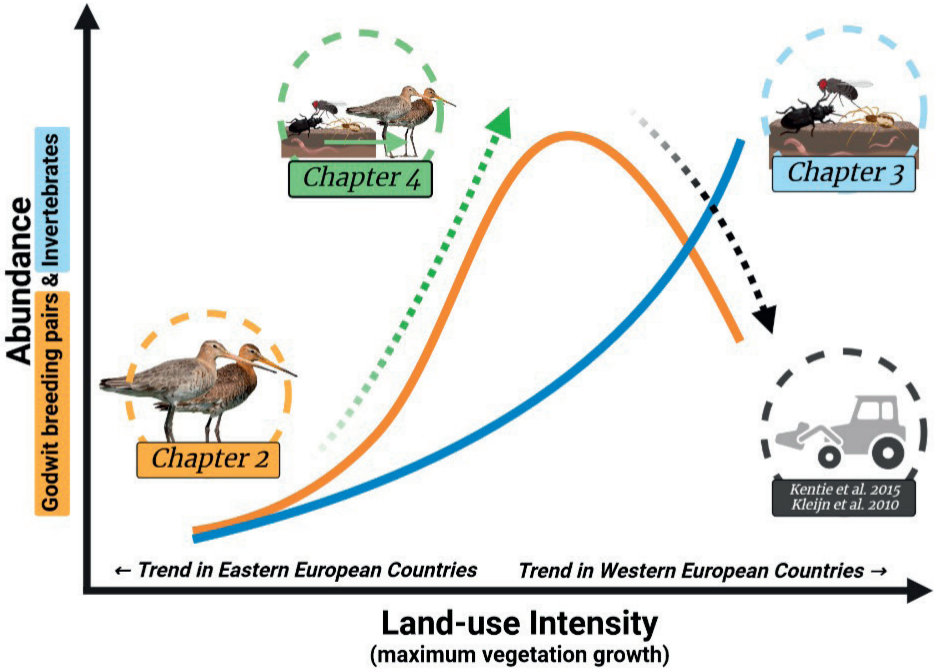


Figure 7.2. Conceptual model demonstrating the relationships between the land-use intensity gradient, defined as the maximum vegetation growth a breeding area can generate, with the abundance of Godwit breeding pairs (orange bold line) and abundance of invertebrate communities (blue bold line). While the drop in Godwit breeding pairs on the more intensified side of the land-use gradient represents the direct and indirect consequences of intensified agricultural activities (black dotted line), the rapid increase in the more natural and extensive side of the land-use gradient is caused by the growing availability of food resources for both chicks and adults (green dotted line). Specific habitats belonging to those two contrasting sides of the land-use gradient can be mostly found in western and eastern European countries respectively.

We can observe that the sampled sites with the highest Godwit breeding densities were extremely abundant in both chick and adult invertebrate food, belonging to both medium and high land-use intensity class habitats (Fig 7.3b, orange and red dots). These locations are characterized by higher vegetation productivity presumably achieved through fertilizer input or controlled water tables. Chapter 3 demonstrates that locations with greater vegetation growth can generate a higher abundance of both invertebrate communities, through cascading effects of nutrient availability (live or decaying plant biomass; Haddad et al., 2000; Siemann, 1998). Yet, smaller, less dense Godwit populations are also able to breed in sites abundant in chick invertebrate food but mostly absent of adult invertebrate food, with these sites belonging to natural and low land-use intensity habitats (Fig 7.3b, blue and green dots).

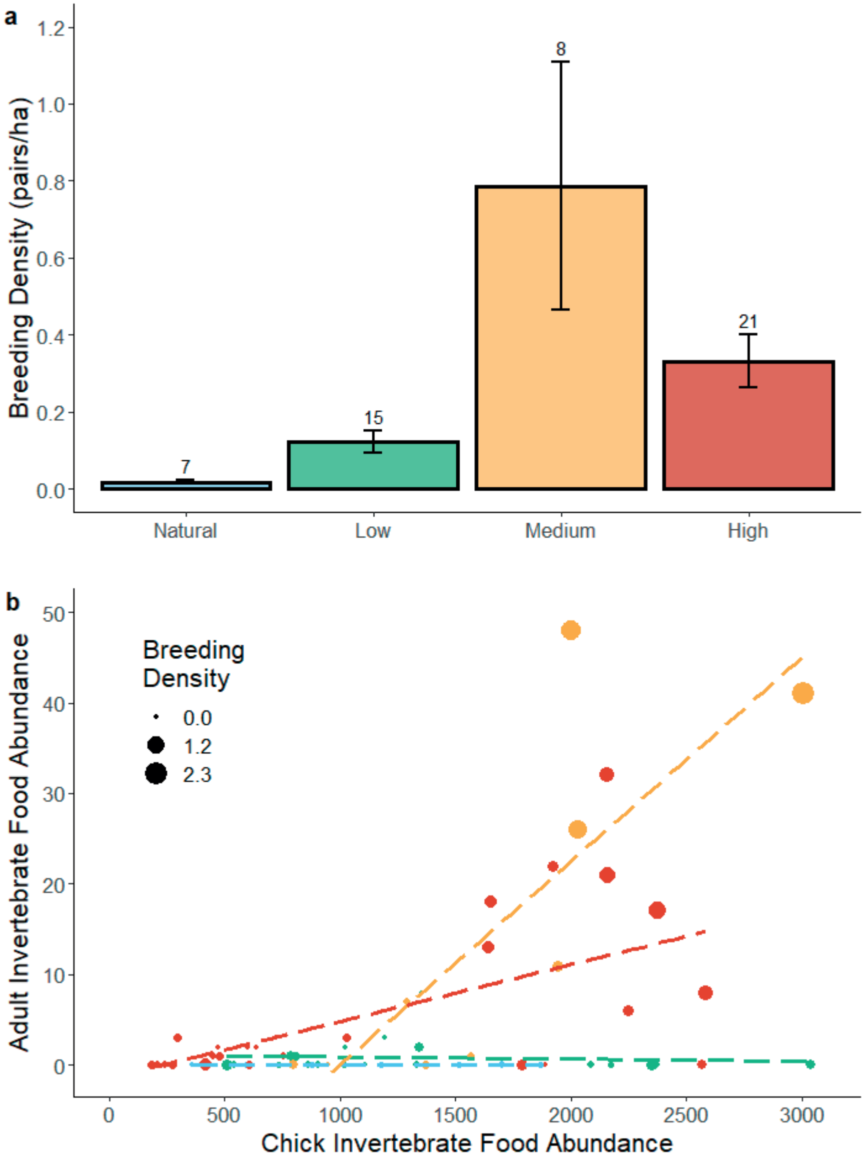


Figure 7.3. (**a**) Average Godwit breeding densities observed in our study system sites, excluding the areas that did not have breeding couples in the respective sampled season (n=51), following the same land-use intensity classes defined in Chapter 2 ("Natural" includes bogs and fens; "Low" includes coastal and floodplain grasslands; "Medium" includes bird meadow reserves and extensive farmland; "High" includes improved farmland with varying levels of fertilizer input). Numbers above bars represent sample sizes while error bars represent standard error intervals; (**b**) The relationship between the relative abundances of chick invertebrate food (ground-active and flying arthropods) at clutch hatching time and adult invertebrate food (soil-dwelling invertebrates) at clutch laying time (28 days apart), is represented by the dotted lines for each land-use intensity class. Study system sites (n=63) are classified according to land-use intensity (in point colours), and the respective Godwit breeding densities observed on site (in point size). Due to small sample sizes within land-use intensity classes, lines are merely illustrative of the relationship.

It is interesting to point out that while we found evidence that food supply for both adults and chicks plays a prominent role in the breeding densities of the species, we did not find such evidence for the studied structural and functional habitat characteristics necessary for the Godwit couple to establish a breeding territory. Whereas the distinct sampled invertebrate communities are dependent on vegetation growth to reach higher abundances (Chapter 3), the abundance of Godwit couples was not significantly related to any environmental variable, such as vegetation growth or soil moisture (Chapter 4). This seems to suggest that Godwits can potentially breed in any open wetland habitat, while food availability will determine its achievable local breeding density.

NEW INSIGHTS INTO GODWIT PREDATOR RELATIONSHIPS

While the relative effect of the habitat requirements was straightforward to sample and inspect, measuring the effect of predator pressure remains a challenging topic. The main predator species of ground-nesting birds in Europe are elusive by nature (Macdonald & Bolton 2008, Teunissen *et al.* 2008a). A study that could assess their local abundances and relative time spent inside breeding areas across our study system would be ideal, but practically unfeasible, considering the diverse range of existing predators and material needed to detect them. Thus, taking advantage of the breeding bird surveys conducted in Chapter 4, I alternatively examined the incubating behaviour of Godwit nests found, by inspecting the frequency and duration of long incubation recesses (≥20 minutes), which could give some insight into some characteristics of the relative predation pressures that the species might locally perceive (Cervencl *et al.* 2011).

Although the sample size of Godwit nests that I could monitor in each country was relatively low, the predation rates observed in Chapter 5 were very similar to what has been previously documented in the same general locations, giving a fair overview of the current nest predation panorama affecting the species along the land-use intensity gradient of our study system (Fig. 7.5). In France and the Netherlands, where the highest end of the land-use intensity gradient is located, the clutch predation rates fell between the interval of 30 to 50%, similar to previous reports (Teunissen *et al.* 2008a, Kentie *et al.* 2015). Additionally, intensified farmland also sampled in Finland demonstrated the lowest predation rates, being completely absent of predation to be more exact, as commonly observed in the Oulu area (Timonen personal observations). However, towards the lower end of the land-use intensity gradient, in habitats such as fens as well as coastal and floodplain grasslands located in Estonia, the predation rates were high (69%). Although in similar habitats in Poland, wader nest predation rates usually have values comparable to the ones observed in Estonia (Ławicki & Kruszyk 2011, Niemczynowicz *et al.* 2017), the ones presented in Chapter 5 are half lower due to the presence of a protective electrical fence around the sampled area, that restricts the entrance of large mammal predators (e.g. Red Fox, *Vulpes vulpes*; Korniluk personal observations).

Surprisingly no relationships between the long incubation recess variables and the relative nest predation rates observed were found, contrary to what has been found in one other wader species (Cervencl *et al.* 2011). All variables analysed in Chapter 5 varied considerably between countries, but seemingly couples that employed this behaviour more often, or for a longer duration, were not consistently from populations that experienced high predation pressures (Fig 7.5a). For example, all nests successfully hatched in Finland but those registered the highest number of long incubation recesses. Moreover, Estonia had a similar frequency of recesses to France, but the predation rates were substantially higher. However, performing long incubation recesses increased the nest survival probabilities, especially in the previously mentioned countries, where predation rates were considerably higher. Thus, although the existence of long incubation recesses as a potential anti-predator mechanism is a novel behaviour description for the species, it seems that it is broadly employed across populations. Because we lack direct visual evidence that all these long incubation recesses were caused by the presence of predators, we cannot assume that they were only executed as direct means to increase nest survival probabilities. It is also possible that those long recesses might be consequences of foraging opportunities (Bulla *et al.* 2015) or unfavourable weather conditions (Smith *et al.* 2012).

Nevertheless, there is visual evidence for other wader species, such as the Common Redshank or the Northern Lapwing, sharing the same breeding areas as the Godwit in the studied Estonian sites, performing this long incubation recess behaviour when in the presence of a roaming predator (Silva-Monteiro & Kaasiku personal observations). Thus, it is highly plausible that the Godwit is also capable to perceive the risk of returning to clutch incubation duty too early when a roaming predator is still nearby. An early return to the incubation would likely facilitate the predator to detect the nest and consume the eggs (Cervencl *et al.* 2011). However, performing this behaviour is still not enough to counteract the large predation rates observed in some breeding sites, as noted by recent research pointing out the continuously increasing predation rates in both western and eastern regions of Europe (Laidlaw *et al.* 2021).

The influence of the Polish electrical fence in the frequency of the long incubation recess behaviour gives evidence of how impactful the presence of especially larger mammal predators can be. The fact that couples breeding within the electrical fence engaged in half less long incubation recesses compared to all the other populations (Fig. 7.5a) could indicate that this behaviour is mostly applied when in the presence of larger predators (e.g. Red Fox), which are the current major nest predators for the species (Teunissen *et al.* 2008a, Ławicki & Kruszyk 2011, Salewski & Schmidt 2022). Nevertheless, we still do not know to which extent these long incubation recesses might negatively affect breeding Godwits. Those indirect impacts can range from development constrictions in the chick embryos (Webb 1987, Olson *et al.* 2006) to increasing predation probability, or even hatching failure by extending the necessary clutch incubation duration (Cervencl *et al.* 2011). Therefore, the consequences of long incubation recesses should be further explored to grasp how directly and indirectly impactful they are to the overall Godwit clutch hatching success.

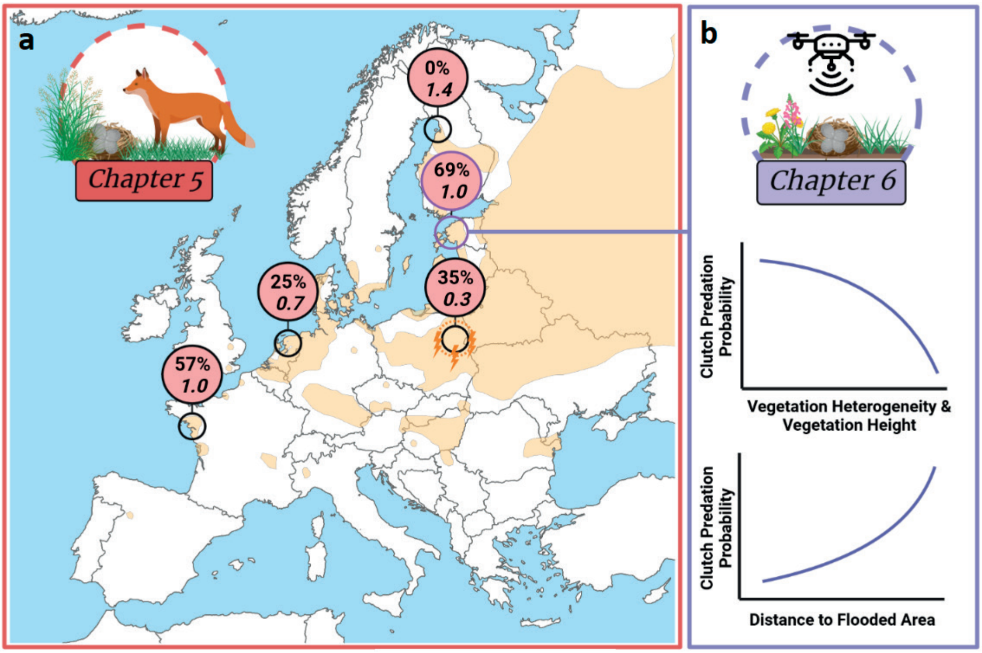


Figure 7.5. (**a**) Godwit clutch predation rates (% of the total sampled nests) and respective average frequency of long incubation recesses performed per day by breeding couples in our study system countries; (**b**) The relationships between the whole wader community's clutch predation probability and the vegetation heterogeneity and height, and distance to large flooded areas (>20m^2) in Estonian coastal grasslands.

Unexpectedly, the environmental conditions affecting wader clutch survival seem not to substantially differ in the low land-use intensity coastal grasslands found in Estonia compared to more intensified agricultural grasslands (Chapter 6). In intensified grasslands, agricultural management often leaves nest locations conspicuous to predators (Kentie *et al.* 2015), while the reduced vegetation heterogeneity and sward heights usually facilitate predators foraging movements (Laidlaw *et al.* 2015). Additionally, a lack of water bodies or flooded areas might further increase predator mobility in wader breeding areas (Laidlaw *et al.* 2017). In the eastern side of Europe, it has been pointed out that afforestation of coastal grasslands, due to the cessation of agricultural activities, leads to an increase in predation rates as the area where mammal predators roam increases substantially, augmenting the chances of finding wader nests close to the forest edge (Kaasiku *et al.* 2022). In Chapter 6 I contribute to the evidence base on the topic. Similar to more intensified grasslands, vegetation sward heterogeneity and height, together with flooded feature distance, are the key variables explaining nest survival in the wader communities breeding in coastal grasslands (Fig. 7.5b). Thus, it is likely that the foraging movement dynamics and clutch visual detection of the main wader nest predator, the broadly distributed Red Fox, might be dependent on the same set of landscape characteristics, although to my knowledge not yet has been tested with a cross-habitat analysis. Additionally, the fact that the grassland's functional and structural habitat characteristics play a dominant role in wader nest survival probability across the land-use intensity gradient, demonstrates how fundamental the management and conservation of those features is in Godwit breeding areas.

Therefore, while the invertebrate food supply is the main habitat requirement that mediates the number of breeding pairs a breeding site can sustain, its inner structural and functional habitat characteristics are potentially the ones that mediate the local predator pressures.

CONSERVATION IMPLICATIONS AND FUTURE RESEARCH DIRECTIONS

Understanding how wader breeding densities fluctuate between distinct habitats, urbanization levels or agricultural management has been widely used to infer where and how to modify certain conditions for the benefit of targeted species (Fuller *et al.* 1986, Reijnen *et al.* 1996, Tharme *et al.* 2001, Jóhannesdóttir *et al.* 2019, Douglas *et al.* 2021). In this thesis, through the same method, I reviewed and added further knowledge of where and through which ecological processes Godwit populations are currently being threatened. Hopefully, this will encourage the application of more effective conservation practices that can lead to stable or growing Godwit populations in Europe.

The remaining available space for wildlife in Europe continues to be threatened by severe biodiversity declines (EEA 2020). Current times demand the most efficient use of the few suitable areas available. A potential major action to revert the overall negative Godwit population trend would be to improve existing habitats to their suitability peak for the species. Targeting the habitat requirement that seems to be primarily driving the density of breeding populations, the chick's invertebrate food resources (Chapter 4), could potentially lead to an increase in their populations using the same areas. This would require modifications in both directions of the land-use intensity: either moderately intensifying agricultural productivity in low land-use habitats or reducing it in highly productive farmland, such as monocultures. However, one should never modify whole landscapes without assessing the potential impacts it might cause on other species and communities that share the same areas. This is especially true for low land-use habitats, mostly located in eastern Europe. There, bird communities have higher species richness, by both species that are more geographically restricted to the eastern European region and species that are practically extinct from western European farmlands and are now threatened in the eastern ones. Species such as the Great Snipe (*Gallinago media*) or the Ruff (*Calidris pugnax*), coexist with the Godwit and are often specialized in those unique types of low land-use intensity habitats (e.g. floodplain grasslands; Chapter 2). The intensification of semi-natural grasslands, either through the appliance of fertilisers, creating ditches or by increasing the grazing regimes, would likely raise the Godwit abundance, but on the other hand lead to a decrease in the breeding populations of those, already threatened, wader species (Zöckler 2002, Korniluk *et al.* 2021).

Hence, ideal land-use modifications would have to be focused primarily on highly intensified grasslands. These would be mostly located in western countries, where local bird communities are less intricate and already subject to heavy, constant habitat modifications (Chapter 2). Decreasing the land-use intensity to medium levels would still enable to have a sufficiently abundant food supply for both chicks and adults (Chapter 3) while bringing some vegetation characteristics, such as sward density and heterogeneity, to a more beneficial level, helping to both reduce the high nest and chick predation pressures and losses due to intensive agricultural activities (Schekkerman & Beintema 2007, Laidlaw *et al.* 2015). The only current strategy to reduce land-use intensity in the most intensive European agricultural landscapes for the benefit of many farmland-specialized species is through Agri-Environmental Schemes (AES), which have not been able to revert the negative Godwit population trends (Schekkerman *et al.* 2008, Oosterveld *et al.* 2011, Kentie *et al.* 2013). Due to AES sites being often integrated within mosaics of agricultural monocultures, continuing to invest solely in the breeding habitat quality of those scattered areas would likely continue to be an ineffective strategy for Godwit conservation. Country and European-level decisions on whole agricultural land-use changes are urgently needed (Pe'er *et al.* 2014, 2022, Clough *et al.* 2020). Although an ambitious goal, the definitive halt and reversion of the negative Godwit population trend is likely dependent on this, as projections for the species populations in these farmland habitats continue to point to overall declines if no further measures are applied (Kentie 2015).

Instead, low land-use intensity habitats should aim to protect current land management that promotes high vegetation sward heterogeneity and plant richness, to continue to be a stronghold for many endangered bird species that rely on them. Yet, even considering those ideal conditions, nest (and potentially chick) predation pressures continue to be at an all-time high for both the Godwit and whole bird communities (Chapters 5 and 6). These already minor Godwit populations are therefore at further risk of completely disappearing in many sites. In order to reduce predator abundance and/or accessibility, the urgent improvement of low land-use grasslands through artificial processes should be considered. Electrical fences that exclude predator presence have shown promising results, with extremely high Godwit fledgling success (Smith *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022b). On the other hand, enhancing some landscape features, such as increasing landscape openness by removing aforestated patches (Kaasiku *et al.* 2019), augmenting the presence of constantly flooded areas through higher control of water tables (Bellebaum & Bock 2008) or implementing more diverse grazing systems to increase vegetation sward heterogeneity (Villoslada *et al.* 2021), could potentially lead to similar increases in Godwit fledgling success as the electric fences demonstrate, without the heavy land modifications and logistically complex maintenance they require. Moreover, this would lend an opportunity to test these methods and verify and compare their cost/effectiveness, while studying many knowledge gaps on the predator pressure dynamics in these little-researched habitats.

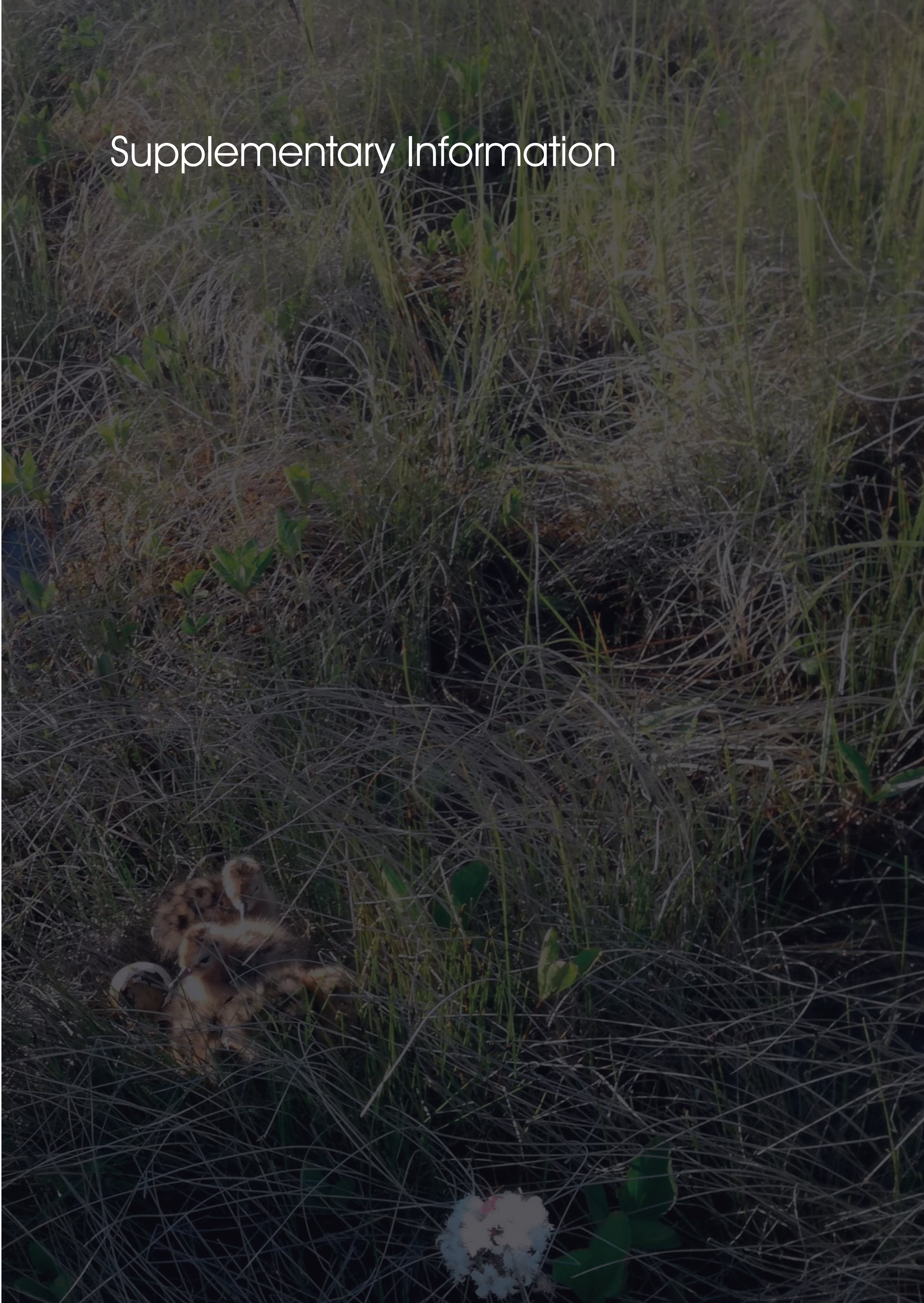
One such major knowledge gap is Godwit chick predation. This thesis, like much of the previous research, focused solely on clutch predation research, due to being more logistically feasible to conduct in several countries. However, chick predation is also a key factor in the current decline of many ground-nesting species (Roodbergen *et al.* 2012, Mason *et al.* 2018). More research needs to be conducted, especially investigating how habitat conditions affect the foraging dynamics, home ranges and survival probability of both wader chicks and their main predators along the land-use gradient.

