Links between agricultural management and wader populations in sub-arctic landscapes

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Dissertation submitted in partial fulfilment of a
Philosophiae Doctor degree in biology

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Abstract

The development and expansion of agriculture throughout the world has been a major driver of biodiversity loss in recent decades. Icelandic agriculture is currently not as intense and widespread as in many other western countries, and the effects of agriculture on biodiversity in Iceland and similar farming systems are largely unknown. Iceland supports big populations of several wader species of international importance and the aim of this thesis is to explore the links between agriculture and breeding wader populations. This was done by surveying waders in agricultural landscapes across Iceland and by carrying out a questionnaire survey among farmers. Surveys of wader density in areas of varying agricultural management intensity throughout lowland Iceland revealed high densities of breeding waders in all three management categories. However densities are generally lower on more intensely managed land, suggesting possible negative effects of future expansion of agriculture, given that the majority of farmers questioned for the study reported they were likely to expand cultivated land in the coming years. The volcanic nature of Iceland and varying temperatures have a strong influence on bird distribution and abundance, and interact with the effects of cultivated land on birds. In areas further from volcanic activity, wader density increases when there is more cultivated land around but the reverse occurs in areas with high levels of historic volcanic ash fall. This suggests that the location of cultivated land expansion can partly determine future effects on birdlife. Currently there are few efforts towards protecting these species in Iceland and, when questioned about their views towards birdlife, farmers reported that they do not currently take bird conservation into consideration in their land use management, although they do consider it important to have rich birdlife on their land and were positive towards participating in proposed conservation management. Cooperation with farmers, who own most of the lowlands, will therefore be crucial in maintaining these widespread and internationally important wader breeding populations.

Útdráttur

Hnignun líffræðilegrar fjölbreytni í heiminum á síðustu áratugum má að stórum hluta rekja til aukinnar útbreiðslu og ákefðar í landbúnaði. Íslenskur landbúnaður hefur enn ekki náð sömu ákefð og útbreiðslu og víða í vestrænum ríkjum og áhrif landbúnaðar á líffræðilega fjölbreytni eru að mestu óþekkt hérlendis, sem og í öðrum sambærilegum landbúnaðarkerfum. Ísland er mikilvægt varpsvæði margra ábyrgðartegunda og hér finnast stórir stofnar vaðfugla. Markmið doktorsverkefnisins er að skýra tengsl landbúnaðar og vaðfuglastofna á norrænum slóðum með mælingum á Íslandi. Þetta var gert bæði með að meta þéttleika vaðfugla á landbúnaðarsvæðum sem og að spyrja bændur um fyrirætlanir þeirra í landnýtingu og viðhorf þeirra til fuglalífs á landi þeirra. Mat á þéttleika vaðfugla á svæðum undir mismiklum áhrifum landbúnaðar sýnir að almennt er hár þéttleiki á öllum svæðunum en þéttleikinn er lægri á svæðum undir meiri landbúnaðaráhrifum. Þetta bendir til að ef flatarmál ræktað lands eykst muni það hafa neikvæð áhrif á þéttleika vaðfugla en meirihluti þeirra bænda sem rætt var við fyrir verkefnið sögðust stefna á að auka ræktað land á komandi árum. Eldvirkni og hitastig hafa umtalsverð áhrif á fuglalíf á Íslandi, en að auki geta áhrif ræktaðs lands á þéttleika vaðfugla ráðist af þessum tveimur þáttum. Á sumum svæðum minnkar þéttleiki með aukinni útbreiðslu ræktað lands en á öðrum svæðum eykst þéttleikinn. Áhrif aukningar ræktaðs lands á vaðfuglastofna ráðast því að hluta til af staðsetningu. Það eru litlar áherslur lagðar á vernd þessara tegunda á Íslandi og þegar bændur voru spurðir út í viðhorf þeirra til fuglalífs á landi þeirra sögðust þeir almennt ekki taka mikið tillit þess við landnýtingu þrátt fyrir að telja mikilvægt að hafa ríkulegt fuglalíf. Aftur á móti voru bændur jákvæðir gagnvart þeim verndaðgerðum sem lagðar voru til en vitað er að samvinna við landeigendur er lykilatriði ef á að viðhalda þeim þáttum líffræðilegrar fjölbreytni sem hafa víðtæka útbreiðslu.

List of publications

This thesis is based on the following papers. Within the thesis, references to these papers will be by their Roman numerals.

Paper I: Jóhannesdóttir, L., Gill, J. A., Alves, J. A., & Gunnarsson, T. G. (201X). Icelandic meadow breeding waders: status, threats and conservation challenges. *International Wader Study - Submitted*.

Paper II: Jóhannesdóttir, L., Alves, J. A., Gill, J. A., & Gunnarsson, T. G. (201X). Use of agricultural land by breeding waders in low-intensity farming landscapes. *In review*.

Paper III: Gunnarsson, T. G., Jóhannesdóttir, L., Alves, J. A., Þórisson, B., & Gill, J. A. (2016). Effects of spring temperature and