Likewise, natural, undisturbed habitats remain extremely understudied. These are wader diversity hotspots sprinkled out across northern Europe, and the only breeding refuge found in the continent for many habitat specialists waders, such as the Wood Sandpiper (*Tringa glareola*) or the Eurasian Golden Plover (*Pluvialis apricaria*; Chapter 2). However, many ecological processes affecting breeding waders there remain unknown. How predator pressures, available suitable nesting areas or how wader diets differ in mires compared to grasslands are just some examples. Mires are logistically challenging locations to set up research experiments (Chapter 2). However, these habitats are massively threatened due to the current high demand for peat extraction (Andersen *et al.* 2017) and extremely vulnerable to climate change (Essl *et al.* 2012). Research there should be prioritised, aiming for their legal protection as key bird breeding areas (Fraixedas *et al.* 2017). Additionally, although not a crucial breeding habitat for Godwits, they might act as a refuge, signalling when the nearby grasslands have lost their suitability (Lebedeva 1998).

CONCLUDING REMARKS

The Godwit is a bird that many farmers across Europe recognize as an iconic, integral piece of their farmland landscapes (Vredenbregt 2019). Cooperation between farmers, nature-lovers and researchers has yielded excellent conservation research and led to develop several on-site practices targetting the protection of the Godwit in many countries. However, this thesis unveils that some critical ecological knowledge for the species can only be revealed beyond independent, within-country research, through cross-continental analyses of the species' habitat requirements. Thus, as successful conservation requires collaboration across international borders (Kark *et al.* 2015), the future of the Godwit, and many other endangered animal species, is dependent on how we, as Europeans, cooperate.

Supplementary Information



S2.1. Web of Science search protocol

Search of the Web of Science on 01-11-2018, using the search terms Topic=wader$ AND Topic=(farmland OR wetland OR grassland OR meadow OR peatland OR bog) AND Topic=breeding AND Topic=densit* AND Topic=habitat$ AND Topic=selection AND Topic=communit*.

S2.2. List of references of studies used in the analysis of breeding density data

Altenburg, W. & Hazelhorst, H. (1990). Effecten van grondwaterwinning op de weidevogels van het Noordijkerveld

Altenburg, W. & Jalving, R. (1998). Weidevogels in de relatienotagebieden Sauwerd en Zuidelijk westerkwartier in de periode 1986-1997

Altenburg, W. & Wymenga, E. (1988). Vegetatie en weidevogels in het relatienotagebied Het Reestal: natuurwerenschappelijk onderzoek voor de evaluatie van het beheersplan Reestal

Baines, D., 1988. The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wading birds (Charadriiformes) in northern England. Biol. Conserv. 45, 221–236. https://doi.org/10.1016/0006-3207(88)90141-3

Bakker, N.J. (1986). Kraaien en weidevogels in het Zuidelijk Westerkwartier

Bakker, N.J. (1996). Vegetatie- en weidevogelonderzoek in een aantal Gelderse Uiterwaarden in 1995

Berg, J.J. van den, Gleichman, J.M. & Sanders, G.M. (1988). Broedvogel-Inventarisatie Zuidelijke Gelderse Vallei 1987

Bijtel, H.J.V. van (1991). Inventarisatie van vogels in enkele graslandgebieden in de provincie Utrecht in 1991

Bijtel, H.J.V. van den & Slagboom, T. (1987). Weidevogels in het Noorderpark in 1986

Bontenbal, M.M. (1979). Onderzoek t.b.v. beheer en inrichting van het graslandgebied tussen Harderwijk en Doornspijk 1979

Bostrom, U., Nilsson, S.G., 1983. Latitudinal gradients and local variations in species richness and structure of bird communities on raised peat-bogs in Sweden. Ornis Scand. 14, 213–226. https://doi.org/10.2307/3676155

Bracken, F., McMahon, B.J., Whelan, J., 2008. Breeding bird populations of Irish peatlands. Bird Study 55, 169–178. https://doi.org/10.1080/00063650809461519

Bracken, F., Smiddy, P., 2012. Lowland bogs, fens and reedswamps, in: Bird Habitats in Ireland. The Collins Press.

Brandsma, O.H. (1997). Onderzoek Geen beheer en bodemfauna in het reservaatsgebied Giethoorn-Wannepervee VIII (1992-1996)

Brink, H. van den & Fijn, R. (1989). Effekten van het relatienotabeleid op weidevogels en vegetatie in Groningen

Brown, A.F., Shepherd, K.B., 1993. A method for censusing upland breeding waders. Bird Study 40, 189–195. https://doi.org/10.1080/00063659309477182

Buel, H van & Vergeer, J.W. (1995). Weidevogels van de relatienotagebieden Waterland en Zeevang in 1993

Buel, H. van (1996). Weidevogels binnen en buiten relatienotagebieden in Zeeland in 1995

Buel, H. van (1998). Weidevogels van de relatienotagebieden Nieuwkoop en Driebruggen in 1997

Bureau Waardenburg (1979). Broedvogels en vegetatie in het C.R.M- reservaat Bossche Broek

Colhoun, K., Mawhinney, K. and Peach, W. J. (2015) 'Population estimates and changes in abundance of breeding waders in Northern Ireland up to 2013', Bird Study. Taylor and Francis Ltd., 62(3), pp. 394–403. doi: 10.1080/00063657.2015.1058746.

Damm, T. & Groen, F.M. (2012). Broedvogels in de Bergermeer Inventarisatie 2012

Dijk, G. van(1974). Weidevogeltellingen in Zuidwest-Drenthe.

Dongen, R. van & Buel, H. van (1996). Weidevogels in het "Ruime Jas"-gebied De Venen in 1996

Eyerman, C. (1975). De weidevogels van de Eilandspolder

Fuller, R.J., Reed, T.M., Buxton, N.E., Webb, A., Williams, T.D., Pienkowski, M.W., 1986. Populations of breeding waders charadrii and their habitats on the crofting lands of the outer hebrides, Scotland. Biol. Conserv. 37, 333–361. https://doi.org/10.1016/0006-3207(86)90077-7

Groen, N.M. & Buker, J.B. (1991). Weidevogels in de Schaalsmeerpolder

Grotenhuis, J. (1984). Weidevogels in blok 41 – 24

Guldemond, J.A., Sosa Romero, M.C. & Terwan, P. (1991). Weidevogels, waterpeil en nestbescherming: tien jaar onderzoek aan Kievit Vanellus vanellus, Grutto Limosa limosa en Tureluur Tringa totanus in een veenweidegebied

Hancock, M., Avery, M., 1998. Changes in breeding bird populations in peatlands and young forestry in north east Sutherland and Caithness between 1988 and 1995 . Scottish Birds 19, 195–205.

Hancock, M.H., Grant, M.C., Wilson, J.D., 2009. Associations between distance to forest and spatial and temporal variation in abundance of key peatland breeding bird species. Bird Study 56, 53–64. https://doi.org/10.1080/00063650802648176

Hazelhorst, H. (!995). Weidevogels van laaggelegen gebieden in Salland

Hazelhorst, H. (1996). Weidevogels van het Dalfserveld

Hazelhorst, H. (1997). Weidevogels in enkele laaggelegen gebieden in Overijssel

Hazelhorst, H. (1998). Weidevogels in laaggelegen delen van West-Twente in 1998

Hazelhorst, H. (2000). Weidevogels met een te krappe jas in de Ijsseldelta

Hazelhorst, H. (2001). Weidevogels in de polder Mastenbroek en Haerst-Genne

Hazelhorst, H. (2001). Weidevogels in het Haersterbroek, De Ruiten-Veenekampen en de Tohuislanden in 2001

Heijden, H.G. van der (1997). Weidevogeloderzoek landinrichting Reeuwijk 1996

Heikkila, R., Lindholm, T., Tahvanainen, T., 2006. Mires of Finland – Daughters of the Baltic Sea.

Heinen, M.A. & Mensink, E.G.W. (2005). Weidevogels in het Staphorsterveld en omgeving in 2004

Heinen, M.A. (2004). Weidevogels in de zuidelijke Ijsseldelta en de polders bij Wilsum in 2003

Heinen, M.A. (2005). Weidevogels in lage delen van Salland in 2005

Hollander, H. & Vliet, F. van der (1995). Weidevogelinventarisatie Krimpenerwaard Uitgangssituatie 1995

Holzer, T.J., Beardall, C.H., Dryden, R.C., 1989. Breeding Waders And Other Waterfowl On Suffolk Estuaries In 1988.

Houten, M. van (2002). Broedvogels van de Zuidpolder te Veld in 2002

Hut, H. (1985). Weidevogels: relatienotagebied Sauwerd

Jackson, D.B., Fuller, R.J., Campbell, S.T., 2004. Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (Erinaceus europaeus). Biol. Conserv. 117, 151–166. https://doi.org/10.1016/S0006-3207(03)00289-1

Jeugd, H. van der (1993). Broedvogels van Arkemheen in 1993

Jonkers, D.A. & Leurs, F. (2005). Resultaten van weidevogelinventarisaties in delen van de Eempolders (Eemnes) en polder Zeldert (Hoogland) in 2004

Kleunen, A. van (1997). Weidevogelinventarisatie in (extra) proefvlakken in 1997 ten behoeven van de valuatie van het Convenant Albasserwaard/Vijfheerenlanden

Kleunen, A. van (1999). Monitoring weidevogels Convenant Landbouw-Natuur Zuid-Holland-Oost in 1999

Kuijk, F. & Dijk, G. van (1983). Weidevogeltellingen in West-Utrecht in 1976 met aanvullende gegevens over de jaren t/m 1983

Ławicki, Ł., Kruszyk, R., 2011. Long-term decline of the grassland waders in Western Poland, VOGELWELT 132, 101-108

Larsson, T., 1976. Composition and Density of the Bird Fauna in Swedish Shore Meadows. Ornis Scand. 7, 1. https://doi.org/10.2307/3676169

Lebedeva, E.A., 1998. Waders in agricultural habitats of European Russia. Wader Study Gr. Bull.

Lehikoinen, A., Fraixedas, S., Burgas, D., Eriksson, H., Henttonen, H., Laakkonen, H., Lehikoinen, P., Lehtomäki, J., Leppänen, J., Mäkeläinen, S., Niemimaa, J., Pihlajaniemi, M., Santaharju, J., Välimäki, K., 2016. The impact of weather and the phase of the rodent cycle on breeding populations of waterbirds in Finnish Lapland. Ornis Fenn. 93, 31–46.

Leito, A., Elts, J., Mägi, E., Truu, J., Ivask, M., Kuu, A., Ööpik, M., Meriste, M., Ward, R., Kuresoo, A., Pehlak, H., Sepp, K., Luigujõe, L., Elts, J., Truu, J., Ööpik, M., Kuresoo, A., Pehlak, H., Sepp, K., Luigujõe, L., 2014. Coastal grassland wader abundance in relation to breeding habitat characteristics in Matsalu Bay, Estonia. Ornis Fenn. 91, 149–165.

Leivits, A., Leivits, M., 2016. Using density surface modelling for estimating abundance of breeding birds in heterogeneous mire habitats: a case study in Estonia.

Linde, H.F. van der, Jonkers, A.L. & Diermen, J. van (1975). Weidevogelonderzoek in Eemland

Magi, E., Kastepõld, T., Lotman, A., 2004. Ornithological Monitoring and Wetland Management in Matsalu, Bird Census News.

Magnin. G. (1985). Weidevogels in de AE's 1985: een broedvogelinventarisatie in de Staatsbosbeheerreservaten in de gemeente Slochteren

Mayenburg, F.J. (1987). Ontwikkeling van de weidevogelstand in Zuid-Hollandse SBB Reservaten

Mes, R.G. & Wal, R.J. van der (1982). Sneekermeer: een relatiestudie waterrecreatie en weidevogels

Ministerie van Landbouw en Visserij (1970). Inventarisatie weidevogels in ruilverkavelingen in 1969 en 1970. Ministerie van Landbouw en Visserij

Mischenko, A.L., Sukhanova, O. V., 1998. Waders of the Novgorod Region: Peculiarities of their Distribution and Important Breeding Areas. Int. Wader Stud. 285–290.

Mischenko, A.L., Sukhanova, O. V., 2016. Response of wader populations in the vinogradovo floodplain (Moscow region, Russia) to changes in agricultural land use and spring flooding. Wader Study 123, 136–142. https://doi.org/10.18194/ws.00039

Norris, K. et al. (1998) ‘Is the density of redshank Tringa totanus nesting on saltmarshes in Great Britain declining due to changes in grazing management?’, Journal of Applied Ecology. Blackwell Publishing Ltd., 35(5), pp. 621–634. doi: 10.1046/j.1365-2664.1998.355339.x.

O’ Brien, M., Murray, S., 1998. Estimating the breeding wader populations on farmland in northern England in 1993.

O’Brien, M. and Bainbridge, I. (2002) ‘The evaluation of key sites for breeding waders in lowland Scotland’, Biological Conservation, 103(1), pp. 51–63. doi: 10.1016/S0006-3207(01)00115-X.

O’brien, M., Tharme, A. and Jackson, D. (2002) ‘Changes in breeding wader numbers on Scottish farmed land during the 1990s’, Scottish Birds e, 23(1), pp. 10–21. Available at: https://eurekamag.com/research/010/292/010292990.php (Accessed: 26 April 2021).

Ottvall, R., Smith, H.G., 2006. Effects of an agri-environment scheme on wader populations of coastal meadows of southern Sweden. Agric. Ecosyst. Environ. 113, 264–271. https://doi.org/10.1016/j.agee.2005.10.018

Pakanen, V. M. et al. (2017) ‘Between-patch natal dispersal declines with increasing natal patch size and distance to other patches in the endangered Southern Dunlin Calidris alpina schinzii’, Ibis. Blackwell Publishing Ltd, 159(3), pp. 611–622. doi: 10.1111/ibi.12463.

Pearce-Higgins, J.W., Grant, M.C., 2006. Relationships between bird abundance and the composition and structure of moorland vegetation. Bird Study 53, 112–125. https://doi.org/10.1080/00063650609461424

Pienkowski, M.W., Fuller, R.J., Jackson, D.B., Percival, S.M., 1986. Breeding waders of blackland, moorland and agriculturally improved moorland in the Uists and Benbecula. Scottish Birds 14.

Prak, B.J. (1999). De weide- en akkervogels van Middag-Humsterland in 1999

Radford, D.J., 1995. Breeding waders around the Duddon estuary in 1994. Wader Study Gr. Bull 77, 27–31.

Rebergen, B. (1988). Weidevogels in de Terschellingerpolder

Robin, F. et al. (2012) ‘Current state of Black-tailed Godwits Limosa limosa limosa breeding in France’, Wader Study Group Bulletin, 119, pp. 133–136

Rol, W. (1985). Weidevogels in de Saendertocht

Scharringa, C.J.G. (1984). Weidevogels in het zuidelijk deel van Noord-Holland

Scharringa, C.J.G. (1994). Weidevogels binnen en buiten relatienotagebieden

Shepherd, K., Shepherd, K.B., Stroud, D., 1991. Breeding waders and their conservation on the wetlands of Tiree and Coll, Inner Hebrides. Wildfowl 42, 108–117.

Sim, I.M.W., Gregory, R.D., Hancock, M.H., Brown, A.F., 2005. Recent changes in the abundance of British upland breeding birds. Bird Study 52, 261–275. https://doi.org/10.1080/00063650509461399

Smart, J. et al. (2006) ‘Grassland-breeding waders: identifying key habitat requirements for management’, Journal of Applied Ecology. John Wiley & Sons, Ltd, 43(3), pp. 454–463. doi: 10.1111/j.1365-2664.2006.01166.x.

Smart, J. et al. (2013) ‘Managing uplands for biodiversity: Do agri-environment schemes deliver benefits for breeding lapwing Vanellus vanellus?’, Journal of Applied Ecology. Edited by M. Frederiksen. John Wiley & Sons, Ltd, 50(3), pp. 794–804. doi: 10.1111/1365-2664.12081.

Stillman, R.A., Brown, A.F., 1994. Population sizes and habitat associations of upland breeding birds in the south Pennines, England. Biol. Conserv. 69, 307–314. https://doi.org/10.1016/0006-3207(94)90431-6

Terlouw, R.J.S. & Wijs, W.J.R. de (1989). Weidevogelonderzoek in het landinrichtingsgebied Eemland 1989

Terlouw, R.J.S. (1991). Weidevogelinventarisaties in het Utrechtse westelijk veenweidegebied

Tharme, A.P., Green, R.E., Baines, D., Bainbridge, I.P., O’Brien, M., 2001. The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. J. Appl. Ecol. 38, 439–457. https://doi.org/10.1046/j.1365-2664.2001.00597.x

Uilhoorn, H.M.G. (1999). Weidevogelonderzoek 1997 in Midden-Opsterland en Polder Henswoude

Valkama, J., Currie, D. and Korpimäki, E. (1999) ‘Differences in the intensity of nest predation in the curlew Numenius arquata: A consequence of land use and predator densities?', Ecoscience. Universite Laval, 6(4), pp. 497–504. doi: 10.1080/11956860.1999.11682552.

Veen, P.J. van, Winden, J. van der & Dirksen, S. (1994). Weidevogels in Polder Mijnden, Westbroek c.a. en Polder Achttienhoven in 1994

Verhagen, F. & Verheggen, L. (1988). Weidevogels in de Gouw (West-Friesland)

Visser, D. (1986). Weidevogel-inventarisatie Vijfheerenlanden 1986

Vogelwacht Veenwouden (1980). Weidevogels in het C.R.M.-reservaat 'Het Houtwiel', Gemeente Dantumadeel (1972-1980)

Weijer, W. de (1976). De relaties tussen broedplaatsen van weidevogels en de vegetatie in de Riperkrite

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1981

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1980

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1975

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1979

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1976

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1982

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1978

Werkgroep Ontwikkeling Eemland (1976). Verslag van de vogeltellingen in de broedseizoenen 1973-1974-1977

Wilson, A. M., Ausden, M. and Milsom, T. P. (2004) 'Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions', Ibis. John Wiley & Sons, Ltd, 146(SUPPL. 2), pp. 32–40. doi: 10.1111/j.1474-919X.2004.00371.x.

Wilson, A., Vickery, J. and Pendlebury, C. (2007) 'Agri-environment schemes as a tool for reversing declining populations of grassland waders: Mixed benefits from Environmentally Sensitive Areas in England', Biological Conservation. Elsevier, 136(1), pp. 128–135. doi: 10.1016/j.biocon.2006.11.010.

Winden, A. van der (1986). De weidevogels van het Molenblok (West-Betuwe)

Wymenga, E. & Alma, R. (1998). Onderzoek naar de achteruitgang van weidevogels in het natuurreservaat de Gouden Bodem

Wymenga, E. & Heider, Y. van der (1995). Weidevogels en vliegende hectaren in Friesland in 1995

Figure S2.1. The breeding pairs' abundance of selected wader species in relation to its surveyed area' size. No relationship was found between the two variables in any species. Data distribution indicates that surveyed area' size is also independent of the land-use intensity class. Colors represent different land-use intensity classes from where the data was sampled (see table 2.3). Surveyed area' size was log-transformed for better visualization of the data's distribution. Not all data was possible to be represented in this figure due the lack of surveyed area size information in some articles, which prevented us to calculate the respective number of breeding pairs.

Table S3.1. Selected sampled sites' geographical location and habitat classification. A short description of the local farming practices is given. Agricultural grassland (E): Regular agricultural grasslands that are extensively managed; Agricultural grassland (I): Regular agricultural grasslands that are intensively managed.

Country	Site Name	Geographical Coordinates	Habitat	Local agricultural practices
Estonia	Avaste	58°41' 24,91"N 24°12' 46,23"E	Bog	Natural areas with no agricultural activities or human disturbance. Vegetation mostly comprising of sphagnum mosses.
	Agusalu	59° 4' 22,23"N 27°31' 53,53"E	Bog	
	Muraka	59° 7' 6,86"N 27° 4' 6,27"E	Bog	
	Lihula	58°39' 40,76"N 23°53' 32,41"E	Bog	
	Volla	58°24' 44,14"N 24° 7' 42,60"E	Bog	
	Kiive	58°37' 37,19"N 23°54' 26,67"E	Fen	Natural areas with no agricultural activities or human disturbance. Vegetation mostly comprising tall swards of grass constantly submerged.
	Tuhu	58°33' 56,33"N 23°49' 40,32"E	Fen	
	Pogari	58°48' 7,58"N 23°30' 10,65"E	Coastal Meadow	Herb-rich semi-natural pastures with no fertilizer input. Grazing starts by mid-May.
	Pikla	58°11' 21,75"N 24°28' 15,52"E	Coastal Meadow	
	Puise	58°45' 55,67"N 23°26' 52,17"E	Coastal Meadow	
	Haeska	58°46' 50,12"N 23°41' 0,18"E	Coastal Meadow	
	Esikula	58°48' 53,65"N 22°50' 1,38"E	Coastal Meadow	
	Pulgoja	58° 5' 49,44"N 24°28' 48,39"E	Coastal Meadow	
	Tagukula	58°47' 14,88"N 22°52' 36,70"E	Coastal Meadow	
	Vennati	58°15' 23,87"N 22°20' 0,75"E	Floodplain Meadow	Semi-natural grasslands nearby water streams that are submerged during winter with no fertilizer input. Mowing starts by the mid July.
	Kloostri	58°45' 28,00"N 23°49' 17,97"E	Floodplain Meadow	
Finland	Maijala	64°51' 28,461"N 25°16' 15,072"E	Coastal Meadow	Herb-rich semi-natural pastures with no fertilizer input. Grazing or mowing starts by mid-June.
	Nena	64°53' 20,592"N 25°23' 28,949"E	Coastal Meadow	
	Kuppi	64°54' 33,145"N 25° 7' 46,169"E	Coastal Meadow	
	Routunkarin CM	64°49' 59,710"N 25°20' 25,570"E	Coastal Meadow	
	Kempeleenlathi	64° 57' 7,398"N 25°28' 36,899"E	Coastal Meadow	
	Temmesjoen	64°51' 20,498"N 25°22' 31,965"E	Coastal Meadow	
	Jarvenpaa	64°52' 29,422"N 25° 23' 5,273"E	Agricultural Grassland (I)	Cultivated grasslands, with varying fertilizer inputs ranging 50-200 kg N $ha^{-1}yr^{-1}$. Mowing starts by the beginning of June.

	Routunkarin pellot A	64°49' 14,344"N 25°19' 25,382"E	Agricultural Grassland (I)	
	Monkkasenranta	64°55' 41,502"N 25°26' 54,703"E	Agricultural Grassland (I)	
	Selkamaantien	64° 50' 5,997"N 25°26' 52,477"E	Agricultural Grassland (I)	
	Tupos	64°52' 26,401"N 25°30' 51,370"E	Agricultural Grassland (I)	
	Kylanpuoli	64°55' 23,254"N 25°24' 43,704"E	Agricultural Grassland (I)	
	Teppola	64°56' 11,896"N 25°28' 12,327"E	Agricultural Grassland (I)	
France	La Chausson	46°52' 49,60"N 2° 2' 38,59"W	Agricultural Grassland (E)	Pasture grasslands with no fertilizer input. Grazing starts by the beginning of April.
	Le Daviaud	46°52' 23,58"N 2° 5' 46,84"W	Agricultural Grassland (E)	
	La Boissellerie	46°52 '26,11"N 2° 3' 57,21"W	Agricultural Grassland (E)	
	La Grande ministiere	46°53' 11,71"N 2° 3' 5,76"W	Agricultural Grassland (E)	
	La Voie	46°55' 58,40"N 2° 2' 53,49"W	Agricultural Grassland (E)	
	La Petite Ramoniere	46°51' 0,59"N 2° 4' 25,25"W	Agricultural Grassland (E)	
	La Cavoleau	46°51' 17,39"N 2° 6' 0,69"W	Agricultural Grassland (E)	
	Les Abbayes	46°54' 33,56"N 2° 4' 10,52"W	Agricultural Grassland (E)	
	Dixemerie	46°24' 56,52"N 1°13' 19,53"W	Agricultural Grassland (E)	
	La Vacherie	46°23' 58,03"N 1° 6' 13,48"W	Agricultural Grassland (E)	
	Le Query Cellier	46°51' 17,01"N 2° 5' 27,77"W	Agricultural Grassland (E)	
	Le Giraubeau	46°53' 55,39"N 2° 2' 37,44"W	Agricultural Grassland (E)	
Netherlands	St. - Zuidermeerpolder	52°52' 31,15"N 5°23' 19,25"E	Agricultural Grassland (E)	Meadow bird reserves. Extensive grasslands managed specifically for meadow bird conservation. Low fertilizer input. Grazing starts by the end of April.
	Workumerbinnenwaard	52°59' 18,88"N 5°24' 45,78"E	Agricultural Grassland (E)	
	Makkumermeerpl.	53° 3 '8,31"N 5°26' 15,19"E	Agricultural Grassland (E)	
	Koudum - samenvoeging	52°54' 44,05"N 5°28' 2,47"E	Agricultural Grassland (E)	
	It H. - Feandyk	52°56' 27,61"N 5°29' 34,95"E	Agricultural Grassland (I)	Agricultural grasslands with agri-environment schemes that delay the first annual cut, but does not restrict management such as fertilizer application in any other way. Grazing starts by the end of April.
	Kl. Gaastmeer	52°58' 31,90"N 5°30' 37,65"E	Agricultural Grassland (I)	
	St. - Zuidermeerpolder (b)	52°52' 42,86"N 5°22' 52,73"E	Agricultural Grassland (I)	
	Workumerveld - it Heid.	52°58' 8,94"N 5°27' 51,98"E	Agricultural Grassland (I)	

	It H. - Feandyk (i)	52°56' 31,12"N 5°29' 47,37"E	Agricultural Grassland (I)	Intensive monoculture grasslands. High fertilizer input. Mowing starts by mid-April.
	Kl. Gaastmeer (i)	52°58' 42,36"N 5°30' 31,32"E	Agricultural Grassland (I)	
	Hindeloopen	52°56' 25,81"N 5°24' 44,97"E	Agricultural Grassland (I)	
	Ex. Parregaasterpolder	53° 1' 58,25"N 5°27' 7,42"E	Agricultural Grassland (I)	
Poland	Brzeziny	53°13' 43,43"N 22°30' 49,10"E	Floodplain Grassland	Natural pastures nearby water streams that are submerged during winter. No fertilizer input, although in some years Zajki is occasionally fertilized up to 60 kg N/ha. Most mown once or twice yearly.
	Zajki	53°12' 45,91"N 22°36' 40,69"E	Floodplain Grassland	
	Kaniuki	52°54' 12,47"N 23°17' 49,92"E	Floodplain Grassland	
	Trzescianka	52°55' 5,32"N 23°27' 4,21"E	Floodplain Grassland	
	Zajaczki	52°54' 53,02"N 23° 9' 53,10"E	Floodplain Grassland	
	Zuki	52°35' 43,32"N 23°13' 12,25"E	Agricultural Grassland (E)	Farmland with extensive agricultural practices. Sites usually receive fertilizer input up to 60 kg N/ha. Sites mowed twice yearly and occasionally a third time. Grazing cattle introduced in some sites by mid-June.
	Ogrodniki	53° 7' 6,67"N 23° 1' 4,98"E	Agricultural Grassland (E)	
	Zabiele	53°34' 11,96"N 22°56' 23,69"E	Agricultural Grassland (E)	
	Sokolka1	53°23' 29,79"N 23°30' 54,99"E	Agricultural Grassland (E)	
	Sokolka2	53°26' 52,41"N 23°36' 49,75"E	Agricultural Grassland (E)	
	Grodek	53° 4' 18,35"N 23°40' 5,91"E	Agricultural Grassland (E)	

Table S3.2. Table of generalized linear mixed models where VegGrowth.across (vegetation growth across countries), VegGrowth.within (vegetation growth within countries), SoilMoist.across (soil moisture content across countries), SoilMoist.within (soil moisture content within countries), TempSum.within (daily temperature sums within countries, fixed term) were considered as explanatory variables affecting the response variables. Country was considered as a random factor. The presented models were used to calculate the model-averaged parameter estimates presented in Table 3.1, with selected models having corrected Akaike Information Criterion (AICc) less than 2 from the best model. The degrees of freedom (df), log-likelihood (logLik) and model corrected weight (Wc) are also given. *single model with ΔAICc<2, estimates not averaged.

Response variable	**Model number**	**df**	**logLik**	**AICc**	**ΔAICc**	**Wc**
Ground-active invertebrate abundance	1. TempSum.within + VegGrowth.across	5	-353.44	717.92	0	0.54
	2. TempSum.within + VegGrowth.across + VegGrowth.within	6	-352.37	718.22	0.31	0.46
Ground-active invertebrate biomass	1. TempSum.within + VegGrowth.across	5	-498.37	1007.78	0	0.29
	2. TempSum.within	4	-499.85	1008.38	0.6	0.21
	3. TempSum.within + VegGrowth.across + SoilMoist.within	6	-497.89	1009.25	1.46	0.14
	4. TempSum.within + VegGrowth.across + VegGrowth.within	6	-497.96	1009.39	1.61	0.13
	5. TempSum.within + SoilMoist.within	5	-499.32	1009.67	1.88	0.11
	6. TempSum.within + VegGrowth.across + SoilMoist.across	6	-498.11	1009.69	1.91	0.11
Ground-active invertebrate average body weight	1. TempSum.within + SoilMoist.within	5	-155.37	321.77	0	0.36
	2. TempSum.within + SoilMoist.across + SoilMoist.within	6	-154.16	321.8	0.03	0.35
	3. TempSum.within + VegGrowth.across + SoilMoist.within	6	-154.99	323.46	1.7	0.15
	4. TempSum.within + VegGrowth.within + SoilMoist.within	6	-155.12	323.72	1.95	0.13
Aerial invertebrate abundance	1. TempSum.within + VegGrowth.within	5	-490.24	991.52	0	0.35
	2. TempSum.within + VegGrowth.within + SoilMoist.within	6	-489.26	991.99	0.47	0.28
	3. TempSum.within + SoilMoist.within	5	-490.72	992.47	0.94	0.22
	4. TempSum.within + VegGrowth.within + SoilMoist.across	6	-489.86	993.19	1.67	0.15
Aerial invertebrate biomass	1. TempSum.within	4	-487.9	984.49	0	0.42
	2. TempSum.within + VegGrowth.across	5	-487.45	985.94	1.46	0.2
	3. TempSum.within + SoilMoist.within	5	-487.5	986.03	1.54	0.19
	4. TempSum.within + VegGrowth.across + SoilMoist.across	6	-486.36	986.19	1.7	0.18
Aerial invertebrate average body weight	1. TempSum.within + VegGrowth.across + VegGrowth.within *	6	-42.97	97.9		
Soil invertebrate abundance	1. TempSum.within + VegGrowth.across	5	-99.56	210.16	0	0.39
	2. TempSum.within	4	-100.79	210.25	0.1	0.38
	3. TempSum.within + SoilMoist.across	5	-100.1	211.24	1.09	0.2

Table S4.1. Selected sampled sites' geographical location, habitat classification, surveyed area size and the number of breeding Black-tailed Godwit pairs observed. A short description of the local farming practices is given. All sites without breeding pairs in our study were known to host breeding pairs in the three years prior to our field work, based on observations by the local ornithological researchers involved in this study.

Country	Site Name	Geographical Coordinates	Habitat	Local Agricultural Practices	Surveyed Area (ha)	Breeding Pairs
Estonia	Avaste	58°41' 24,91"N 24°12' 46,23"E	Bog	Natural areas with no agricultural activities or human disturbance. Vegetation mostly comprising of sphagnum mosses.	47.8	1
	Agusalu	59° 4' 22,23"N 27°31' 53,53"E	Bog		111.0	1
	Muraka	59° 7' 6,86"N 27° 4' 6,27"E	Bog		72.4	1
	Lihula	58°39' 40,76"N 23°53' 32,41"E	Bog		616.8	5
	Volla	58°24' 44,14"N 24° 7' 42,60"E	Bog		547.5	2
	Kiive	58°37' 37,19"N 23°54' 26,67"E	Fen	Natural areas with no agricultural activities or human disturbance. Vegetation mostly comprising tall swards of grass constantly submerged.	39.1	1
	Tuhu	58°33' 56,33"N 23°49' 40,32"E	Fen		24.1	1
	Pogari	58°48' 7,58"N 23°30' 10,65"E	Coastal Meadow	Herb-rich semi-natural pastures with no fertilizer input. Grazing starts by mid-May.	25.5	1
	Pikla	58°11' 21,75"N 24°28' 15,52"E	Coastal Meadow		32.1	2
	Puise	58°45' 55,67"N 23°26' 52,17"E	Coastal Meadow		4.7	1
	Haeska	58°46' 50,12"N 23°41' 0,18"E	Coastal Meadow		36.6	1
	Esikula	58°48' 53,65"N 22°50' 1,38"E	Coastal Meadow		36.0	2
	Pulgoja	58° 5' 49,44"N 24°28' 48,39"E	Coastal Meadow		13.3	2
	Tagukula	58°47' 14,88"N 22°52' 36,70"E	Coastal Meadow		13.7	1
	Vennati	58°15' 23,87"N 22°20' 0,75"E	Floodplain Meadow	Semi-natural grasslands nearby water streams that are submerged during winter with no fertilizer input. Mowing starts by the mid July.	70.2	1
	Kloostri	58°45' 28,00"N 23°49' 17,97"E	Floodplain Meadow		27.5	0
Finland	Maijala	64°51' 28,461"N 25°16' 15,072"E	Coastal Meadow	Herb-rich semi-natural pastures with no fertilizer input. Grazing or mowing starts by mid-June.	47.4	2
	Nena	64°53' 20,592"N 25°23' 28,949"E	Coastal Meadow		19.3	4
	Kuppi	64°54' 33,145"N 25° 7' 46,169"E	Coastal Meadow		15.4	5
	Routunkari CM	64°49' 59,710"N 25°20' 25,570"E	Coastal Meadow		47.1	3
	Kempeleenlahti	64° 57' 7,398"N 25°28' 36,899"E	Coastal Meadow		33.2	1

	Temmesjoen	64°51' 20,498"N 25°22' 31,965"E	Coastal Meadow		8.8	3
	Jarvenpaa	64°52' 29,422"N 25° 23' 5,273"E	Agricultural Grassland	Cultivated grasslands, with varying fertilizer inputs ranging 50-200 kg N $ha^{-1}yr^{-1}$. Mowing starts by the beginning of June.	6.6	0
	Routunkari pellot A	64°49' 14,344"N 25°19' 25,382"E	Agricultural Grassland		24.6	2
	Monkkasenranta	64°55' 41,502"N 25°26' 54,703"E	Agricultural Grassland		12.5	5
	Selkamaantie	64° 50' 5,997"N 25°26' 52,477"E	Agricultural Grassland		13.7	5
	Tupos	64°52' 26,401"N 25°30' 51,370"E	Agricultural Grassland		40.0	8
	Kylanpuoli	64°55' 23,254"N 25°24' 43,704"E	Agricultural Grassland		15.6	2
	Teppola	64°56' 11,896"N 25°28' 12,327"E	Agricultural Grassland		19.3	2
France	La Chausson	46°52' 49,60"N 2° 2' 38,59"W	Agricultural Grassland	Pasture grasslands with no fertilizer input. Grazing starts by the beginning of April.	16.1	0
	Le Daviaud	46°52' 23,58"N 2° 5' 46,84"W	Agricultural Grassland		17.4	0
	La Boissellerie	46°52 '26,11"N 2° 3' 57,21"W	Agricultural Grassland		15.6	1
	La Grande ministiere	46°53' 11,71"N 2° 3' 5,76"W	Agricultural Grassland		15.4	0
	La Voie	46°55' 58,40"N 2° 2' 53,49"W	Agricultural Grassland		14.9	1
	La Petite Ramoniere	46°51' 0,59"N 2° 4' 25,25"W	Agricultural Grassland		16.1	2
	La Cavoleau	46°51' 17,39"N 2° 6' 0,69"W	Agricultural Grassland		14.4	2
	Les Abbayes	46°54' 33,56"N 2° 4' 10,52"W	Agricultural Grassland		18.3	2
	Dixemerie	46°24' 56,52"N 1°13' 19,53"W	Agricultural Grassland		25.3	2
	La Vacherie	46°23' 58,03"N 1° 6' 13,48"W	Agricultural Grassland		26.1	0
	Le Query Cellier	46°51' 17,01"N 2° 5' 27,77"W	Agricultural Grassland		15.5	2
	Le Giraubeau	46°53' 55,39"N 2° 2' 37,44"W	Agricultural Grassland		15.2	0
Netherlands	St. - Zuidermeerpolder	52°52' 31,15"N 5°23' 19,25"E	Meadow Bird Reserve	Protected semi-natural meadows with high botanical value managed for meadow bird conservation. Low fertilizer input. Grazing starts by the end of April.	3.5	5
	Workumerbinnenwaard	52°59' 18,88"N 5°24' 45,78"E	Meadow Bird Reserve		16.2	5
	Makkumermeerpl.	53° 3 '8,31"N 5°26' 15,19"E	Meadow Bird Reserve		2.6	6
	Koudum - samenvoeging	52°54' 44,05"N 5°28' 2,47"E	Meadow Bird Reserve		2.3	4

	It H. - Feandyk	52°56' 27,61"N 5°29' 34,95"E	Agricultural Grassland with Agri-environment schemes	Farmland with extensive agricultural practices for biodiversity enhancement. Low fertilizer input. Grazing starts by the end of April.	2.9	3
	Kl. Gaastmeer	52°58' 31,90"N 5°30' 37,65"E	Agricultural Grassland with agri-environment schemes		7.1	5
	St. - Zuidermeerpolder (b)	52°52' 42,86"N 5°22' 52,73"E	Agricultural Grassland with Agri-environment schemes		5.0	2
	Workumerveld - it Heid.	52°58' 8,94"N 5°27' 51,98"E	Agricultural Grassland with Agri-environment schemes		3.6	4
	It H. - Feandyk (i)	52°56' 31,12"N 5°29' 47,37"E	Intensive Monoculture Grassland	Intensive monoculture grasslands. High fertilizer input. Mowing starts by mid-April.	2.8	2
	Kl. Gaastmeer (i)	52°58' 42,36"N 5°30' 31,32"E	Intensive Monoculture Grassland		9.8	3
	Hindeloopen	52°56' 25,81"N 5°24' 44,97"E	Intensive Monoculture Grassland		14.2	5
	Ex. Parregaasterpolder	53° 1' 58,25"N 5°27' 7,42"E	Intensive Monoculture Grassland		10.5	4
Poland	Brzeziny	53°13' 43,43"N 22°30' 49,10"E	Floodplain Grassland	Natural pastures nearby water streams that are submerged during winter. No fertilizer input, although in some years Zajki is occasionally fertilized up to 60 kg N/ha. Most mown once or twice yearly.	4.2	0
	Zajki	53°12' 45,91"N 22°36' 40,69"E	Floodplain Grassland		10.0	2
	Kaniuki	52°54' 12,47"N 23°17' 49,92"E	Floodplain Grassland		10.6	0
	Trzescianka	52°55' 5,32"N 23°27' 4,21"E	Floodplain Grassland		7.1	0
	Zajaczki	52°54' 53,02"N 23° 9' 53,10"E	Floodplain Grassland		5.5	0
	Zuki	52°35' 43,32"N 23°13' 12,25"E	Agricultural Grassland	Farmland with extensive agricultural practices. Sites usually receive fertilizer input up to 60 kg N/ha. Sites mowed twice yearly and occasionally a third time. Grazing cattle introduced in some sites by mid-June.	26.2	2
	Ogrodniki	53° 7' 6,67"N 23° 1' 4,98"E	Agricultural Grassland		13.4	2
	Zabiele	53°34' 11,96"N 22°56' 23,69"E	Agricultural Grassland		14.8	1
	Sokolka1	53°23' 29,79"N 23°30' 54,99"E	Agricultural Grassland		14.3	0
	Sokolka2	53°26' 52,41"N 23°36' 49,75"E	Agricultural Grassland		18.6	3

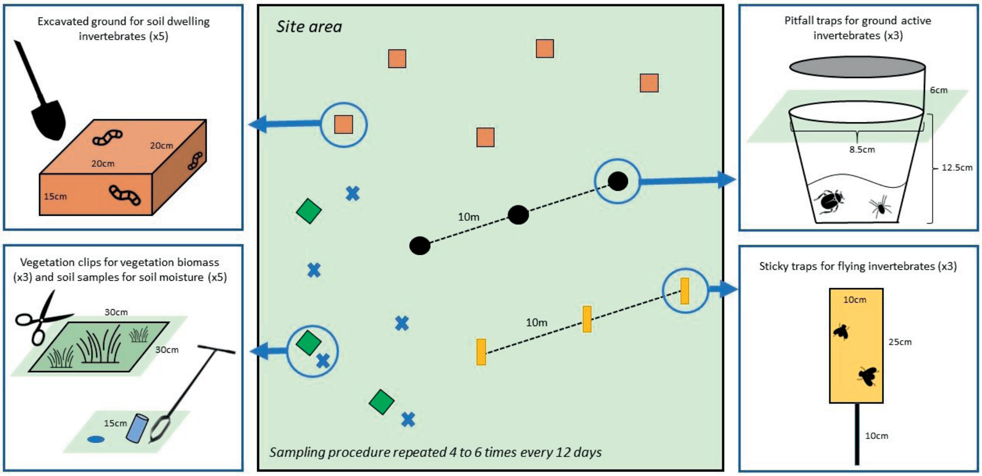


Figure S3.1. Invertebrate and environmental sampling procedure' visual concept.

Table S4.2. Sampled site's average Black-tailed Godwit laying date (LD) and respective environmental variables at that precise date. Bellow ground invertebrate abundance is the average between the two sampled periods.

Country	Site Name	Average Laying Date (Julian)	Vegetation Biomass at LD (g)	Soil Moisture at LD (%)	Above Ground Invertebrate Abundance at LD	Bellow Ground Invertebrate Abundance
Estonia	Agusalu	118	3.6	100.0	68	0
	Avaste	128	4.8	93.6	607	0
	Esikula	130	4.7	62.6	2123	0
	Haeska	117	0.0	57.9	0	0
	Kiive	120	0.0	100.0	3751	0
	Kloostri	128	10.2	71.2	1433	0
	Lihula	128	13.7	100.0	2237	0
	Muraka	127	3.1	100.0	2544	0
	Pikla	136	19.1	48.9	752	0
	Pogari	128	2.6	29.9	1014	0
	Puise	128	7.0	37.0	1060	0
	Pulgoja	128	22.1	67.9	646	1
	Tagukula	128	10.4	46.2	701	0
	Tuhu	116	0.0	100.0	3176	0
	Vennati	127	24.8	60.7	536	0
	Volla	131	0.0	100.0	1064	0
Finland	Jarvenpaa B	132	9.2	46.3	0	0
	Kempeleenlathi	132	13.8	30.9	0	0
	Kuppi	138	15.9	74.1	379	2
	Kylanpuoli B	127	15.7	27.4	102	0
	Maijala	128	18.8	41.0	0	0
	Monkkasenranta	128	21.2	22.4	41	0
	Nena	136	24.4	66.7	831	0

	Routunkarin CM	136	12.8	64.5	615	0
	Routunkarin pellot A	129	9.0	22.4	9	0
	Selkamaantien	127	5.7	40.9	10	0
	Temmesjoen	137	16.3	71.0	462	0
	Teppola B	130	26.5	31.7	42	0
	Tupos	133	18.5	39.8	790	0
France	Dixemerie	104	24.3	26.1	761	1
	La Boissellerie	104	22.7	24.6	597	2
	La Cavoleau	104	28.8	28.4	940	2
	La Chausson	104	34.6	24.5	489	2
	La Grande ministiere	104	26.5	22.8	1016	2
	La Petite Ramoniere	102	25.8	30.9	553	2
	La Vacherie	104	18.2	21.4	959	2
	La Voie	98	18.6	22.7	779	1
	Le Daviaud	104	47.8	31.1	981	3
	Le Giraubeau	104	31.4	25.4	1145	1
	Le Query Cellier	100	23.4	25.3	1091	2
	Les Abbayes	125	50.9	21.3	454	1
Netherlands	Ex. Parregaasterpolder	105	23.4	47.6	827	15
	Hindeloopen	117	24.8	26.4	1938	4
	It H. - Feandyk	109	6.7	43.4	1065	14
	It H. - Feandyk (i)	109	14.1	41.3	1066	19
	Kl. Gaastmeer	108	7.1	41.2	784	4
	Kl. Gaastmeer (i)	114	16.6	41.2	1069	14
	Koudum - samenvoeging	104	3.9	44.9	614	25
	Makkumermeerpl.	109	8.2	44.3	1028	24
	St. - Zuidermeerpolder	105	10.0	43.3	748	17
	St. - Zuidermeerpolder (b)	92	0.3	65.0	496	7

	Workumerbinnenwaard	102	3.5	49.3	491	15
	Workumerveld - it Heid.	111	16.0	41.5	1488	13
Poland	Brzeziny	107	0.9	43.0	314	3
	Kaniuki	107	1.1	55.6	238	2
	Ogrodniki	105	0.3	71.0	365	0
	Sokolka1	107	1.1	68.0	181	0
	Sokolka2	110	2.3	68.7	487	0
	Trzescianka	107	0.8	58.3	322	0
	Zabiele	106	0.0	68.4	150	3
	Zajaczki	107	1.7	58.4	341	6
	Zajki	107	0.0	36.8	0	4
	Zuki	107	0.0	69.3	107	4

Table S4.3. Sampled site's average Black-tailed Godwit hatching date (HD) and respective environmental variables at that precise date. Bellow ground invertebrate abundance is the average between the two sampled periods.

Country	Site Name	Average Hatching Date (Julian)	Vegetation Biomass at HD (g)	Soil Moisture at HD (%)	Above Ground Invertebrate Abundance at HD	Bellow Ground Invertebrate Abundance
Estonia	Agusalu	146	5.8	100.0	1513	0
	Avaste	156	6.8	93.3	597	0
	Esikula	158	23.1	43.3	1330	0
	Haeska	145	14.0	41.7	1017	0
	Kiive	148	13.0	100.0	1869	0
	Kloostri	156	32.7	47.7	1333	0
	Lihula	156	17.5	100.0	879	0
	Muraka	155	6.3	100.0	1177	0
	Pikla	164	27.2	43.9	904	0
	Pogari	156	4.7	27.2	861	0
	Puise	156	12.9	36.5	788	0
	Pulgoja	156	46.9	47.3	810	1
	Tagukula	156	25.3	44.7	540	0
	Tuhu	144	14.1	100.0	1702	0
	Vennati	155	26.2	47.9	736	0
	Volla	159	15.8	100.0	359	0
Finland	Jarvenpaa B	160	14.4	34.4	1889	0
	Kempeleenlathi	160	18.9	69.7	2173	0
	Kuppi	166	16.6	56.4	510	2
	Kylanpuoli B	155	21.7	21.7	185	0
	Maijala	156	15.4	42.4	2370	0
	Monkkasenranta	156	12.3	18.7	418	0

	Nena	164	15.6	60.2	3039	0
	Routunkarin CM	164	15.8	55.9	2088	0
	Routunkarin pellot A	157	12.9	22.8	244	0
	Selkamaantien	155	13.2	28.2	1788	0
	Temmesjoen	165	17.8	67.0	2349	0
	Teppola B	158	25.2	27.3	273	0
	Tupos	161	17.8	34.2	2569	0
France	Dixemerie	132	53.8	17.6	211	1
	La Boissellerie	132	32.7	22.1	452	2
	La Cavoleau	132	42.6	21.5	607	2
	La Chausson	132	27.0	24.3	601	2
	La Grande ministiere	132	37.2	23.8	722	2
	La Petite Ramoniere	130	42.5	20.0	476	2
	La Vacherie	132	37.0	20.2	541	2
	La Voie	126	24.9	16.9	756	1
	Le Daviaud	132	48.1	21.3	474	3
	Le Giraubeau	132	56.0	23.2	637	1
	Le Query Cellier	128	46.5	24.3	1027	2
	Les Abbayes	153	69.8	16.2	296	1
Netherlands	Ex. Parregaasterpolder	133	31.0	38.8	1653	15
	Hindeloopen	145	3.4	18.9	2249	4
	It H. - Feandyk	137	17.4	35.8	2156	14
	It H. - Feandyk (i)	137	16.5	33.5	2155	19
	Kl. Gaastmeer	136	19.1	33.2	2583	4
	Kl. Gaastmeer (i)	142	16.9	29.4	1920	14
	Koudum - samenvoeging	132	21.7	33.5	2001	25

	Makkumermeerpl.	137	28.6	33.0	3005	24
	St. - Zuidermeerpolder	133	14.0	27.8	2028	17
	St. - Zuidermeerpolder (b)	120	19.5	61.9	1643	7
	Workumerbinnenwaard	130	5.2	48.1	1944	15
	Workumerveld - it Heid.	139	47.3	35.9	2376	13
Poland	Brzeziny	135	6.9	43.2	1020	3
	Kaniuki	135	10.6	55.8	1191	2
	Ogrodniki	133	6.9	72.7	1368	0
	Sokolka1	135	6.5	65.3	947	0
	Sokolka2	138	10.2	69.3	798	0
	Trzescianka	135	11.0	55.3	1109	0
	Zabiele	134	7.4	63.3	1565	3
	Zajaczki	135	16.0	60.6	1352	6
	Zajki	135	6.2	37.6	1343	4
	Zuki	135	5.9	68.9	1289	4

Table S5.1. Black-tailed Godwit breeding habitat description of the sampled clutches in this study.

Country	Habitats sampled	Main Geographical Area
Finland	**Cultivated grasslands**, with varying fertilizer inputs ranging 50-200 kg N $ha^{-1}yr^{-1}$	**Bothnian Bay, Oulo region**. 64.87, 25.43
Estonia	**Fens**, no agricultural activities or human disturbance. Vegetation mostly comprises tall swards of grass constantly submerged. **Herb-rich semi-natural coastal pastures**, with no fertilizer input.	**West mainland Estonia and Islands**. 58.77, 23.68
Poland	**Farmland grassland**, a single fenced site with extensive agricultural practices. Grazed and mowed twice yearly.	**East Poland, Bialystok region**. 53.07, 22.89
Netherlands	**Farmland grassland**, with extensive agricultural practices for biodiversity enhancement. Low fertilizer input. **Intensive monoculture grasslands**, with high fertilizer input and early mowing (mid-April).	**Northwest Netherlands, Friesland region**. 52.99, 5.41
France	**Pasture grasslands**, with no fertilizer input and grazed.	**Midwest France, Beauvoir-sur-mer region**. 46.88, -2.05

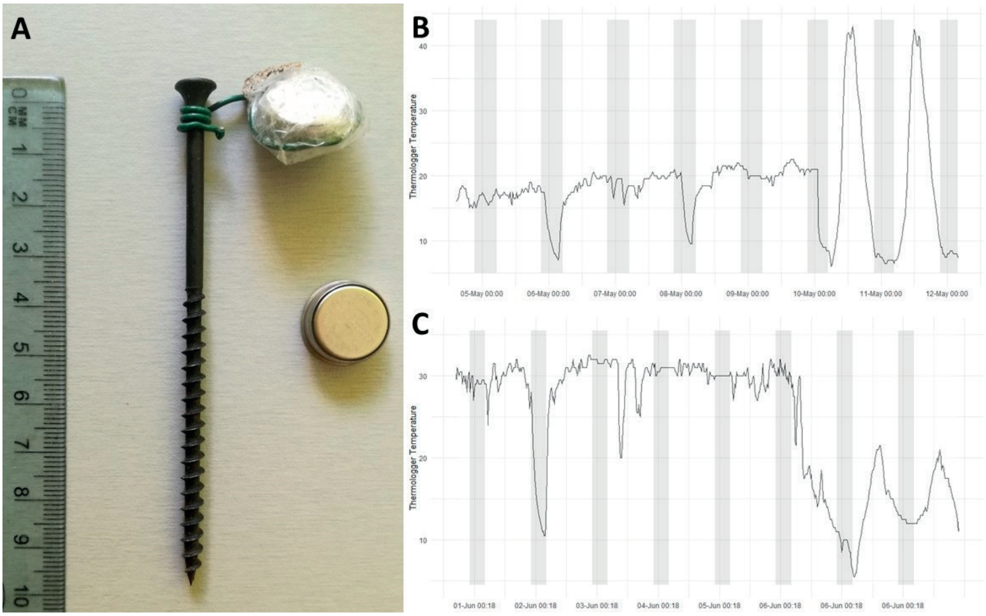


Figure S5.1. (**A**) Thermologger used to sample clutch incubation temperatures. The device was wrapped in plastic to avoid direct contact with water. The device was inserted under the eggs and stuck to a nail to avoid removal by the breeding birds; (**B**) Incubation temperatures of a predated clutch. Grey bars represent the nighttime period of the day. We can observe a sharp decline in the incubation temperatures close to midnight of May 10th, representing the time of predation, and then resuming to the environmental temperatures characterized by the continuous increasing and decreasing of temperatures along the day; (**C**) Incubation temperatures of a successfully hatched clutch. Grey bars represent the nighttime period of the day. We can observe a slow decline in the incubation temperatures starting at midnight of June 6th, representing the beginning of the hatching process, ending around midday of the same day, then resuming the environmental temperatures characterized by the continuous increasing and decreasing of temperatures along the day. In both incubation temperature plots, long incubation recesses are visible, when the temperature drops for some hours and then quickly resumes back to the constant incubation temperature.

Table S5.2: Wilcoxon rank-sum test results for the daily hours spent in a Long Incubation Recess (LIR) across countries and the percentage of the day and nighttime period spent in a LIR. Significant results are highlighted in bold.

		Sample Size	Statistic Test	P-value
Daily hours spent in a LIR	Across Countries			
	Estonia - Finland	32 - 19	402	0.06
	Estonia - France	32 - 14	205	0.67
	Estonia - Netherlands	32 - 12	208	0.67
	Estonia - Poland	**32 - 17**	**410**	**<0.01**
	Finland - France	19 - 14	180	0.09
	Finland - Netherlands	**19 - 12**	**199**	**<0.01**
	Finland - Poland	**19 - 17**	**313**	**<0.01**
	France - Netherlands	14 - 12	104	0.32
	France - Poland	**14 - 17**	**205**	**<0.01**
	Netherlands - Poland	**12 - 17**	**169**	**<0.01**
% of the day/night time in a LIR	Within Countries			
	Estonia: Day - Night	(32)	112	0.07
	Finland: Day - Night	(19)	95	1.00
	France: Day - Night	(14)	58	0.76
	Netherlands: Day - Night	(12)	63	0.06
	Poland: Day - Night	**(17)**	**57**	**0.04**

Table S5.3. Wilcoxon rank-sum test results for the daily frequency of Long Incubation Recess (LIR) across countries and the hourly frequency of LIRs during the day and nighttime period. Significant results are highlighted in bold.

		Sample Size	Statistic Test	P-value
Daily frequency of LIR	Across Countries			
	Estonia - Finland	**32 - 19**	**406**	**0.05**
	Estonia - France	32 - 14	246	0.61
	Estonia - Netherlands	32 - 12	243	0.18
	Estonia - Poland	**32 - 17**	**427**	**<0.01**
	Finland - France	**19 - 14**	**202**	**0.01**
	Finland - Netherlands	**19 - 12**	**200**	**<0.01**
	Finland - Poland	**19 - 17**	**302**	**<0.01**
	France - Netherlands	14 - 12	85	0.98
	France - Poland	**14 - 17**	**198**	**<0.01**
	Netherlands - Poland	**12 - 17**	**169**	**<0.01**
Hourly frequency of LIR	Within Countries			
	Estonia: Day - Night	(32)	148	0.33
	Finland: Day - Night	(19)	120	0.33
	France: Day - Night	**(14)**	**96**	**<0.01**
	Netherlands: Day - Night	**(12)**	**74**	**<0.01**
	Poland: Day - Night	**(17)**	**66**	**<0.01**

Table S5.4. Wilcoxon rank-sum test results for the Long Incubation Recess (LIR) length across countries and the LIR length during the day and nighttime period. Significant results are highlighted in bold.

		Sample Size	**Statistic Test**	**P-value**
LIR length	Across Countries			
	Estonia - Finland	32 - 19	378	0.15
	Estonia - France	**32 - 14**	**133**	**0.03**
	Estonia - Netherlands	32 - 12	136	0.14
	Estonia - Poland	32 - 17	493	0.66
	Finland - France	19 - 14	107	0.35
	Finland - Netherlands	19 - 12	114	1.00
	Finland - Poland	19 - 17	197	0.27
	France - Netherlands	14 - 12	102	0.36
	France - Poland	**14 - 17**	**168**	**0.05**
	Netherlands - Poland	12 - 17	133	0.17
LIR length	Within Countries			
	Estonia: Day - Night	(32)	94	0.11
	Finland: Day - Night	(19)	120	0.83
	France: Day - Night	(14)	24	0.14
	Netherlands: Day - Night	(12)	15	0.41
	Poland: Day - Night	(17)	45	0.31

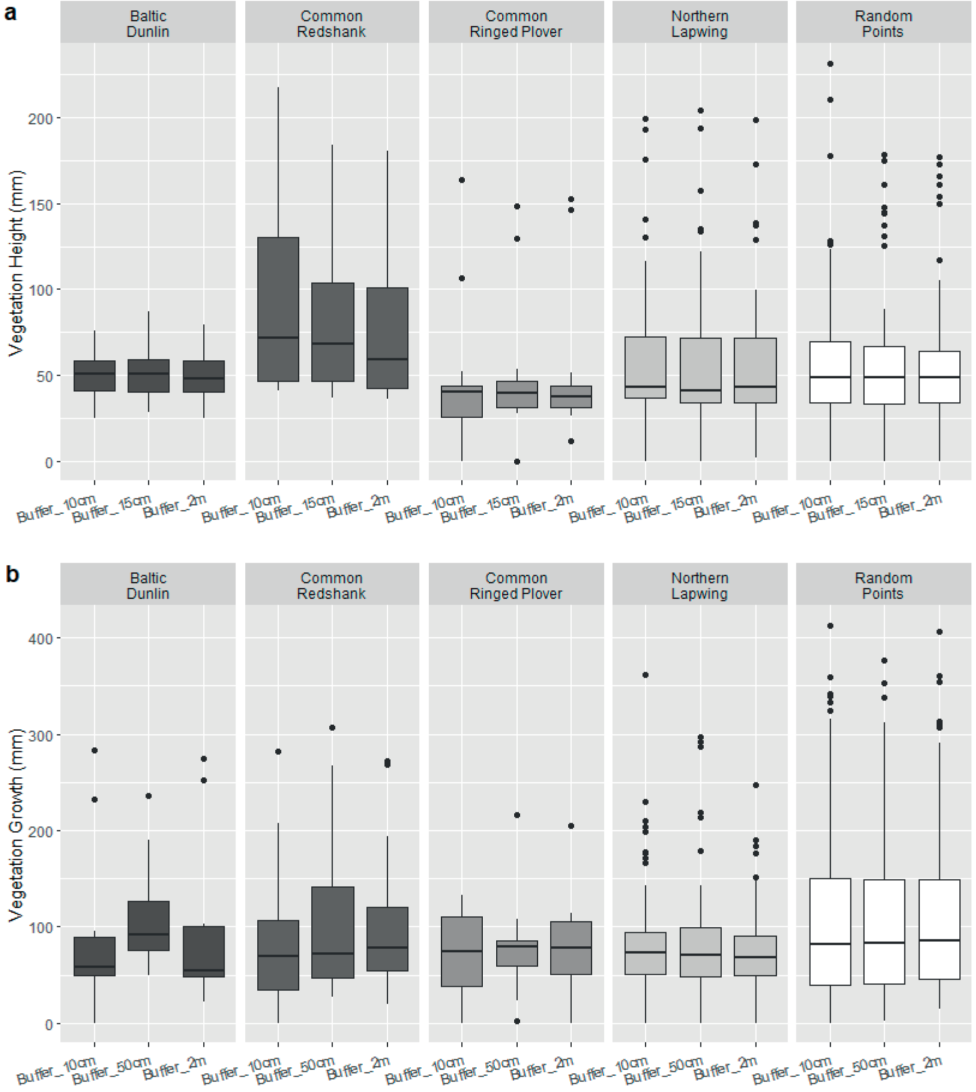


Figure S6.1. Boxplots representing the vegetation sward height (**a**) and vegetation height growth (**b**) averages according to different nest buffer radii (10cm, 50cm and 2m), between wader species and randomly selected points.

Table S6.1. List of vegetation indices selected in the present study to predict standing above-ground biomass.

Vegetation index	**Equation**	**Reference**
Normalized Difference Vegetation Index (NDVI)	(NIR-R)/(NIR + R)	Rouse et al. (1974)
Soil Adjusted Vegetation Index (SAVI)	[(NIR-R)/(NIR + R + L)](1 + L) L (soil adjustment factor) = 0.5	Huete (1988), Ullah et al. (2012)
Modified Soil Adjusted Vegetation Index (MSAVI)		Jin et al. (2014)
2-band Enhanced Vegetation Index (EVI2)	2.5[(NIR-R)/(NIR + 2.4R + 1)]	Jiang et al. (2008), Jin et al. (2014)
Difference Vegetation Index (DVI)	NIR-αR $\alpha = 0.96916$	Richardson and Everitt (1992), Maguigan et al. (2016)
Green Normalized Vegetation Index (GNDVI)	(NIR-G)/(NIR + G)	Gitelson et al. (1996), Naidoo et al. (2019)
Green Ratio Vegetation Index (GRVI)	NIR/G	Sripada et al. (2006), Naidoo et al. (2019)
Green Difference Index(GDI)	NIR-R + G	Gianelle and Vescovo (2007)
Green Red Difference Index (GRDI)	(G-R)/(G + R)	Gianelle and Vescovo (2007)
Red edge normalized difference vegetation index (NDVIre)	(NIR-Rededge)/(NIR + Rededge)	Gitelson and Merzlyak (1994), Kross et al. (2015)
Red edge simple ratio (SRre)	NIR/Rededge	Gitelson and Merzlyak (1994), Kross et al. (2015), Naidoo et al. (2019)
Red edge triangular vegetation index (core only) (RTVIcore)	100(NIR-Rededge)-10(NIR-G)	Kross et al. (2015), Clausen et al. (2013)
Datt4	R/G*Rededge	Datt (1998)

S


-pühaste-
EDZE

References

Adade, R., **A.M. Aibinu**, **B. Ekumah** & **J. Asaana**. 2021. Unmanned Aerial Vehicle (UAV) applications in coastal zone management—a review. *Environmental Monitoring and Assessment* 193: 1–12.

AEWA. 2008. *International Single Species Action Plan for the Conservation of the Black-tailed Godwit (TS No. 37) | AEWA*. Agreement on the Conservation of African-Eurasian Migratory Waterbirds.

Amar, A., **M. Grant**, **G. Buchanan**, **I. Sim**, **J. Wilson**, **J.W. Pearce-Higgins** & **S. Redpath**. 2011. Exploring the relationships between wader declines and current land-use in the British uplands. *Bird Study* 58: 13–26.

An, S. & **J.T.A. Verhoeven**. 2019. Wetland Functions and Ecosystem Services: Implications for Wetland Restoration and Wise Use. Pages 1–10 in: *Wetlands: Ecosystem Services, Restoration and Wise Use*.

Andersen, R., **C. Farrell**, **M. Graf**, **F. Muller**, **E. Calvar**, **P. Frankard**, **S. Caporn** & **P. Anderson**. 2017. An overview of the progress and challenges of peatland restoration in Western Europe. *Restoration Ecology* 25: 271–282.

Andrey, A., **J. Humbert**, **C. Pernollet** & **R. Arlettaz**. 2014. Experimental evidence for the immediate impact of fertilization and irrigation upon the plant and invertebrate communities of mountain grasslands. *Ecology and Evolution* 4: 2610–2623.

Atkinson, P.W., **R.J. Fuller**, **J.A. Vickery**, **G.J. Conway**, **J.R.B. Tallowin**, **R.E.N. Smith**, **K.A. Haysom**, **T.C. Ings**, **E.J. Asteraki** & **V.K. Brown**. 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *Journal of Applied Ecology* 42: 932–942.

Aune, S., **A. Hofgaard** & **L. Söderström**. 2011. Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola PeninsulaThis article is a contribution to the series Tree recruitment, growth, and distribution at the circumpolar forest–tundra transition. *Canadian Journal of Forest Research* 41: 437–449.

Babyak, M.A. 2004. What you see may not be what you get: A brief, nontechnical introduction to overfitting in regression-type models. *Psychosomatic Medicine* 66: 411–421.

Baines, D. 1990. The Roles of Predation, Food and Agricultural Practice in Determining the Breeding Success of the Lapwing (Vanellus vanellus) on Upland Grasslands. *The Journal of Animal Ecology* 59: 915.

Bakker, W., **B.J. Ens**, **A. Dokter**, **H.J. van der Kolk**, **K. Rappoldt**, **M. van de Pol**, **K. Troost**, **H.W. van der Veer**, **A.I. Bijleveld**, **J. van der Meer**, **K. Oosterbeek**, **E. Jongejans** & **A.M. Allen**. 2021. Connecting foraging and roosting areas reveals how food stocks explain shorebird numbers. *Estuarine, Coastal and Shelf Science* 259: 107458.

Barton, K. 2020. MuMIn: Multi-Model Inference. R Package version 1.43.17. Accessed 8 Feb 2021 at: *https://cran.r-project.org/web/packages/MuMIn/index.html*.

Batáry, P. & **A. Báldi**. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology*.

Bates, D., **M. Mächler**, **B.M. Bolker** & **S.C. Walker**. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Beintema, A.J. 1983. Meadow birds as indicators. *Environmental Monitoring and Assessment* 3: 391–398.

Beintema, A.J., **O. Moedt** & **D. Ellinger**. 1995. *Ecologische atlas van de Nederlandse weidevogels*.

Beintema, A.J. & **G.H. Visser**. 1989. The effect of weather on time budgets and development of chicks of meadow birds. *Ardea* 77: 181–192.

Beintema, A.J., **J.B. Thissen**, **D. Tensen** & **G.H. Visser**. 1991. Feeding ecology of charadriiform chicks in agricultural grassland. *Ardea* 79: 31–44.

Bell, J.R., **C. Philip Wheater** & **W. Rod Cullen**. 2001. The implications of grassland and heathland management for the conservation of spider communities: A review. *Journal of Zoology* 255: 377–387.

Bell, M. V. & **J. Calladine**. 2017. The decline of a population of farmland breeding waders: a twenty-five-year case study. *Bird Study* 64: 264–273.

Bellebaum, J. & **C. Bock**. 2008. Influence of ground predators and water levels on Lapwing Vanellus vanellus breeding success in two continental wetlands. *Journal of Ornithology 2008 150:1* 150: 221–230.

Benton, T.G., **D.M. Bryant**, **L. Cole** & **H.Q.P. Crick**. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39: 673–687.

Berg, Å. 1996. Predation on artificial, solitary and aggregated wader nests on farmland. *Oecologia* 107: 343–346.

Berg, Å., **S.G. Nilsson** & **U. Bostrom**. 1992. Predation on artificial wader nests on large and small bogs along a south-north gradient. *Ornis Scandinavica* 23: 13–16.

Bergamo, T.F., **R.D. Ward**, **C.B. Joyce**, **M. Villoslada** & **K. Sepp**. 2022. Experimental climate change impacts on Baltic coastal wetland plant communities. *Scientific Reports 2022 12:1* 12: 1–13.

Bertholdt, N.P., **J.A. Gill**, **R.A. Laidlaw** & **J. Smart**. 2016. Landscape effects on nest site selection and nest success of Northern Lapwing Vanellus vanellus in lowland wet grasslands. *Bird Study* 64: 30–36.

Bibby, C., **N. Burgess** & **D. Hill**. 1992. *Bird Census Techniques - 1st Edition*.

Bignal, E.M. & **D.I. McCracken**. 1996. Low-Intensity Farming Systems in the Conservation of the Countryside. *The Journal of Applied Ecology* 33: 413.

Bijlsma, R.G., **F. Hustings** & **C.J. Camphuysen**. 2001. *Algemene en schaarse vogels van Nederland. Avifauna van Nederland, 2.*

BirdLife International. 2017. Limosa limosa (Black-tailed Godwit). *Limosa limosa (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2017: e.T22693150A111611637*. Accessed 25 Jan 2021 at: *https://dx.doi.org/10.2305/IUCN.UK.2017-1.RLTS.T22693150A111611637.en*.

Blake, S., **G. Foster**, **M. Eyre** & **M. Luff**. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* 38: 502–512.

Bolton, M., **G. Tyler**, **K. Smith** & **R. Bamford**. 2007. The impact of predator control on lapwing Vanellus vanellus breeding success on wet grassland nature reserves. *Journal of Applied Ecology* 44: 534–544.

Bostrom, U. & **S.G. Nilsson**. 1983. Latitudinal gradients and local variations in species richness and structure of bird communities on raised peat-bogs in Sweden. *Ornis Scandinavica* 14: 213–226.

Breeuwer, A., **F. Berendse**, **F. Willems**, **R. Foppen**, **W. Teunissen**, **H. Schekkerman** & **P. Goedhart**. 2009. Do meadow birds profit from agri-environment schemes in Dutch agricultural landscapes? *Biological Conservation* 142: 2949–2953.

Breiman, L. 2001. Random forests. *Machine Learning* 45: 5–32.

Brooks, M.E., **K. Kristensen**, **K.J. van Benthem**, **A. Magnusson**, **C.W. Berg**, **A. Nielsen**, **H.J. Skaug**, **M. Mächler** & **B.M. Bolker**. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9: 378–400.

Brown, A.F. & **K.B. Shepherd**. 1993. A method for censusing upland breeding waders. *Bird Study* 40: 189–195.

Brzeziński, M., **M. Żmihorski**, **A. Zarzycka** & **A. Zalewski**. 2019. Expansion and population dynamics of a non-native invasive species: the 40-year history of American mink colonisation of Poland. *Biological Invasions* 21: 531–545.

Buchanan, G.M., **M.C. Grant**, **R.A. Sanderson** & **J.W. Pearce-Higgins**. 2006. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis* 148: 615–628.

Bulla, M., **E. Stich**, **M. Valcu** & **B. Kempenaers**. 2015. Off-nest behaviour in a biparentally incubating shorebird varies with sex, time of day and weather. *Ibis* 157: 575–589.

Burnham, E. & **D. Anderson**. 2001. Model Selection and Inference. A Practical Information–Theoretic Approach. Kenneth P. Burnham and David R. Anderson, Springer-Verlag, Heidelberg, 1998. No. of pages: xix+353. Price: DM 149.00. ISBN 0-387-98504-2. *Statistics in Medicine* 20: 1144–1146.

Burnham, K.P., **D.R. Anderson** & **K.P. Huyvaert**. 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*.

Burns, F., **M.A. Eaton**, **I.J. Burfield**, **A. Klvaňová**, **E. Šilarová**, **A. Staneva** & **R.D. Gregory**. 2021. Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. *Ecology and Evolution* 11: 16647–16660.

Burnside, N.G., **C.B. Joyce**, **E. Puurmann** & **D.M. Scott**. 2007. Use of vegetation classification and plant indicators to assess grazing abandonment in Estonian coastal wetlands. *Journal of Vegetation Science* 18: 645–654.

Camps-Valls, G., **M. Campos-Taberner**, **Á. Moreno-Martínez**, **S. Walther**, **G. Duveiller**, **A. Cescatti**, **M.D. Mahecha**, **J. Muñoz-Marí**, **F.J. García-Haro**, **L. Guanter**, **M. Jung**, **J.A. Gamon**, **M. Reichstein** & **S.W. Running**. 2021. A unified vegetation index for quantifying the terrestrial biosphere. *Science Advances* 7: 7447–7473.

Cervencl, A., **W. Esser**, **M. Maier**, **N. Oberdiek**, **S. Thyen**, **A. Wellbrock** & **K.M. Exo**. 2011. Can differences in incubation patterns of Common Redshanks Tringa totanus be explained by variations in predation risk? *Journal of Ornithology* 152: 1033–1043.

Chamberlain, D.E., **R.J. Fuller**, **R.G.H. Bunce**, **J.C. Duckworth** & **M. Shrubb**. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology* 37: 771–788.

Clough, Y., **S. Kirchweger** & **J. Kantelhardt**. 2020. Field sizes and the future of farmland biodiversity in European landscapes. *Conservation Letters* 13: e12752.

Clucas, B., **J.M. Marzluff**, **B. Clucas** & **J.M. Marzluff**. 2015. A cross-continental look at the patterns of avian species diversity and composition across an urbanisation gradient. *Wildlife Research* 42: 554–562.

Comaniciu, D. & **P. Meer**. 2002. Mean shift: A robust approach toward feature space analysis. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 24: 603–619.

Cramp, S. & **C.M. Perrins**. 1983. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic: 3. Waders to gulls. *Oxford University Press*: Volume III.

Cunningham, J.A., **D.C. Kesler** & **R.B. Lanctot**. 2016. Habitat and social factors influence nest-site selection in Arctic-breeding shorebirds. *The Auk* 133: 364–377.

De Felici, L., **T. Piersma** & **R.A. Howison**. 2019. Abundance of arthropods as food for meadow bird chicks in response to short- And long-term soil wetting in Dutch dairy grasslands. *PeerJ* 2019.

Dennis, P., **J. Skartveit**, **D.I. McCracken**, **R.J. Pakeman**, **K. Beaton**, **A. Kunaver** & **D.M. Evans**. 2007. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* 45: 279–287.

Donald, P.F., **R.E. Green** & **M.F. Heath**. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences* 268: 25–29.

Donald, P.F., **G. Pisano**, **M.D. Rayment** & **D.J. Pain**. 2002. The common agricultural policy, EU enlargement and the conservation of Europe's farmland birds. *Agriculture, Ecosystems and Environment* 89: 167–182.

Donald, P.F., **F.J. Sanderson**, **I.J. Burfield** & **F.P.J. van Bommel**. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. *Agriculture, Ecosystems and Environment* 116: 189–196.

Douglas, D.J.T., **M. Lewis**, **Z. Thatey** & **E. Teuten**. 2021. Wetlands support higher breeding wader densities than farmed habitats within a nature-rich farming system. *Bird Study* 68: 112–123.

Douglas, D.J.T.T., **P.E. Bellamy**, **L.S. Stephen**, **J.W. Pearce–Higgins**, **J.D. Wilson**, **M.C. Grant**, **J.W. Pearce-Higgins**, **J.D. Wilson** & **M.C. Grant**. 2014. Upland land use predicts population decline in a globally near-threatened wader. *Journal of Applied Ecology* 51: 194–203.

Doxa, A., **Y. Bas**, **M.L. Paracchini**, **P. Pointereau**, **J.-M. Terres** & **F. Jiguet**. 2010. Low-intensity agriculture increases farmland bird abundances in France. *Journal of Applied Ecology* 47: 1348–1356.

Dugan, P. 1993. *Wetlands In Danger: a World Conservation Atlas*. *Oxford university press*.

Duncan, P., **A.J.M. Hewison**, **S. Houte**, **R. Rosoux**, **T. Tournebize**, **F. Dubs**, **F. Burel** & **V. Bretagnolle**. 1999. Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *Journal of Applied Ecology* 36: 11–23.

Durant, D., **M. Tichit**, **E. Kernéïs** & **H. Fritz**. 2008a. Management of agricultural wet grasslands for breeding waders: Integrating ecological and livestock system perspectives - A review. *Biodiversity and Conservation*.

Durant, D., **M. Tichit**, **H. Fritz** & **E. Kernéïs**. 2008b. Field occupancy by breeding lapwings Vanellus vanellus and redshanks Tringa totanus in agricultural wet grasslands. *Agriculture, Ecosystems & Environment* 128: 146–150.

EBCC. 2016. *PanEuropean Common Bird Monitoring Scheme*.

EEA, E.E.A. 2020. *State of nature in the EU - Results from reporting under the nature directives 2013-2018*. Luxembourg.

Eglington, S.M., **M. Bolton**, **M.A. Smart**, **W.J. Sutherland**, **A.R. Watkinson** & **J.A. Gill**. 2010. Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. *Journal of Applied Ecology* 47: 451–458.

Ejsmond, M. 2008. The effect of mowing on next-year predation of grassland bird nests : experimental study. *Polish Journal of Ecology* Vol. 56: 299–307.

Ekroos, J., **D. Kleijn**, **P. Batáry**, **M. Albrecht**, **A. Báldi**, **N. Blüthgen**, **E. Knop**, **A. Kovács-Hostyánszki** & **H.G. Smith**. 2020. High land-use intensity in grasslands constrains wild bee species richness in Europe. *Biological Conservation* 241: 108255.

Elek, Z., **L. Drag**, **P. Pokluda**, **L. Cizek** & **S. Berces**. 2014. Dispersal of individuals of the flightless grassland ground beetle, Carabus hungaricus (Coleoptera: Carabidae), in three populations and what they tell us about mobility estimates based on mark-recapture. *European Journal of Entomology* 111: 663–668.

Ens, B.J., **M. Kersten**, **A. Brenninkmeijer** & **J.B. Hulscher**. 1992. Territory Quality, Parental Effort and Reproductive Success of Oystercatchers (Haematopus ostralegus). *The Journal of Animal Ecology* 61: 703.

Essl, F., **S. Dullinger**, **D. Moser**, **W. Rabitsch** & **I. Kleinbauer**. 2012. Vulnerability of mires under climate change: Implications for nature conservation and climate change adaptation. *Biodiversity and Conservation* 21: 655–669.

Estonian Environmental Agency. 2019. *Breeding birds of coastal grasslands monitoring scheme report - in Estonian*.

Estonian Land Board. 2020. Estonian Topographic Database.

European Commission. 2019. *Fertilisers in the EU: Prices, trade and use*.

European Environment Agency. 2017. Landscapes in Transition. An account of 25 years of land cover change in Europe. *EEA Report*. https://doi.org/10.2800/81075.

Ewing, S.R., **E.S. Scragg**, **N. Butcher** & **D.J.T. Douglas**. 2018. GPS tracking reveals temporal patterns in breeding season habitat use and activity of a globally Near Threatened wader, the Eurasian Curlew. *Wader Study* 124: 206–214.

Flade, M., **H. Plachter**, **R. Schmidt** & **A. Werner**. 2006. *Nature Conservation in Agricultural Ecosystems. Results of the Schorfheide-Chorin Research Project*.

Fletcher, K., **N.J. Aebischer**, **D. Baines**, **R. Foster** & **A.N. Hoodless**. 2010a. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology* 47: 263–272.

Fletcher, K., **N.J. Aebischer**, **D. Baines**, **R. Foster** & **A.N. Hoodless**. 2010b. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology* 47: 263–272.

Fluet-Chouinard, E., **B.D. Stocker**, **Z. Zhang**, **A. Malhotra**, **J.R. Melton**, **B. Poulter** & **J.O. Kaplan**. 2023. Extensive global wetland loss over the past three centuries. *Kees Klein Goldewijk* 614: 26.

Forbes, B.C., **M.M. Fauria** & **P. Zetterberg**. 2010. Russian Arctic warming and “greening” are closely tracked by tundra shrub willows. *Global Change Biology* 16: 1542–1554.

Fraixedas, S., **A. Lindén**, **K. Meller**, **Å. Lindström**, **O. Keišs**, **J.A. Kålås**, **M. Husby**, **A. Leivits**, **M. Leivits** & **A. Lehikoinen**. 2017. Substantial decline of Northern European peatland bird populations: Consequences of drainage. *Biological Conservation* 214: 223–232.

Fuller, R.J. 2012. *Birds and Habitat: Relationships in Changing Landscapes*.

Fuller, R.J., **T.M. Reed**, **N.E. Buxton**, **A. Webb**, **T.D. Williams** & **M.W. Pienkowski**. 1986. Populations of breeding waders charadrii and their habitats on the crofting lands of the outer hebrides, Scotland. *Biological Conservation* 37: 333–361.

Gamero, A., **L. Brotons**, **A. Brunner**, **R. Foppen**, **L. Fornasari**, … **P. Voříšek**. 2017. Tracking Progress Toward EU Biodiversity Strategy Targets: EU Policy Effects in Preserving its Common Farmland Birds. *Conservation Letters* 10: 395–402.

Gill, J.A., **R.H.W. Langston**, **J.A. Alves**, **P.W. Atkinson**, **P. Bocher**, … **T. Piersma**. 2007. Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. *Wader Study Group Bulletin* 114: 43–50.

Gochfeld, M. 1984. Antipredator Behavior: Aggressive and Distraction Displays of Shorebirds. *Shorebirds*: 289–377.

Goss-Custard, J.D. 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. *Journal of Applied Ecology* 28: 1004–1026.

Goss-Custard, J.D. & **A.D. West**. 1997. The concept of carrying capacity and shorebirds.

Goulson, D. 2019. The insect apocalypse, and why it matters. *Current Biology*.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.

Green, R.E. 1988. Effects of Environmental Factors on the Timing and Success of Breeding of Common Snipe Gallinago gallinago (Aves: scolopacidae). *The Journal of Applied Ecology* 25: 79.

Green, R.E., **J. Hawell** & **T.H. Johnson**. 1987. Identification of predators of wader eggs from egg remains. *Bird Study* 34: 87–91.

Green, R.E., **G.J.. M. Hironsl** & **J.S. Kirby**. 1990. The Effectiveness Of Nest Defence By Black-tailed Godwits Limosa limosa. *Ardea* 78: 405–413.

Gregory, R.D., **D. G. Noble** & **J. Custance**. 2004. The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* 146: 1–13.

Gregory, R.D., **A. van Strien**, **P. Vorisek**, **A.W. Gmelig Meyling**, **D.G. Noble**, **R.P.. Foppen** & **D.W. Gibbons**. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 269–288.

Groen, N.M. 1993. Breeding site tenacity and natal philopatry in the Black-tailed Godwit Limosa l. limosa. *Ardea* 81: 107–113.

Groen, N.M., **R. Kentie**, **P. de Goeij**, **B. Verheijen**, **J.C.E.W. Hooijmeijer** & **T. Piersma**. 2012. A Modern Landscape Ecology of Black-Tailed Godwits: Habitat Selection in Southwest Friesland, The Netherlands. *Ardea* 100: 19–28.

Haddad, N.M., **J. Haarstad** & **D. Tilman**. 2000. The effects of long-term nitrogen loading grassland insect communities. *Oecologia* 124: 73–84.

Hallmann, C.A., **M. Sorg**, **E. Jongejans**, **H. Siepel**, **N. Hofland**, **H. Schwan**, **W. Stenmans**, **A. Müller**, **H. Sumser**, **T. Hörren**, **D. Goulson** & **H. de Kroon**. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE* 12: e0185809.

Hallmann, C.A., **T. Zeegers**, **R. van Klink**, **R. Vermeulen**, **P. van Wielink**, **H. Spijkers**, **J. van Deijk**, **W. van Steenis** & **E. Jongejans**. 2019. Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity* 13: 127–139.

Hallmann, C.A. & **E. Jongejans**. 2021. *Long-term trends and drivers of aquatic insects in the Netherlands*.

Hancock, M.H., **M.C. Grant** & **J.D. Wilson**. 2009. Associations between distance to forest and spatial and temporal variation in abundance of key peatland breeding bird species. *Bird Study* 56: 53–64.

Hartig, E.K., **O. Grozev** & **C. Rosenzweig**. 1997. Climate change, agriculture and wetlands in Eastern Europe: Vulnerability, adaptation and policy. *Climatic Change*.

Haverschmidt, F. 1963a. The black-tailed godwit. *E. J. Brill, Leiden*.

Haverschmidt, F. 1963b. The black-tailed godwit. *E. J. Brill, Leiden*.

Hegyi, Z. & **L. Sasvári**. 1998. Parental Condition and Breeding Effort in Waders. *Journal of Animal Ecology* 67: 41–53.

Heijmans, M.M.P.D., **Y.A.M. van der Knaap**, **M. Holmgren** & **J. Limpens**. 2013. Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. *Global Change Biology* 19: 2240–2250.

Heisler-White, J.L., **J.M. Blair**, **E.F. Kelly**, **K. Harmoney** & **A.K. Knapp**. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Global Change Biology* 15: 2894–2904.

Hellstrom, M. & **Å. Berg**. 2014. Effects of restoration and management regime on the avifaunal composition on Swedish wet meadows.

Herzog, F., **B. Steiner**, **D. Bailey**, **J. Baudry**, **R. Billeter**, **R. Bukácek**, **G. De Blust**, **R. De Cock**, **J. Dirksen**, **C.F. Dormann**, **R. De Filippi**, **E. Frossard**, **J. Liira**, **T. Schmidt**, **R. Stöckli**, **C. Thenail**, **W. Van Wingerden** & **R. Bugter**. 2006. Assessing the intensity of temperate European agriculture at the landscape scale. *European Journal of Agronomy* 24: 165–181.

Hesselbarth, M.H.K., **M. Sciaini**, **K.A. With**, **K. Wiegand** & **J. Nowosad**. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42: 1648–1657.

Hijmans, R.J., **J. van Etten** & **J. Cheng**. 2015. Raster Geographic Data Analysis and Modeling.

Hockey, P.A.R., **R.A. Navarro**, **B. Kalejta** & **C.R. Velasquez**. 1992. The riddle of the sands: why are shorebird densities so high in southern estuaries? *American Naturalist* 140: 961–979.

Howison, R.A., **T. Piersma**, **R. Kentie**, **J.C.E.W. Hooijmeijer** & **H. Olff**. 2018. Quantifying landscape-level land-use intensity patterns through radar-based remote sensing. *Journal of Applied Ecology* 55: 1276–1287.

Huk, T. & **B. Kühne**. 1999. Substrate selection by Carabus clatratus (Coleoptera, Carabidae) and its consequences for offspring development. *Oecologia* 121: 348–354.

Ibáñez-álamo, J.D., **R.D. Magrath**, **J.C. Oteyza**, **A.D. Chalfoun**, **T.M. Haff**, **K.A. Schmidt**, **R.L. Thomson** & **T.E. Martin**. 2015. Nest predation research: recent findings and future perspectives. *Journal of Ornithology 2015 156:1* 156: 247–262.

Järvinen, O., **R.A. Väisänen**, **O. Jarvinen** & **R.A. Vaisanen**. 1978. Ecological Zoogeography of North European Waders, or Why Do So Many Waders Breed in the North? *Oikos* 30: 496.

Jensen, F.P. & **C. Perennou**. 2007. *Management plan for Black-tailed Godwit (Limosa limosa) 2007-2009. Directive 79/409/EEC on the conservation of wild birds.*

Jóhannesdóttir, L., **J.A. Gill**, **J.A. Alves**, **S.H. Brink**, **Ó. Arnalds**, **V. Méndez** & **T.G. Gunnarsson**. 2019. Interacting effects of agriculture and landscape on breeding wader populations. *Agriculture, Ecosystems & Environment* 272: 246–253.

Johansson, O.C. & **D. Blomqvist**. 1996. Habitat Selection and Diet of Lapwing Vanellus vanellus Chicks on Coastal Farmland in S. W. Sweden. *The Journal of Applied Ecology* 33: 1030.

Johansson, T. 2001. Habitat selection, nest predation and conservation biology in a black-tailed godwit (Limosea limosa) population.

Jourdan, J., **V. Baranov**, **R. Wagner**, **M. Plath** & **P. Haase**. 2019. Elevated temperatures translate into reduced dispersal abilities in a natural population of an aquatic insect. *Journal of Animal Ecology* 88: 1498–1509.

Joyce, C.B. & **P.M. (P. M. Wade**. 1998. European wet grasslands : biodiversity, management, and restoration. 340.

Kaasiku, T., **R. Rannap** & **T. Kaart**. 2019. Managing coastal grasslands for an endangered wader species can give positive results only when expanding the area of open landscape. *Journal for Nature Conservation* 48: 12–19.

Kaasiku, T., **R. Rannap** & **& P. Männil**. 2022. Predation-mediated edge effects reduce survival of wader nests at a wet grassland-forest edge. *Animal Conservation*. https://doi.org/10.1111/ACV.12774

Kaasiku, T., **J. Praks**, **K. Jakobson** & **R. Rannap**. 2021. Radar remote sensing as a novel tool to assess the performance of an agri-environment scheme in coastal grasslands. *Basic and Applied Ecology*. https://doi.org/10.1016/J.BAAE.2021.07.002

Kamp, J., **A. Reinhard**, **M. Frenzel**, **S. Kämpfer**, **J. Trappe** & **N. Hölzel**. 2018. Farmland bird responses to land abandonment in Western Siberia. *Agriculture, Ecosystems and Environment* 268: 61–69.

Kark, S., **A. Tulloch**, **A. Gordon**, **T. Mazor**, **N. Bunnefeld** & **N. Levin**. 2015. Cross-boundary collaboration: key to the conservation puzzle. *Current Opinion in Environmental Sustainability* 12: 12–24.

Keller, V., **S. Herrando**, **P. Voříšek**, **M. Franch**, **M. Kipson**, **P. Milanesi**, **D. Martí**, **M. Anton**, **A. Klvaňová**, **M.V. Kalyakin**, **H.-G. Bauer** & **R.P.B. Foppen**. 2021. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. European Bird Census Council & Lynx Edicions, Barcelona.

Kentie, R. 2015. *Spatial demography of black-tailed godwits: metapopulation dynamics in a fragmented agricultural landscape*. University of Groningen.

Kentie, R., **J.C.E.W. Hooijmeijer**, **K.B. Trimbos**, **N.M. Groen** & **T. Piersma**. 2013. Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *Journal of Applied Ecology* 50: 243–251.

Kentie, R., **C. Both**, **J.C.E.W. Hooijmeijer** & **T. Piersma**. 2014. Age-dependent dispersal and habitat choice in black-tailed godwits *Limosa limosa limosa* across a mosaic of traditional and modern grassland habitats. *Journal of Avian Biology* 45: 396–405.

Kentie, R., **C. Both**, **J.C.E.W. Hooijmeijer** & **T. Piersma**. 2015. Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits Limosa limosa. *Ibis* 157: 614–625.

Kentie, R., **N.R. Senner**, **J.C.E.W. Hooijmeijer**, **R. Márquez-Ferrando**, **J. Figuerola**, **J.A. Masero**, **M.A. Verhoeven** & **T. Piersma**. 2016. Estimating the Size of the Dutch Breeding Population of Continental Black-Tailed Godwits from 2007–2015 Using Resighting Data from Spring Staging Sites. *Ardea* 104: 213–225.

Kentie, R., **T. Coulson**, **J.C.E.W. Hooijmeijer**, **R.A. Howison**, **A.H.J. Loonstra**, **M.A. Verhoeven**, **C. Both** & **T. Piersma**. 2018. Warming springs and habitat alteration interact to impact timing of breeding and population dynamics in a migratory bird. *Global Change Biology* 24: 5292–5303.

Kirby, J.S. 1984. Aspects of the breeding biology of the black-tailed godwit (limosa limosa) with particular reference to coloniality and anti-predator defence.

Kleijn, D. & **D. Bos**. 2010. Een pilotstudie naar de interacties tussen broedende weidevogels en Brandganzen. *De Levende Natuur* 111: 64–67.

Kleijn, D., **F. Berendse**, **R. Smit** & **N. Gilissen**. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413: 723–725.

Kleijn, D., **W.J. Dimmers**, **R.J.M. van Kats** & **T.C.P. Melman**. 2009a. Het belang van hoog waterpeil en bemesting voor de Grutto: I. de vestigingsfase. *De Levende Natuur* 110: 180–183.

Kleijn, D., **W.J. Dimmers**, **R.J.M. van Kats** & **T.C.P. Melman**. 2009b. *De relatie tussen gebruiksintensiteit en de kwaliteit van graslanden als foerageerhabitat voor gruttokuikens*. Alterra.

Kleijn, D., **W.J. Dimmers**, **R.J.M. van Kats** & **T.C.P. Melman**. 2009c. Het belang van hoog waterpeil en bemesting voor de Grutto: I. de vestigingsfase. *De Levende Natuur* 110: 180–183.

Kleijn, D., **D. Lammertsma** & **G. Müskens**. 2011a. *Het belang van waterpeil en bemesting voor de voedselbeschikbaarheid van weidevogels pp. 41-60. SOVON onderzoeksrapport 2011/10*.

Kleijn, D. & **W.J. Sutherland**. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*.

Kleijn, D., **H. Schekkerman**, **W.J. Dimmers**, **R.J.M. Van Kats**, **D. Melman** & **W.A. Teunissen**. 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits Limosa l. limosa in the Netherlands. *Ibis* 152: 475–486.

Kleijn, D., **M. Rundlöf**, **J. Scheper**, **H.G. Smith** & **T. Tscharntke**. 2011b. Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution* 26: 474–481.

Kleijn, D., **F. Kohler**, **A. Báldi**, **P. Batáry**, **E.. Concepción**, **Y. Clough**, **M. Díaz**, **D. Gabriel**, **A. Holzschuh**, **E. Knop**, **A. Kovács**, **E.J.. Marshall**, **T. Tscharntke** & **J. Verhulst**. 2009d. On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B: Biological Sciences* 276: 903–909.

Klomp, H. 1954. De terreinkeus van de Kievit, Vanellus vanellus (L.). *Ardea*: 1–2.

Knisley, C.B., **C. Gowan** & **C. Wirth**. 2018. Effects of soil moisture, vegetation and food on adult activity, oviposition and larval development in the tiger beetle, Cicindela albissima Rumpp. *Journal of Insect Conservation* 22: 443–449.

Koleček, J., **P. Procházka**, **N. El-Arabany**, **M. Tarka**, **M. Ilieva**, **S. Hahn**, **M. Honza**, **J. de la Puente**, **A. Bermejo**, **A. Gürsoy**, **S. Bensch**, **P. Zehtindjiev**, **D. Hasselquist** & **B. Hansson**. 2016. Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology* 47: 756–767.

Korniluk, M., **P. Białomyzy**, **G. Grygoruk**, **Ł. Kozub**, **M. Sielezniew**, **P. Świętochowski**, **T. Tumiel**, **M. Wereszczuk** & **P. Chylarecki**. 2021. Habitat selection of foraging male Great Snipes on floodplain meadows: importance of proximity to the lek, vegetation cover and bare ground. *Ibis* 163: 486–506.

Kose, M., **M. Kose** & **A. Klein**. 2004. *Coastal meadow management: Best Practice Guidelines*.

Kose, M., **K. Heinsoo**, **K. Kaljund** & **K. Tali**. 2021. Twenty years of Baltic Boreal coastal meadow restoration: has it been long enough? *Restoration Ecology* 29: e13266.

Krebs, J.R. (John R.. & **N.B. (Nicholas B.. Davies**. 1997. Behavioural ecology : an evolutionary approach. 456.

Krüger, H., **V.M. Väänänen**, **S. Holopainen** & **P. Nummi**. 2018. The new faces of nest predation in agricultural landscapes—a wildlife camera survey with artificial nests. *European Journal of Wildlife Research* 64: 1–11.

Kruk, M., **M.A.W. Noordervliet** & **W.J.T. Keurs**. 1998. Natal philopatry in the Black-tailed Godwit Limosa limosa L. And its possible implications for conservation. *Ringing and Migration* 19: 13–16.

Kruk, M., **M.A.W. Noordervliet** & **W.J. Ter Keurs**. 1997. Survival of black-tailed godwit chicks Limosa limosa in intensively exploited grassland areas in the Netherlands. *Biological Conservation* 80: 127–133.

Kubelka, V., **V. Zámečník**, **K. Slabeyová**, **V. Škorpíková** & **M. Šálek**. 2018. Threats and conservation of meadow-breeding shorebirds in the Czech Republic and Slovakia. *Wader Study* 125: 164–174.

Kuresoo, A. & **E. Mägi**. 2004. *Changes of bird communities in relation to management of coastal meadows in Estonia*. Tallinn.

Laake, J. 2013. RMark : an R Interface for analysis of capture-recapture data with MARK. *AFSC Processed Rep. 2013-01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA*.

Laca, E.A. & **G. Lemaire**. 2000. Measuring sward structure. *Field and laboratory methods for grassland and animal production research*: 103–121.

Laidlaw, R.A., **T.G. Gunnarsson**, **V. Méndez**, **C. Carneiro**, **B. Þórisson**, **A. Wentworth**, **J.A. Gill** & **J.A. Alves**. 2020. Vegetation structure influences predation rates of early nests in subarctic breeding waders. *Ibis* 162: 1225–1236.

Laidlaw, R.A., **J. Smart**, **M.A. Smart** & **J.A. Gill**. 2015. The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis* 157: 700–712.

Laidlaw, R.A., **J. Smart**, **M.A. Smart** & **J.A. Gill**. 2017. Scenarios of habitat management options to reduce predator impacts on nesting waders. *Journal of Applied Ecology* 54: 1219–1229.

Laidlaw, R.A., **J. Smart**, **M.A. Smart**, **T.W. Bodey**, **T. Coledale** & **J.A. Gill**. 2019. Foxes, voles, and waders: drivers of predator activity in wet grassland landscapes. *Avian Conservation and Ecology* 14.

Laidlaw, R.A., **J. Smart**, **H. Ewing**, **S.E. Franks**, **H. Belting**, … **J.A. Gill**. 2021. Predator management for breeding waders: A review of current evidence and priority knowledge gaps. *Wader Study* 128: 44–55.

Larsen, T. 1991. Anti-predator behaviour and mating systems in waders: aggressive nest defence selects for monogamy. *Animal Behaviour* 41: 1057–1062.

Ławicki, Ł. & **P.W. Bull**. 2011. *Recent data on the declining breeding population of Eurasian Curlew Numenius arquata in western Poland*.

Ławicki, Ł. & **R. Kruszyk**. 2011. *Long-term decline of the grassland waders in Western Poland*.

Lebedeva, E.A. 1998. Waders in agricultural habitats of European Russia. *International Wader Studies* 10: 315–324.

Lehikoinen, A., **S. Fraixedas**, **D. Burgas**, **H. Eriksson**, **H. Henttonen**, **H. Laakkonen**, **P. Lehikoinen**, **J. Lehtomäki**, **J. Leppänen**, **S. Mäkeläinen**, **J. Niemimaa**, **M. Pihlajaniemi**, **J. Santaharju** & **K.**

Välimäki. 2016. The impact of weather and the phase of the rodent cycle on breeding populations of waterbirds in Finnish Lapland. *Ornis Fennica* 93: 31–46.

Leito, A., **J. Elts**, **E. Mägi**, **J. Truu**, **M. Ivask**, … **L. Luigujõe**. 2014. Coastal grassland wader abundance in relation to breeding habitat characteristics in Matsalu Bay, Estonia. *Ornis Fennica* 91: 149–165.

Leivits, A. & **M. Leivits**. 2016. Using density surface modelling for estimating abundance of breeding birds in heterogeneous mire habitats: a case study in Estonia.

Leivits, A., **M. Leivits** & **H. Pehlak**. 2013. Reconstruction of population trends of waders using historical and repeated mire bird survey data in Estonia. Reconstruction of population trends of waders using historical and repeated mire bird survey data in Estonia. https://doi.org/10.13140/2.1.3999.2005

Lenth, R., **H. Singman**, **J. Love**, **P. Buerkner** & **M. Herve**. 2018. R package emmeans: Estimated marginal means. *R package version 1.15-15*. https://doi.org/10.1080/00031305.1980.10483031>.

Lesiv, M., **D. Schepaschenko**, **E. Moltchanova**, **R. Bun**, **M. Dürauer**, … **S. Fritz**. 2018. Data descriptor: Spatial distribution of arable and abandoned land across former Soviet Union countries. *Scientific Data* 5: 1–12.

Li, Y., **T. Piersma**, **J.C.E.W. Hooijmeijer** & **R.A. Howison**. 2023. Land-use intensity impacts habitat selection of ground-nesting farmland birds in The Netherlands. *Ecological Solutions and Evidence* 4: e12201.

Liaw, A. & **M. Wiener**. 2002. Classification and Regression by randomForest. 2.

Librán-Embid, F., **F. Klaus**, **T. Tscharntke** & **I. Grass**. 2020. Unmanned aerial vehicles for biodiversity-friendly agricultural landscapes - A systematic review. *Science of The Total Environment* 732: 139204.

Liebezeit, J.R., **P.A. Smith**, **R.B. Lanctot**, **H. Schekkerman**, **I. Tulp**, **S.J. Kendall**, **D.M. Tracy**, **R.J. Rodrigues**, **H. Meltofte**, **J.A. Robinson**, **C. Gratto-Trevor**, **B.J. Mccaffery**, **J. Morse** & **S.W. Zack**. 2007. Assessing the Development of Shorebird Eggs Using the Flotation Method: Species-Specific and Generalized Regression Models. *The Condor* 109: 32–47.

Lieth, H. 1975. Modeling the Primary Productivity of the World. 237–263.

Lister, B.C. & **A. Garcia**. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences of the United States of America* 115: E10397–E10406.

Logan, J.D., **W. Wolesensky** & **A. Joern**. 2006. Temperature-dependent phenology and predation in arthropod systems. *Ecological Modelling* 196: 471–482.

Loonstra, A.H.J., **M.A. Verhoeven**, **N.R. Senner**, **J.C.E.W. Hooijmeijer**, **T. Piersma** & **R. Kentie**. 2019. Natal habitat and sex-specific survival rates result in a male-biased adult sex ratio. *Behavioral Ecology* 30: 843–851.

Loonstra, A.H.J., **M.A. Verhoeven** & **T. Piersma**. 2017. Sex-specific growth in chicks of the sexually dimorphic Black-tailed Godwit. *Ibis*: n/a-n/a.

Macdonald, M.A. & **M. Bolton**. 2008. Predation on wader nests in Europe. *Ibis* 150: 54–73.

Machín, P., **J. Fernández-Elipe**, **J. Hungar**, **A. Angerbjörn**, **R.H.G. Klaassen** & **J.I. Aguirre**. 2019. The role of ecological and environmental conditions on the nesting success of waders in sub-Arctic Sweden. *Polar Biology* 42: 1571–1579.

Machín, P., **J. Fernández-Elipe**, **H. Flinks**, **M. Laso**, **J.I. Aguirre** & **R.H.G. Klaassen**. 2017. Habitat selection, diet and food availability of European Golden Plover Pluvialis apricaria chicks in Swedish Lapland. *Ibis* 159: 657–672.

Magi, E., **T. Kastepõld** & **A. Lotman**. 2004. *Ornithological Monitoring and Wetland Management in Matsalu*.

Mägi, M. 2017. Predation of ground-nesting birds’ nests on Pärnu coastal meadows. *Hirundo*.

Malpas, L.R., **R.J. Kennerley**, **G.J.M. Hirons**, **R.D. Sheldon**, **M. Ausden**, **J.C. Gilbert** & **J. Smart**. 2013. The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *Journal for Nature Conservation* 21: 37–47.

Mandel, J.T., **G. Bohrer**, **D.W. Winkler**, **D.R. Barber**, **C.S. Houston** & **K.L. Bildstein**. 2011. Migration path annotation: cross-continental study of migration-flight response to environmental conditions. *Ecological Applications* 21: 2258–2268.

Manton, M., **P. Angelstam**, **P. Milberg** & **M. Elbakidze**. 2016. Wet Grasslands as a Green Infrastructure for Ecological Sustainability: Wader Conservation in Southern Sweden as a Case Study. *Sustainability* 8: 340.

Mason, L.R., **J. Smart** & **A.L. Drewitt**. 2018. Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis* 160: 71–88.

Mayfield, H.F. 1975. Suggestions for calculating nest success. *JSTOR*.

Mccracken, D.I. & **J.R. Tallowin**. 2004. Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands. *Ibis* 146: 108–114.

McKinnon, L., **M. Picotin**, **E. Bolduc**, **C. Juillet** & **J. Bêty**. 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology* 90: 961–971.

Meisner, K., **P. Sunde**, **K.K. Clausen**, **P. Clausen**, **C.C. Fælled** & **M. Hoelgaard**. 2014. Foraging ecology and spatial behaviour of the red fox (Vulpes vulpes) in a wet grassland ecosystem. *Acta Theriologica* 59: 377–389.

Melman, T.C.P., **A.G.M. Schotman**, **S. Hunink** & **G.R. de Snoo**. 2008. Evaluation of meadow bird management, especially black-tailed godwit (Limosa limosa L.), in the Netherlands. *Journal for Nature Conservation* 16: 88–95.

Meltofte, H., **T.T. Høye**, **N.M. Schmidt** & **M.C. Forchhammer**. 2007. Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. *Polar Biology* 30: 601–606.

Menne, M.J., **Imke Durre**, **Bryant Korzeniewski**, **Shelley McNeal**, **Kristy Thomas**, **Xungang Yin**, **Steven Anthony**, **Ron Ray**, **Russell S. Vose**, **Byron E.Gleason** & **Tamara G. Houston**. 2012. Global Historical Climatology Network - Daily (GHCN-Daily). *NOAA National Climatic Data Center*. Accessed 25 Jan 2021 at: *https://data.noaa.gov/dataset/dataset/global-historical-climatology-network-daily-ghcn-daily-version-3*.

Meyer, N., **L. Bollache**, **F.X. Dechaume-Moncharmont**, **J. Moreau**, **E. Afonso**, … **O. Gilg**. 2020. Nest attentiveness drives nest predation in arctic sandpipers. *Oikos* 129: 1481–1492.

Meyer, N., **L. Bollache**, **M. Galipaud**, **J. Moreau**, **F.X. Dechaume-Moncharmont**, … **O. Gilg**. 2021. Behavioural responses of breeding arctic sandpipers to ground-surface temperature and primary productivity. *Science of The Total Environment* 755: 142485.

Milsom, T.P., **S.D. Langton**, **W.K. Parkin**, **S. Peel**, **J.D. Bishop**, **J.D. Hart** & **N.P. Moore**. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *Journal of Applied Ecology* 37: 706–727.

Mischenko, A. 2020. Meadow-breeding waders in European Russia: Main habitat types, numbers, population trends and key affecting factors. *Wader Study* 127: 43–52.

Mischenko, A.L., **O. V. Sukhanova**, **V.N. Melnikov** & **P.N. Amosov**. 2019. Meadow Birds under Waning Traditional Pasture Animal Husbandry. *Biology Bulletin* 46: 1431–1441.

Mischenko, A.L. & **O. V. Sukhanova**. 2016. Response of wader populations in the vinogradovo floodplain (Moscow region, Russia) to changes in agricultural land use and spring flooding. *Wader Study* 123: 136–142.

Møller, A.P. 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution* 9: 6581–6587.

Møller, A.P., **O. Thorup** & **K. Laursen**. 2018. Predation and nutrients drive population declines in breeding waders. *Ecological Applications* 28: 1292–1301.

Mulder, T. 1972. *De Grutto (Limosa limosa (L.)) in Nederland: aantallen, verspreiding, terreinkeuze, trek en overwintering*.

Musters, C. j. m., **W. j. ter Keurs** & **G.R. de Snoo**. 2010. Timing of the Breeding Season of Black-Tailed Godwit Limosa limosa and Northern Lapwing Vanellus vanellus in The Netherlands. *Ardea* 98: 195–202.

Nethersole-Thompson, D. & **M. Nethersole-Thompson**. 1986. *Waders: their Breeding, Haunts and Watchers*. Poyser, Calton.

Newton, I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579–600.

Niemczynowicz, A., **P. Świętochowski**, **M. Brzeziński** & **A. Zalewski**. 2017. Non-native predator control increases the nesting success of birds: American mink preying on wader nests. *Biological Conservation* 212: 86–95.

Nordström, M., **J. Högmander**, **J. Laine**, **J. Nummelin**, **N. Laanetu** & **E. Korpimäki**. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biological Conservation* 109: 359–368.

OECD & **BirdLife**. 2019. Common farmland bird index. Accessed 13 Feb 2020 at: *https://ec.europa.eu/eurostat/web/products-datasets/-/env_bio2*.

Ohl, C., **M. Drechsler**, **K. Johst** & **F. Wätzold**. 2008. Compensation payments for habitat heterogeneity: Existence, efficiency, and fairness considerations. *Ecological Economics* 67: 162–174.

Oliveira, M.O., **B.M. Freitas**, **J. Scheper** & **D. Kleijn**. 2016. Size and Sex-Dependent Shrinkage of Dutch Bees during One-and-a-Half Centuries of Land-Use Change. *PLOS ONE* 11: e0148983.

Olsen, H. & **N.M. Schmidt**. 2004. Impacts of wet grassland management and winter severity on wader breeding numbers in eastern Denmark. *Basic and Applied Ecology* 5: 203–210.

Olson, C.R., **C.M. Vleck** & **D. Vleck**. 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiological and Biochemical Zoology* 79: 927–936.

Onrust, J., **E. Wymenga**, **T. Piersma** & **H. Olff**. 2019. Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands. *Journal of Applied Ecology* 56: 1333–1342.

Oosterveld, E.B., **F. Nijland**, **C.J.M. Musters** & **G.R. de Snoo**. 2011. Effectiveness of spatial mosaic management for grassland breeding shorebirds. *Journal of Ornithology* 152: 161–170.

Ospina, E.A., **L. Merrill** & **T.J. Benson**. 2018. Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. *Ecology and Evolution* 8: 3270–3279.

Ottvall, R. & **H.G. Smith**. 2006. Effects of an agri-environment scheme on wader populations of coastal meadows of southern Sweden. *Agriculture, Ecosystems and Environment* 113: 264–271.

Pain, D.J. & **M.W. Pienkowski**. 1997. *Farming and birds in Europe: the common agricultural policy and its implications for bird conservation*.

Pakanen, V.M., **A. Luukkonen** & **K. Koivula**. 2011. Nest predation and trampling as management risks in grazed coastal meadows. *Biodiversity and Conservation* 20: 2057–2073.

Parra-Torres, Y., **F. Ramírez**, **I. Afán**, **J. Aguzzi**, **W. Bouten**, **M.G. Forero** & **J. Navarro**. 2020. Behavioral rhythms of an opportunistic predator living in anthropogenic landscapes. *Movement Ecology* 8: 17.

Pe'er, G., **J.A. Finn**, **M. Díaz**, **M. Birkenstock**, **S. Lakner**, … **H. Guyomard**. 2022. How can the European Common Agricultural Policy help halt biodiversity loss? Recommendations by over 300 experts. *Conservation Letters* 15: e12901.

Pe'er, G., **L. V. Dicks**, **P. Visconti**, **R. Arlettaz**, **A. Báldi**, … **A. V. Scott**. 2014. EU agricultural reform fails on biodiversity. *Science* 344: 1090–1092.

Pearce-higgins, J.W., **M.C. Grant** & **M. Colin**. 2009. International importance and drivers of change of upland bird populations. Pages 237–255 in: *Drivers of Environmental Change in Uplands*.

Pearce-Higgins, J.W., **C.M. Beale**, **T.H. Oliver**, **T.A. August**, **M. Carroll**, … **H.Q.P. Crick**. 2017. A national-scale assessment of climate change impacts on species: Assessing the balance of risks and opportunities for multiple taxa. *Biological Conservation* 213: 124–134.

Pearce-higgins, J.W., **P. Dennis**, **M.J. Whittingham** & **D.W. Yalden**. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology* 16: 12–23.

Pearce-Higgins, J.W. & **D.W. Yalden**. 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European Golden Plover Pluvialis apricaria chicks. *Ibis* 146: 335–346.

Pehlak, H. & **A. Lõhmus**. 2008. An artificial nest experiment indicates equal nesting success of waders in coastal meadows and mires. *Ornis Fennica* 85: 66–71.

Pienkowski, M.W., **R.J. Fuller**, **D.B. Jackson** & **S.M. Percival**. 1986. Breeding waders of blackland, moorland and agriculturally improved moorland in the Uists and Benbecula. *Scottish Birds* 14.

Piersma, T. 2012. What is habitat quality? Dissecting a research portfolio on shorebirds. Pages 383–407 in: *Birds and Habitat*.

Plard, F., **H.A. Bruns**, **D. V. Cimiotti**, **A. Helmecke**, **H. Hötker**, **H. Jeromin**, **M. Roodbergen**, **H. Schekkerman**, **W. Teunissen**, **H. Jeugd** & **M. Schaub**. 2019. Low productivity and unsuitable management drive the decline of central European lapwing populations. *Animal Conservation*: acv.12540.

Pol, M. Van de, **P.W. Atkinson**, **J. Blew**, **O.P.M. Duriez**, **B.J. Ens**, **B. Hälterlein**, **H. Hötker**, **K. Laursen**, **K.H. Oosterbeek**, **A. Petersen**, **O. Thorup**, **K. Tjørve**, **P. Triplet** & **P. Yésou**. 2014. A global assessment of the conservation status of the nominate subspecies of Eurasian oystercatcher (Haematopus ostralegus ostralegus). *International Wader Studies* 20: 47–61.

Popov, I. & **D. Starikov**. 2015. Recent northward expansion of breeding black-tailed Godwits Limosa limosa in NW Russia. *Wader Study*.

Powell, L.L., **N.J. Cordeiro** & **J.A. Stratford**. 2015. Ecology and conservation of avian insectivores of the rainforest understory: A pantropical perspective. *Biological Conservation* 188: 1–10.

Prins, W.H., **J. Postmus**, **A.M. Reker** & **B. Ruiter**. 1988. Nitrogen use on grassland in spring in the Netherlands and elsewhere in Europe: temperature sum, stage of growth, rate and source of nitrogen. *Netherlands Fertilizer Technical Bulletin (Netherlands)*.

Quinn, G.P. & **M.J. Keough**. 2002. Experimental Design and Data Analysis for Biologists. *Experimental Design and Data Analysis for Biologists*. https://doi.org/10.1017/CBO9780511806384

R Core Team. 2017. R: A language and environment for statistical computing.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Accessed 22 Jul 2020 at: *https://www.r-project.org/*.

R Core Team. 2021. R: A language and environment for statistical computing. *The Journal of Open Source Software*.

Rannap, R., **T. Kaart**, **H. Pehlak**, **S. Kana**, **E. Soomets** & **K. Lanno**. 2017. Coastal meadow management for threatened waders has a strong supporting impact on meadow plants and amphibians. *Journal for Nature Conservation* 35: 77–91.

Ratte, H.T. 1984. Temperature and Insect Development. Pages 33–66 in: *Environmental Physiology and Biochemistry of Insects*.

Raven, P.H. & **D.L. Wagner**. 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 118.

Reijnen, R., **R. Foppen** & **H. Meeuwsen**. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation* 75: 255–260.

Ritchie, E.G. & **C.N. Johnson**. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12: 982–998.

Rogers, L.E., **W.T. Hinds** & **R.L. Buschbom**. 1976. A General Weight vs. Length Relationship for Insects. *Annals of the Entomological Society of America* 69: 387–389.

Rogers, L.E., **R.L. Buschbom** & **C.R. Watson**. 1977. Length-Weight Relationships of Shrub-Steppe Invertebrates1. *Annals of the Entomological Society of America* 70: 51–53.

Rönkä, A., **K. Koivula**, **M. Ojanen**, **V. Pakanen**, **M. Pohjoismäki**, **K. Rannikko** & **P. Rauhala**. 2006. Increased nest predation in a declining and threatened Temminck's Stint Calidris temminckii population. *Ibis* 148: 55–65.

Roodbergen, M., **B. van der Werf** & **H. Hötker**. 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *Journal of Ornithology* 153: 53–74.

Roodbergen, M., **C. Klok** & **H. Schekkerman**. 2008. The Ongoing Decline of the Breeding Population of Black-Tailed Godwits Limosa l. limosa in The Netherlands is Not Explained by Changes in Adult Survival. *https://doi.org/10.5253/078.096.0206* 96: 207–218.

Roodbergen, M. & **W. Teunissen**. 2014. *Meadow bird conservation in The Netherlands-lessons from the past and future developments*.

Roodbergen, M. & **W. Teunissen**. 2019. Meadow birds in the Netherlands. *Wader Study* 126: 7–18.

Roos, S., **J. Smart**, **D.W. Gibbons** & **J.D. Wilson**. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biological Reviews* 93: 1915–1937.

Saalfeld, S.T., **W.C. Conway**, **D.A. Haukos** & **W.P. Johnson**. 2012. Alleviation of nest thermal extremes by incubating Snowy Plovers in the Southern High Plains of Texas. *Wader Study Group Bulletin* 119: 77–83.

Salewski, V. & **L. Schmidt**. 2022. Nest cameras do not affect nest survival in a meadow-nesting shorebird. *Bird Conservation International* 32: 127–136.

Sánchez-Bayo, F. & **K.A.G. Wyckhuys**. 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*.

Sanderson, F.J., **M. Kucharz**, **M. Jobda** & **P.F. Donald**. 2013. Impacts of agricultural intensification and abandonment on farmland birds in Poland following EU accession. *Agriculture, Ecosystems and Environment* 168: 16–24.

Santangeli, A., **A. Lehikoinen**, **A. Bock**, **P. Peltonen-Sainio**, **L. Jauhiainen**, **M. Girardello** & **J. Valkama**. 2018. Stronger response of farmland birds than farmers to climate change leads to the emergence of an ecological trap. *Biological Conservation* 217: 166–172.

Santisteban, L., **C.W. Benkman**, **T. Fetz** & **J.W. Smith**. 2012. Survival and population size of a resident bird species are declining as temperature increases. *Journal of Animal Ecology* 81: 352–363.

Schekkerman, H. & **A.J. Beintema**. 2007. Abundance of Invertebrates and Foraging Success of Black-Tailed Godwit Limosa limosa Chicks in Relation to Agricultural Grassland Management. *Ardea* 95: 39–54.

Schekkerman, H. & **A. Boele**. 2009. Foraging in precocial chicks of the black-tailed godwit Limosa limosa: vulnerability to weather and prey size. *Journal of Avian Biology* 40: 369–379.

Schekkerman, H., **W. Teunissen** & **E. Oosterveld**. 2008. The effect of mosaic management on the demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology* 45: ???-???

Schekkerman, H., **W. Teunissen** & **E. Oosterveld**. 2009. Mortality of Black-tailed Godwit Limosa limosa and Northern Lapwing Vanellus vanellus chicks in wet grasslands: influence of predation and agriculture. *Journal of Ornithology*.

Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. *Movement Ecology 2019 7:1* 7: 1–18.

Seibold, S., **M.M. Gossner**, **N.K. Simons**, **N. Blüthgen**, **J. Müller**, **D. Ambarlı**, **C. Ammer**, **J. Bauhus**, **M. Fischer**, **J.C. Habel**, **K.E. Linsenmair**, **T. Nauss**, **C. Penone**, **D. Prati**, **P. Schall**, **E.D. Schulze**, **J. Vogt**, **S. Wöllauer** & **W.W. Weisser**. 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574: 671–674.

Seymour, A.S., **S. Harris**, **C. Ralston** & **P.C.L. White**. 2010. Factors influencing the nesting success of Lapwings Vanellus vanellus and behaviour of Red Fox Vulpes vulpes in Lapwing nesting sites. *Bird Study* 50: 39–46.

Sharps, E., **A. Garbutt**, **J.G. Hiddink**, **J. Smart** & **M.W. Skov**. 2016. Light grazing of saltmarshes increases the availability of nest sites for Common Redshank Tringa totanus, but reduces their quality. *Agriculture, Ecosystems and Environment* 221: 71–78.

Siemann, E. 1998. Experimental Tests of Effects of Plant Productivity and Diversity on Grassland Arthropod Diversity. *Ecology* 79: 2057.

Silva-Monteiro, M., **H. Pehlak**, **C. Fokker**, **D. Kingma** & **D. Kleijn**. 2021. Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: A review. *Global Ecology and Conservation* 28: e01657.

Silva-Monteiro, M., **J. Scheper**, **H. Pehlak**, **O. Kurina**, **S. Timonen**, … **D. Kleijn**. 2022. Invertebrate abundance increases with vegetation productivity across natural and agricultural wader breeding habitats in Europe. *Biological Conservation* 273: 109670.

Sim, I.M.W., **R.D. Gregory**, **M.H. Hancock** & **A.F. Brown**. 2005. Recent changes in the abundance of British upland breeding birds. *Bird Study* 52: 261–275.

Simons, N.K., **M.M. Gossner**, **T.M. Lewinsohn**, **S. Boch**, **M. Lange**, **J. Müller**, **E. Pašalić**, **S.A. Socher**, **M. Türke**, **M. Fischer** & **W.W. Weisser**. 2014. Resource-Mediated Indirect Effects of Grassland Management on Arthropod Diversity. *PLoS ONE* 9: e107033.

Siriwardena, G.M., **S.R. Baillie**, **S.T. Buckland**, **R.M. Fewster**, **J.H. Marchant** & **J.D. Wilson**. 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology* 35: 24–43.

Sládeček, M., **E. Vozabulová**, **M.E. Šálek** & **M. Bulla**. 2019. Diversity of incubation rhythms in a facultatively uniparental shorebird – the Northern Lapwing. *Scientific Reports 2019 9:1* 9: 1–11.

Smardon, R. 2014. Wetland Ecology Principles and Conservation, Second Edition. *Water* 6: 813–817.

Smart, J., **J.A. Gill**, **W.J. Sutherland** & **A.R. Watkinson**. 2006. Grassland-breeding waders: identifying key habitat requirements for management. *Journal of Applied Ecology* 43: 454–463.

Smith, J.J., **S.T. Hasiotis**, **M.J. Kraus** & **D.T. Woody**. 2009. Transient dwarfism of soil fauna during the Paleocene-Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences of the United States of America* 106: 17655–17660.

Smith, M.W., **J.L. Carrivick** & **D.J. Quincey**. 2015. Structure from motion photogrammetry in physical geography. *http://dx.doi.org/10.1177/0309133315615805* 40: 247–275.

Smith, P., **S. Dauncey**, **H. Gilchrist** & **M. Forbes**. 2012. The influence of weather on shorebird incubation. In: *Video Surveillance of Nesting Birds*.

Smith, R.K., **A.S. Pullin**, **G.B. Stewart** & **W.J. Sutherland**. 2011. Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation*.

Söderström, B. & **T. Pärt**. 2000. Influence of Landscape Scale on Farmland Birds Breeding in Semi-Natural Pastures. *Conservation Biology* 14: 522–533.

Sohlström, E.H., **U. Brose**, **R. van Klink**, **B.C. Rall**, **B. Rosenbaum**, **M. Schädler** & **A.D. Barnes**. 2022. Future climate and land-use intensification modify arthropod community structure. *Agriculture, Ecosystems & Environment* 327: 107830.

SOVON. 2001. *Atlas van de Nederlandse broedvogels 1998-2000*.

Steffan-Dewenter, I., **U. Münzenberg**, **C. Bürger**, **C. Thies** & **T. Tscharntke**. 2002. Scale-dependent Effects Of Landscape Context On Three Pollinator Guilds. *Ecology* 83: 1421–1432.

Strus, Y.M., **I.V. Shydlovskyy** & **I.M. Gorban**. 2018a. Grassland waders in the upper Prypiat’ basin: spatial distribution and number dynamics. *“Branta”: Transactions of the Azov-Black Sea Ornithological Station* 2018: 53–72.

Strus, Y.M., **I.V. Shydlovskyy** & **I.M. Gorban**. 2018b. Grassland waders in the upper Prypiat’ basin: spatial distribution and number dynamics. *“Branta”: Transactions of the Azov-Black Sea Ornithological Station* 2018: 53–72.

Struwe-Juhl, B. 1995a. Habitatwahl und Nahrungsökologie von Uferschnepfen-Familien (Limosa limosa) am Hohner See, Schleswig-Holstein. *Vogelwelt* 116: 61–72.

Struwe-Juhl, B. 1995b. Auswirkungen der Renaturierungsmaßnahmen im Hohner See-Gebiet auf Bestand, Bruterfolg und Nahrungsökologie der Uferschnepfe (Limosa limosa). *Corax* 16: 153–172.

Sutcliffe, L.M.E., **P. Batáry**, **U. Kormann**, **A. Báldi**, **L. V. Dicks**, … **T. Tscharntke**. 2015. Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions* 21: 722–730.

Sutherland, W.J. 2006. *Ecological census techniques: a handbook*.

Symonds, M.R.E. & **A. Moussalli**. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behavioral Ecology and Sociobiology*.

Tanneberger, F., **C. Tegetmeyer**, **S. Busse**, **A. Barthelmes**, **S. Shumka**, … **H. Joosten**. 2017. The peatland map of Europe. *Mires and Peat* 19.

Taylor, D.B., **R.D. Moon**, **J.B. Campbell**, **D.R. Berkebile**, **P.J. Scholl**, **A.B. Broce** & **J.A. Hogsette**. 2010. Dispersal of Stable Flies (Diptera: Muscidae) From Larval Development Sites in a Nebraska Landscape. *Environmental Entomology* 39: 1101–1110.

Teunissen, **H. Schekkerman**, **F. Willems** & **F. Majoor**. 2008a. Identifying predators of eggs and chicks of Lapwing Vanellus vanellus and Black-tailed Godwit Limosa limosa in the Netherlands and the importance of predation on wader reproductive output. *Ibis* 150: 74–85.

Teunissen, **C. Klok**, **D. Kleijn** & **H. Schekkerman**. 2008b. Factoren die de overleving van weidevogelkuikens beïnvloeden. *Natuur en Voedselkwaliteit*.

Teunissen, W., **H. Schekkerman** & **F. Willems**. 2005. *Predatie bij weidevogels; Op zoek naar de mogelijke effecten van predatie op de weidevogelstand*.

Teunissen, W.A. & **L. Soldaat**. 2006. Recente aantalsontwikkeling van weidevogels in Nederland. *De Levende Natuur* 107: 70–74.

Tharme, A.P., **R.E. Green**, **D. Baines**, **I.P. Bainbridge** & **M. O’Brien**. 2001. The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology* 38: 439–457.

Thieurmel, B. & **A. Elmarhraoui**. 2019. Package “suncalc” Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. *https:// CRAN.R-project.org/ package = suncalc*.

Thompson, D.B.A., **A.J. MacDonald**, **J.H. Marsden** & **C.A. Galbraith**. 1995. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*.

Thompson, P.S. & **W.G. Hale**. 1998. Breeding site fidelity and natal philopatry in the Redshank Tringa totanus. *Ibis* 131: 214–224.

Thompson, P.S., **D. Baines**, **J.C. Coulson** & **G. Longrigg**. 1994. Age at first breeding, philopatry and breeding site-fidelity in the Lapwing Vanellus vanellus. *Ibis* 136: 474–484.

Thorp, J.H. & **D.C. Rogers**. 2011. Midges, Mosquitoes, Blackflies, and Other True Flies. Pages 247–260 in: *Field Guide to Freshwater Invertebrates of North America*.

Thorup, O. 2006. Breeding waders in Europe 2000. International Wader Studies 14. *International Wader Study Group* 14.

Thorup, O. 2018. Population sizes and trends of breeding meadow birds in Denmark. *Wader Study* 125: 175–189.

Tichit, M., **D. Durant** & **E. Kernéïs**. 2005. The role of grazing in creating suitable sward structures for breeding waders in agricultural landscapes. *Livestock Production Science*.

Tinarelli, R. & **N. Bacetti**. 1989. Breeding Waders In Italy. *Wader Study Group Bulletin* 56: 7–15.

Tomkovich, P.S. 1992. Breeding conditions for waders m Russian tundras in 1992 Breeding conditions for waders in Russian tundras in 1992. *International Wader Studies* 10: 117–123.

Tryjanowski, P., **B. Gołdyn** & **A. Surmacki**. 2002. Influence of the red fox (Vulpes vulpes, Linnaeus 1758) on the distribution and number of breeding birds in an intensively used farmland. *Ecological Research* 17: 395–399.

Tryjanowski, P., **T. Hartel**, **A. Báldi**, **P. Szymański**, **M. Tobolka**, **I. Herzon**, **A. Goławski**, **M. Konvička**, **M. Hromada**, **L. Jerzak**, **K. Kujawa**, **M. Lenda**, **G. Orłowski**, **M. Panek**, **P. Skórka**, **T.H. Sparks**, **S. Tworek**, **& A.W.** & **M. Żmihorski**. 2011. Conservation of Farmland Birds Faces Different Challenges in Western and Central-Eastern Europe. *Acta Ornithologica* 46: 1–12.

Tulp, I. & **H. Schekkerman**. 2008. Has Prey Availability for Arctic Birds Advanced with Climate Change? Hindcasting the Abundance of Tundra Arthropods Using Weather and Seasonal Variation. *Arctic*.

Valkama, J., **D. Currie** & **E. Korpimäki**. 1999. Differences in the intensity of nest predation in the curlew Numenius arquata: A consequence of land use and predator densities? *Ecoscience* 6: 497–504.

Valle, R. & **F. Scarton**. 1996. Status and distribution of Redshanks Tringa totanus breeding along Mediterranean coasts. *Wader Study Group Bulletin* 81: 66–70.

van de Kam, J., **B. Ens**, **T. Piersma** & **L. Zwarts**. 2004. *Shorebirds: An Illustrated Behavioural Ecology*.

van de Pol, M. & **J. Wright**. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*.

van den Brink, V., **J. Schroeder**, **C. Both**, **P.M. Lourenço**, **J.C.E.W. Hooijmeijer** & **T. Piersma**. 2010. Space use by Black-tailed Godwits Limosa limosa limosa during settlement at a previous or a new nest location. *http://dx.doi.org/10.1080/00063650809461521* 55: 188–193.

Van Der Vliet, R.E., **E. Schuller** & **M.J. Wassen**. 2008. Avian predators in a meadow landscape: consequences of their occurrence for breeding open-area birds. *Journal of Avian Biology* 39: 523–529.

Van Der Vliet, R.E., **J. Van Dijk** & **M.J. Wassen**. 2010. How Different Landscape Elements Limit the Breeding Habitatof Meadow Bird Species. *https://doi.org/10.5253/078.098.0210* 98: 203–209.

van Paassen, A.G., **D.H. Veldman** & **A.J. Beintema**. 1984. A simple device for determination of incubation stages in eggs. *Wildfowl* 35: 173–178.

Van Turnhout, C.A.M., **R.P.B. Foppen**, **R.S.E.W. Leuven**, **A. Van Strien** & **H. Siepel**. 2010. Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation* 143: 173–181.

Vasander, H., **E.-S.S. Tuittila**, **E. Lode**, **L. Lundin**, **M. Ilomets**, **T. Sallantaus**, **R. Heikkilä**, **M.-L.L. Pitkänen** & **J. Laine**. 2003. Status and restoration of peatlands in northern Europe. *Wetlands Ecology and Management* 11: 51–63.

Verhoeven, M.A., **A.H.J. Loonstra**, **A.D. McBride**, **P. Macias**, **W. Kaspersma**, **J.C.E.W. Hooijmeijer**, **E. van der Velde**, **C. Both**, **N.R. Senner** & **T. Piersma**. 2020. Geolocators lead to better measures of timing and renesting in Black-tailed Godwits and reveal the bias of traditional observational methods. *Journal of Avian Biology*: jav.02259.

Verhoeven, M.A., **A.D. McBride**, **J.C.E.W. Hooijmeijer**, **T. Piersma** & **N.R. Senner**. 2022a. Earthworm abundance and availability does not influence the reproductive decisions of black-tailed godwits in an agricultural grassland. *Ecological Solutions and Evidence* 3: e12125.

Verhoeven, M.A., **A.H. Jelle Loonstra**, **T. Pringle**, **W. Kaspersma**, **M. Whiffin**, **A.D. McBride**, **P. Sjoerdsma**, **C. Roodhart**, **M.D. Burgess**, **T. Piersma** & **J. Smart**. 2022b. Do ditch-side electric fences improve the breeding productivity of ground-nesting waders? *Ecological Solutions and Evidence* 3: e12143.

Verhulst, J., **D. Kleijn** & **F. Berendse**. 2006. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. *Journal of Applied Ecology* 44: 70–80.

Verhulst, J., **A. Báldi** & **D. Kleijn**. 2004. Relationship between land-use intensity and species richness and abundance of birds in Hungary. *Agriculture, Ecosystems and Environment* 104: 465–473.

Verhulst, J., **D. Kleijn**, **W. Loonen**, **F. Berendse** & **C. Smit**. 2011. Seasonal distribution of meadow birds in relation to in-field heterogeneity and management. *Agriculture, Ecosystems and Environment* 142: 161–166.

Vessby, K. 2001. Habitat and weather affect reproduction and size of the dung beetle Aphodius fossor. *Ecological Entomology* 26: 430–435.

Vickery, J.A., **J.R. Tallowin**, **R.E. Feber**, **E.J. Asteraki**, **P.W. Atkinson**, **R.J. Fuller** & **V.K. Brown**. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38: 647–664.

Villoslada, M., **T.F. Bergamo**, **R.D. Ward**, **N.G. Burnside**, **C.B. Joyce**, **R.G.H. Bunce** & **K. Sepp**. 2020. Fine scale plant community assessment in coastal meadows using UAV based multispectral data. *Ecological Indicators* 111: 105979.

Villoslada, M., **T.F. Bergamo**, **R.D. Ward**, **C.B. Joyce** & **K. Sepp**. 2021. A novel UAV-based approach for biomass prediction and grassland structure assessment in coastal meadows. *Ecological Indicators* 122: 107227.

Villoslada, M., **T. Bergamo**, **R. Ward**, **C. Joyce** & **K. Sepp**. 2022. A UAV-based approach for biomass prediction and sward structure characterization in coastal meadows. *EGU22*. https://doi.org/10.5194/EGUSPHERE-EGU22-8301

Vince, S.W., **I. Valiela** & **J.M. Teal**. 1981. An experimental study of the structure of herbivorous insect communities in a salt marsh. *Ecology* 62: 1662–1678.

Vredenbregt, S. 2019. The Call of the Godwit : An Exploration of Birds and Farmers in a Landscape of Loss. *Uppsala University, Disciplinary Domain of Humanities and Social Sciences, Faculty of Arts, Department of Archaeology and Ancient History*.

Ward, R.D., **N.G. Burnside**, **C.B. Joyce** & **K. Sepp**. 2016. Importance of Microtopography in Determining Plant Community Distribution in Baltic Coastal Wetlands. *https://doi.org/10.2112/JCOASTRES-D-15-00065.1* 32: 1062–1070.

Webb, D.R. 1987. Thermal Tolerance of Avian Embryos: A Review. *The Condor* 89: 874.

Wheelock, M.J. & **M.E. O'Neal**. 2016. Insect Pollinators in Iowa Cornfields: Community Identification and Trapping Method Analysis. *PLOS ONE* 11: e0143479.

Whitaker, D.M., **A.L. Carroll** & **W.A. Montevecchi**. 2000. Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. *Canadian Journal of Zoology* 78: 740–747.

White, G.C. & **K.P. Burnham**. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139.

Wilson, A.M., **M. Ausden** & **T.P. Milsom**. 2004. Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. *Ibis* 146: 32–40.

Wilson, J.D., **R. Anderson**, **S. Bailey**, **J. Chetcuti**, **N.R. Cowie**, **M.H. Hancock**, **C.P. Quine**, **N. Russell**, **L. Stephen** & **D.B.A. Thompson**. 2014. Modelling edge effects of mature forest plantations on peatland waders informs landscape-scale conservation. *Journal of Applied Ecology* 51: 204–213.

Woud, T.Y. 2014. Impact of increasing landscape openness on waders and avian predators in the Netherlands.

Wylegala, P., **S. Wylegala** & **R. Pinkowski**. 2004. A decline in the Curlew Numenius arquata numbers in the Notec River valley in 1980-2004. *Ornitologiczne*.

Zámečník, V., **V. Kubelka** & **M. Šálek**. 2017. Visible marking of wader nests to avoid damage by farmers does not increase nest predation. *Bird Conservation International*: 1–9.

Zedler, J.B. & **S. Kercher**. 2005. WETLAND RESOURCES: Status, Trends, Ecosystem Services, and Restorability. *Annual Review of Environment and Resources* 30: 39–74.

Zhang, W., **J. Qi**, **P. Wan**, **H. Wang**, **D. Xie**, **X. Wang** & **G. Yan**. 2016. An Easy-to-Use Airborne LiDAR Data Filtering Method Based on Cloth Simulation. *Remote Sensing 2016, Vol. 8, Page 501* 8: 501.

Zharikov, Y. & **G.A. Skilleter**. 2003. Depletion of benthic invertebrates by bar-tailed godwits Limosa lapponica in a subtropical estuary. *Marine Ecology Progress Series* 254: 151–162.

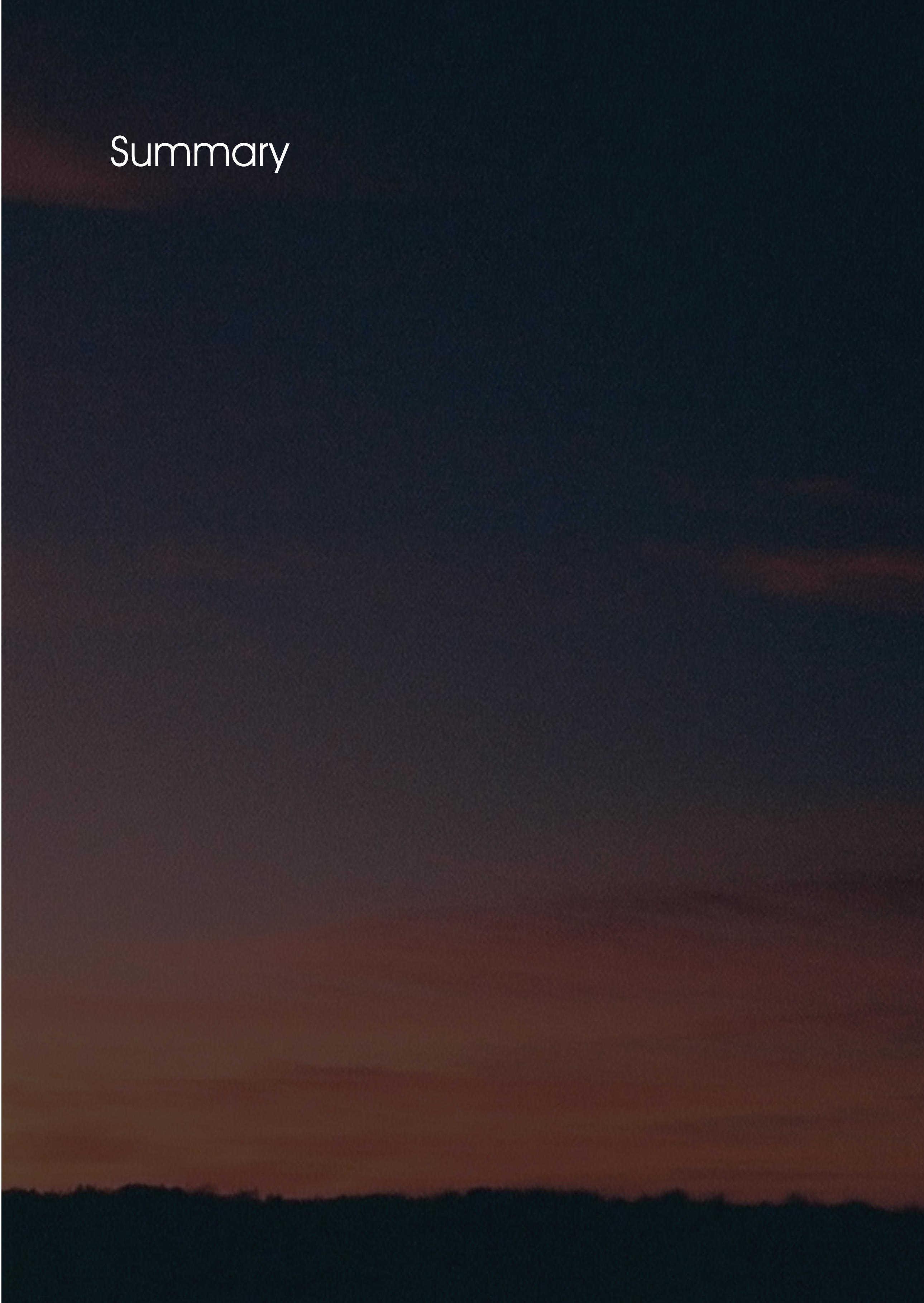
Zhou, H., **X. Wang** & **G. Schaefer**. 2011. Mean shift and its application in image segmentation. *Studies in Computational Intelligence* 339: 291–312.

Żmihorski, M., **D. Krupiński**, **D. Kotowska**, **J. Knape**, **T. Pärt**, **P. Obłoza** & **Å. Berg**. 2018. Habitat characteristics associated with occupancy of declining waders in Polish wet grasslands. *Agriculture, Ecosystems & Environment* 251: 236–243.

Zöckler, C. 2002. *Declining Ruff Philomachus pugnax populations-a response to global warming?*

Zuur, A.F., **E.N. Ieno**, **N. Walker**, **A.A. Saveliev** & **G.M. Smith**. 2009. Mixed effects models and extensions in ecology with R. https://doi.org/10.1007/978-0-387-87458-6

Summary



The Black-tailed Godwit (*Limosa l. limosa*) is a wader bird species currently threatened in most of its European breeding distribution range. While its breeding habitat preferences are known to be fairly broad, with populations occurring in natural undisturbed mires, semi-natural grasslands or highly intensive farmland monocultures, most of the conservation research for the species has been conducted in the highest end of land-use intensity range, where the bulk of the European population predominantly breeds. Thus, much of the knowledge regarding its main habitat requirements has been limited to certain geographical contexts, potentially leaving out crucial ecological knowledge needed to revert the observed declining populations, especially in less-studied habitats and regions. In this thesis, by comparing populations belonging to a wider set of varying breeding habitats available in Europe, I extend the analyses of the species' main habitat requirements. Using a cross-continental approach, I infer broader ecological patterns often undetected by studies that evaluate locations and habitats that are within proximate geographical regions and/or under similar environmental conditions.

The main habitat requirements that would be interesting to explore throughout the Black-tailed Godwit breeding range are the food supply availability, local predator pressures and the presence of specific structural and functional habitat characteristics, all essential for the species' territory settlement and breeding success (**Chapter 1**). Hence, **the overall aim of my PhD thesis** was to evaluate the importance of those three habitat requirements towards potentially attaining larger and denser Black-tailed Godwit breeding populations. As the breeding populations differ in size and density depending on the habitat and its respective land-use intensity, data was collected in a unique study system that covered five European countries (Finland, Estonia, Poland, the Netherlands and France), enabling widely varying land-use intensity habitats to be sampled.

I start by reviewing the current diversity and main population dynamics of wader species and communities present in the breeding habitats of the European continent (**Chapter 2**). Using previously published peer-reviewed and grey-literature data I examined how varying classes of agricultural land-use intensities affect the presence and breeding density of wader species that have general preferences, including the Black-tailed Godwit. I found that while the species is able to successfully breed in habitats with extremely contrasting environmental conditions, its population size and density peak are mainly located within breeding habitats of the “medium” class of the land-use intensity gradient. Those habitats mainly consist in farmland and grasslands that are often managed through agri-environmental schemes or traditional, extensive land management practices, such as low grazing pressures. Additionally, the sharply decreasing population densities towards both extremes of other land-use intensity habitat classes reveal that the species is greatly dependent on unidentified specific habitat requirements that enable denser populations in such “medium” land-use habitats, but not in the other classes. This created a base for assembling the rest of this thesis, further focusing on finding which specific habitat requirements play a major role in the population size and density and understanding its underlying ecological mechanisms.

In **Chapter 3**, using the original study system of Black-tailed Godwit key breeding areas, I began by investigating how the relative abundances of invertebrates, the food supply for both adults and chicks, differ according to different habitat conditions. By sampling three functionally distinct invertebrate communities (soil-dwelling, ground-active and flying), and a set of functional and structural environmental conditions (vegetation growth, soil moisture and temperature sums), I found that the overall abundance and average individual size of such invertebrate communities are mostly positively correlated with the local vegetation productivity. Stronger relationships were especially found with ground-active and soil-dwelling invertebrates while relationships with flying arthropods were less robust. This suggests that the intensification of agricultural management is likely not causing a reduction in the food available for both adults and chicks. Rather, the causes of the decline of the Black-tailed Godwit population observed in such habitats are most likely related to other aspects of land-use intensification, such as poor invertebrate accessibility within dense vegetation, mortality caused by heavy machinery or nest and chick predation enhanced by intensified management practices.

Next, In **Chapter 4** I investigated in the same sites which of the variables measured in Chapter 3 best predicted the Godwit population sizes and densities residing there. I looked into their relative importance during two crucial phenological times for the species: the clutch laying and chick hatching times, which are 28 days apart. The invertebrate food supply at the chick-hatching time was demonstrated to be the major variable enabling larger populations. Additionally, the food supply for adults during the clutch-laying time also played a relevant, yet weaker role. Thus, it seems that the number of breeding territories a location can sustain, or in other words, its carrying capacity, is dependent on the amount of invertebrate food it can generate. Remarkably, the measured environmental conditions played little role, as indirectly demonstrated by the flexibility of the species to breed in distinct, widely varying habitats.

The final habitat requirement investigated was the local predator pressures. This thesis focused on nest predation, as the sampling of the breeding grounds in the previous chapters allowed me to find a reasonable number of Black-tailed Godwit clutches that could be followed using thermologger devices that register incubation temperature fluctuations. In **Chapter 5**, by assessing predation rates and the total duration, frequency and average length of long incubation recesses performed by breeding birds, I investigated potential causes and impacts of such behavioural variables on hatching success across our study system sites. I found that long incubation recesses, the time spent away from incubation for a period longer than 20 minutes, are employed by birds in all countries independently of how large the local predation rates are. Furthermore, it revealed that couples that performed more frequent and lengthier long incubation recesses had higher nest survival probabilities, revealing it to be a potential anti-predatory mechanism. Overall, clutch predation was high in most of the populations sampled, and its impact on the overall population declines deserves to be further explored and targeted through conservation actions and research, especially at the low-intensity end of the land-use range.

Therefore, I found it important to additionally research the influence of functional and structural environmental conditions on the clutch survival probability of whole wader communities. Focusing on Estonian coastal grasslands, an important, under-researched breeding habitat for many wader species, including the Black-tailed Godwit, in **Chapter 6** I conducted an innovative assessment of the breeding areas' vegetation conditions to unveil which variables mainly influence wader nest predation. Using imagery collected by unoccupied aerial vehicles I explored the relative importance of the characteristics of the vegetation immediately surrounding the nest-site (vegetation height, growth and heterogeneity) and landscape level variables (distance to flooded areas and nearby forest cover) on nest predation probabilities. I found that vegetation height and heterogeneity, together with distance towards flooded areas greatly explain the nest predation probability of all found ground-nesting wader species. Interestingly, these variables are extremely similar to the ones found to affect nest predation probabilities in more intensive grassland habitats located in western European countries.

In conclusion, while the main habitat requirement mediating the density of Black-tailed Godwit pairs in a breeding area is the local invertebrate food availability, its inner structural and functional habitat characteristics potentially mediate the occurring predator pressures (**Chapter 7**). Consequently, I propose that to achieve larger and denser populations, a transition is necessary towards agricultural practices and policies that enable an optimal "medium" land-use management level for the species. Alternatively, the employment of some landscape enhancements, such as creating more diverse vegetation structures or experimenting with predator-exclusion methods, will potentially decrease the alarmingly high nest predation levels currently observed.

Cross-continental analyses are, therefore, essential in unveiling hard-to-detect ecological patterns, and much needed for the conservation of this endangered species. However, this can only be achieved if international collaborations between countries, researchers and citizens are kept at the forefront of conservation and nature protection in Europe.

Acknowledgements

One does not start a PhD without some established presumptions, especially about the upcoming challenges and struggles that may come along the journey. Yet, it still managed to completely blow all the expectations of how much I would learn, grow and overcome at both personal and technical levels. The people that accompanied me along this journey are worth more than just a name mention. For helping me accomplish this major achievement in my life I want to personally thank everyone.

First, I want to thank *David*, for never losing the excitement for the project over these years. Your insights and advice into the science we were conducting were always very helpful and continuously gave me the motivation to carry on the work, especially even when in my mind I thought I was reaching a dead end. I also need to thank you for your patience and kindness when I had to go through probably the worst days of my life.

Hannes, my friend and "supervisor": thank you for your enthusiasm while showing me all our beautiful Estonian study sites. There's nothing better than discussing birds, nature and trip schedules over some beers with you. I will be forever grateful to you, *Kadri*, *Lauri*, *Rosi* and little *Tavi* for being so welcoming and easygoing with this legal alien so far from its natal area.

All the top-notch conservation work on this dissertation could not be achieved without the motivation and perseverance of my "Godwit" colleagues: *Sami*, *Mo*, *Jelle*, *Frederic* and *Michał*. Thank you for easily accepting the challenge of running several experiments, exploring breeding sites and going back and forth several times with manuscripts and plans. I am extremely grateful and proud of the science we accomplished.

Although always accompanied by incredible landscapes, doing fieldwork sometimes was lonely. Thankfully my fieldwork needed some extra pair of hands most of the time, so there are plenty of people that were by my side in the field, helping me with all sorts of tasks. *Melissa*, *Kim*, *Morten*, *Jaap*, *Sander*, *Frederik*, *Audrey* and *Sam*: happy to know that I shared the excitement to be in the field with other fellow ecologists.

Interestingly, working in front of the computer was even more challenging and lonely. I need to thank all my colleagues at Wageningen University that helped through the statistics, coding, preliminary presentations or simply discussing ideas. To *Jeroen*, *Runa*, *Eline* and *Thijs*: thank you for spending some time with me in front of our laptops, trying to unlock some gears in my brain. I believe in the power of coffee breaks, and sharing the workspace with this amazing set of scientists is a huge push towards success. Thank you *Maartje*, *Iryna*, *Zakaria*, *Maarten*, *Sina*, *Zulin*, *Chen*, *Petra*, *Gerda*, *Jan*, *Juul*, *Elmar*, *Kalev*, *Olavi* and *Leho*, for making the working days more enjoyable. I wish you all the best in your PhD journeys or your already very well-established careers.

One of the biggest surprises for me was how welcoming and, for the lack of a more accurate adjective, cool, the wader research community is. I need to thank some colleagues that I have met throughout the Wader Study conferences around Europe. I am lucky to belong to a such fascinating set of researchers, which make me want to continue to pursue a career in conservation within this amazing taxa. *José*, *Veronica*, *João*, *Maite*, *Josh*, *Camilo* and all the folks that were behind the *IWSG* conferences, thank you for all your commitment and energy. However, I have to especially thank my colleague and friend *Triin*. Besides being an excellent, hardworking wader researcher herself, she couldn't be a better colleague to discuss and solve many of the challenges that doing fieldwork in Estonia brought. I will always cherish all the help and advice you gave that facilitated me to advance and finish this dissertation.

Academia isn't only about what we learn in our very narrow expertise field. My personal learning experience was incredible in Tartu, which wouldn't be the same without these guys: *Sofia*, *Lisandra*, *Miguelito*, *Thaisa*, *Raul*, *Kai*, *Alain*, *Alfonso*, *Marta*, *Francesca*, *Volha*, *Egor*, *Tauri*, *Toomas*, *Mari* and *James*. Thank you for having the courage to befriend this "bird person". I am glad that the universe managed to align itself for all of us to meet in this strange place called Tartu. Being fresh in a new, unknown place can be difficult, but I am very happy we could make it easier for each other. Partying and enjoying life and nature while discussing the most out-there topics with you all will always remain in my memories. Long live the tripoloski.

I also have to give a special mention to these two guys which every time we are together I feel like we are inside some sort of twisted sitcom: *André* and *Daniela*. Horror movies are not the same without you. Visiting decaying urban or remote natural locations is not the same without you. I am extremely happy that our character development is still evolving and we all feel comfortable sharing. We always have a snark comment ready, and I will be forever eager for our next holidays. Sundays are not the same without you.

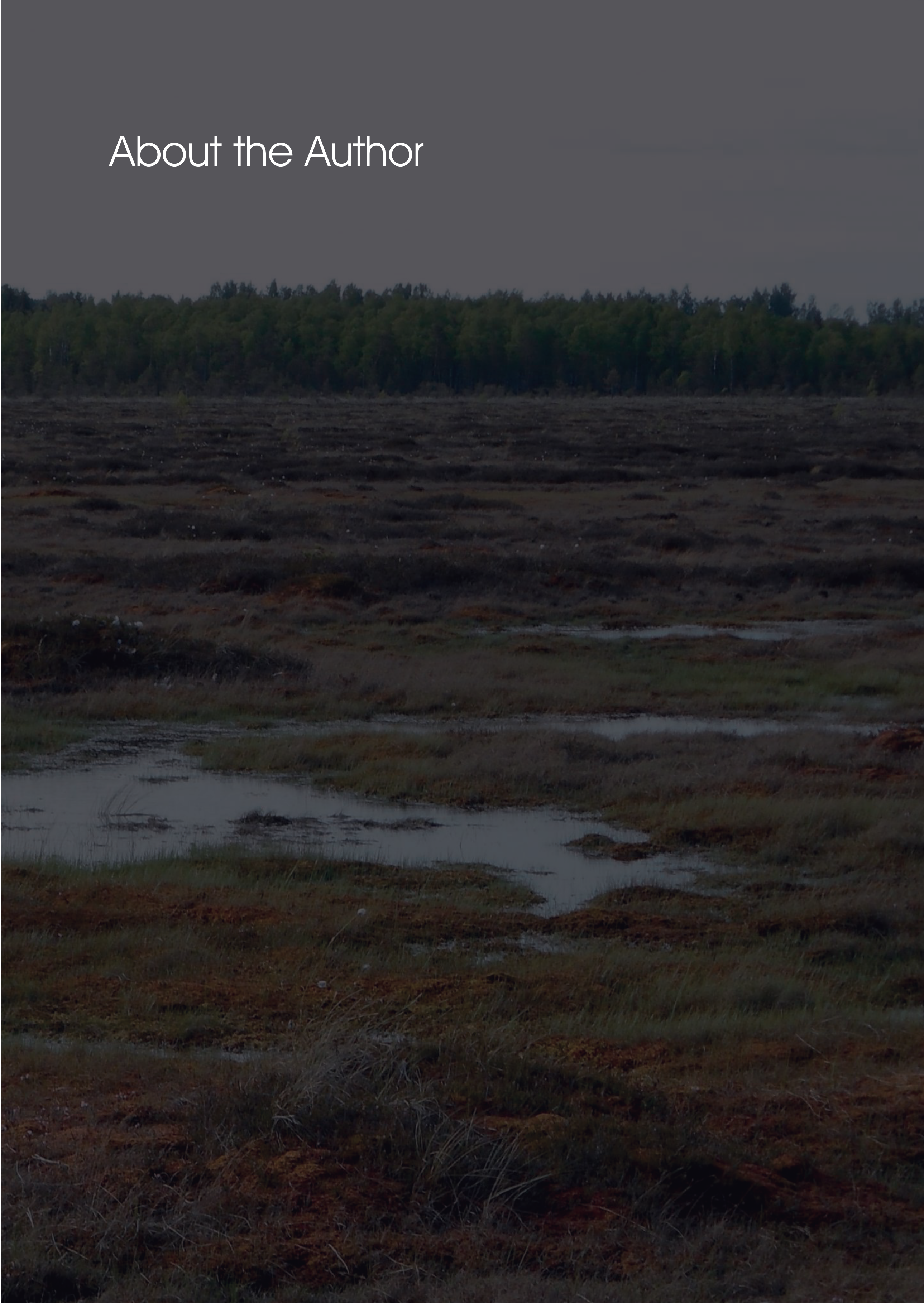
Another set of very special individuals is *Harry*, *Nina* and *Elena*. Thank you for always being by my side. Beyond our unstoppable stream of memes and random conversations, we were and are a truly united and supporting group of friends. You guys understand better than anyone else the struggles of academia and were a role model for me in how to accomplish this. I am so glad we still have the same energy since our Master's degree in Leiden. Just slightly more refined hobbies and tastes I would say!

Props to all my friends who still are part of my life and bring me joy every time we meet. The pandemic truly reinforced how friendship bonds help to overcome everything. These people were there, in one way or another, during very harsh moments of my life. Thank you my beloved Paródia and Aveiro gang: *Bela*, *Carmen*, *Filipa*, *André*, *Pisco*, *Pocah*, *Inês*, *Joanica*, *Maria*, *Miau*, *Piu* (Δ), *Tatxi*, *Teresa*, *Santiago, Valter*, *Eduardo* and *Margarida*. Thank you my Figueira-da-Foz gang: *Telmo*, *Leonor*, *Zeto*, *Tiago*, *Coruche*, *Luís*, *Barão*, *Aninhas*, *Diogo*, *Curado*, *Polter*, *Pamela*, *Inês*, *Rita*, *Jens*, *Dri* and *Caroline*. Thank you for sheltering this bird guy, Droevendaal peeps: *Matika*, *Claire*, *Fotis*, *Marco*, *Romanos*, *Caro*, *Vale* and *Bárbara*.

Probably the person I could write the longest for its well-deserved acknowledgements is *Mariana, "Nana"*. Because we are both very aware of how much we evolved together as humans and scientists this paradoxically makes me want to condensate and minimally write how awesome you are: without hesitating or any demands you were there to pick me up and hug me. I am forever grateful to you, *Renato*, *Pinda* and *Ziggy* for just being near me. I am always longing for the next time I can be near you all.

E não podia acabar sem agradecer à minha família. À minha *Mãe*, por se preocupar e se orgulhar, das grandes às pequenas conquistas. À minha *Irmã*, *Lino* e *Mariana Pequena*, pela energia sempre positiva que me transmitem. À minha madrinha querida, *Tia*, e os meus primos *Marcel* e *Joana*. À *Mariana Grande* também por ter coragem de se enfiar nesta família. Aos meus tios *Zé* e *Madalena* e ao meu primo *Luís* por sempre me querer receber e ouvir. E obrigado aos outros membros familiares que nem se apercebem (ou talvez sim) do quão importante são para mim, *Puki* e *Hobbes*. E claro ao meu *Pai*, que infelizmente não vai conseguir ver este final mas conseguiu ver o quão importante para mim foi ter conseguido inicialo.

About the Author



About the author

Miguel Ângelo Silva Monteiro was born in Figueira-da-Foz, Portugal, on March 13th, 1990. Growing up in a little village near the sea, Miguel dreamt of becoming a mailman (to travel to new, faraway places), an astronaut (to travel to new, faraway places), or a mathematician (because puzzle games are fun). However, learning during high school about the theory of evolution and how animals shift and transform according to the natural laws, made him want to pursue more knowledge in the field of Biology. Therefore, he enrolled in his Biology BSc at Aveiro University, Portugal, where he fell in awe with the topics of ecology, conservation, and particularly, ornithology. In his BSc thesis, he studied the ecology of the iconic White-stork (*Ciconia ciconia*), igniting his curiosity about the migratory habits of birds and how we, as humans, can help them survive in this increasingly threatened world. Not fully satisfied, Miguel continued his academic journey into an MSc degree at Leiden University, the Netherlands, where he sharpened his skills on all his favourite topics. His MSc thesis focused on the invasive Ring-necked parakeet (*Psittacula krameri*) that lives in the urban landscapes of the Netherlands. Throughout his MSc thesis and degree, he was able to learn and combine a number of techniques and methods of both the field and lab work realms. At this point, it was clear to him that having a career in ornithology and conservation was worth pursuing and enrolling in a PhD degree was only logical. Thus, Miguel started his PhD journey at the Plant Ecology and Nature Conservation research group at Wageningen University, the Netherlands, in 2017. Miguel had the privilege of exploring the several breeding habitats of the Black-tailed godwit (*Limosa limosa*) across Europe in a project involving plenty of field and collaborative work. Some highlights of his doctoral project consist in exploring wild bogs and floodplains in Estonia, Belarus and Ukraine, learning the ecological processes affecting invertebrate numbers or capturing and deploying GPS-tracking devices on some individual Black-tailed godwits, to follow their fascinating migratory journeys throughout the world. Another personal achievement was the ability to create and implement his network of several wader researchers into the project, to whom he is forever grateful to be able to translate all the hard work done in the field into this thesis. Currently, during his free time, Miguel enjoys being outdoors, doing yoga, reading sci-fi literature, watching horror movies and MMA matches with his friends, cooking random meals, tasting craft beers and playing around with analogue cameras, while always paying attention to what is flying or singing nearby.

Miguel has recently started a post-doctoral position at the South Bohemian University in the Czech Republic, where he will continue to research wader birds and their ecology and migratory habits, while being able to travel to new, faraway places.

PE&RC TRAINING AND EDUCATION STATEMENT

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review/project proposal (6 ECTS)

- Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: a review

Post-graduate courses (6.2 ECTS)

- Animal movement analysis; Amsterdam University (2017)
- Wetland ecology and conservation; NOVA University Network (2019)
- R and Big data; PE&RC (2019)
- Mixed linear models; PE&RC (2021)

Laboratory training and working visits (1.5 ECTS)

- Breeding habitat selection visit to the field site; Office National Chasse & Faune Sauvage, Ile Olonne, France (2018)

Competence, skills and career-oriented activities (2.7)

- Scientific writing; WGS (2017)
- Scientific integrity; WGS (2017)
- Scientific publishing; WGS (2018)

PE&RC Annual meetings, seminars and PE&RC weekend/retreat (2.1 ECTS)

- PE&RC First years weekend (2017)
- PE&RC Day (2018, 2019)
- PE&RC Midterm weekend (2019)

Discussion groups/local seminars or scientific meetings (6 ECTS)

- International wader study group meeting; Prague, Czech Republic (2017)
- International wader study group meeting; Workum, the Netherlands (2018)
- International wader study group meeting; Morecambe, United Kingdom (2019)
- International wader study group meeting; online (2020)

International symposia, workshops and conferences (5.7 ECTS)

- 2nd European meeting of young ornithologists; Turin, Italy (2018)
- International wader study group conference; online (2021)
- International wader study group conference; Szeged, Hungary (2022)

BSc/MSc thesis supervision (1.5 ECTS)

- Breeding densities and habitat selection of wader species in several field-sites across Europe

LIST OF PUBLICATIONS

Published Papers

Silva-Monteiro M, Pehlak H, Fokker C & Kleijn D (2021) Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: A review. *Global Ecology & Conservation 28:e01657* (**chapter 2** of this thesis)

Silva-Monteiro M, Scheper J, Pehlak H, Kurina O, Timonen S, Pessa J, Pasanen E, Verhoeven M, Loonstra J, Piersma T, Robin F, Korniluk M, Świętochowski P, Onwezen M, Bongers M, Hamelink J, Bik S, Lembreght F, Dunn A & Kleijn D (2022) Invertebrate abundance increases with vegetation productivity across natural and agricultural wader breeding habitats in Europe. *Biological Conservation 273:109670* (**chapter 3** of this thesis)

Silva-Monteiro M, Pehlak H, Timonen S, Pessa J, Pasanen E, Verhoeven M, Loonstra J, Piersma T, Robin F, Korniluk M, Onwezen M, Bongers M, Hamelink J, Lembreght F, Dunn A & Kleijn D (2022) Cross-continental differences in Black-tailed Godwit breeding densities are best explained by arthropod abundance in the chick-hatching period. *Journal of Ornithology 164, pages 287–297* (**chapter 4** of this thesis)

In Preparation

Silva-Monteiro M, Pehlak H, Timonen S, Verhoeven M, Loonstra J, Robin F, Korniluk M, Białomyzy P, Tumiel T, Leeming S, Bik S, Onwezen M, Lembreght F & Kleijn D; Frequent and prolonged incubation recesses across European Black-tailed Godwit populations: a successful nest defence strategy? (**chapter 5** of this thesis) *In preparation*

Silva-Monteiro M*, Villoslada M*, Bergamo T, Kaasiku T, Carneiro C & Kleijn D; UAVs unveil distance to flooded areas, vegetation height and sward heterogeneity in coastal meadows as key variables explaining wader nest survival. (**chapter 6** of this thesis) *In preparation*

* These authors contributed equally

AFFILIATION OF CO-AUTHORS

David Kleijn	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Jeroen Scheper	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Hannes Pehlak	Institute of Agriculture and Life Sciences Estonian University of Life Sciences Tartu, Estonia
Olavi Kurina	Institute of Agriculture and Life Sciences Estonian University of Life Sciences Tartu, Estonia
Sami Timonen	Department of Ecology and Genetics The University of Oulu Oulu, Finland
Jorma Pessa	The Centre for Economic Development, Transport and the Environment North Ostrobothnia, Finland
Esko Pasanen	Nurmikankuja Järvenpää, Finland
Mo Verhoeven	Groningen Institute for Evolutionary Life Sciences University of Groningen Groningen, The Netherlands Department of Animal Ecology Netherlands Institute of Ecology (NIOO-KNAW) Wageningen, The Netherlands
Jelle Loonstra	Groningen Institute for Evolutionary Life Sciences University of Groningen Groningen, The Netherlands
Theunis Piersma	Groningen Institute for Evolutionary Life Sciences University of Groningen Groningen, The Netherlands
Frederic Robin	LPO France Rochefort, France

Michał Korniluk	Museum & Institute of Zoology Polish Academy of Sciences Warsaw, Poland
Piotr Swiętochowski	Nature Association Dubelt Michałowo, Poland
Paweł Białomyzy	Nature Association Dubelt Michałowo, Poland
Tomasz Tumiel	Nature Association Dubelt Michałowo, Poland
Cornelis Fokker	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
David Kingma	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Melissa Onwezen	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Morten Bongers	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Jaap Hamelink	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Sander Bik	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Frederik Lembreght	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Audrey Dunn	Plant Ecology and Nature Conservation Group Wageningen University Wageningen, The Netherlands
Samuel Leeming	Institut für Biologie Graz University Graz, Austria

Miguel Villoslada
Department of Geographical and Historical Studies
University of Eastern Finland
Joensuu, Finland
Institute of Agriculture and Life Sciences
Estonian University of Life Sciences
Tartu, Estonia

Thaisa Bergamo
Department of Geographical and Historical Studies
University of Eastern Finland
Joensuu, Finland
Institute of Agriculture and Life Sciences
Estonian University of Life Sciences
Tartu, Estonia

Triin Kaasiku
Institute of Ecology and Earth Sciences
University of Tartu
Tartu, Estonia

Camilo Carneiro
South Iceland Research Centre
University of Iceland
Iceland
Biology Department & CESAM
University of Aveiro
Aveiro, Portugal

COLOPHON

The research described in this thesis was carried out at the Plant Ecology and Nature Conservation Group of Wageningen University & Research, the Netherlands, and was financially supported by a grant from Wageningen University & Research to David Kleijn (proj. nr. 5160957485). Financial support from Wageningen University & Research for printing this thesis is gratefully acknowledged.

Financial support from Wageningen University for printing this thesis is gratefully acknowledged.

Front Cover photograph by André Pedro Couto

Chapter 3 Cover photograph by Marycha Franken

Printed: ProefschriftMaken.nl on recycled FSC-certified paper
Layout: Dennis Hendriks | ProefschriftMaken.nl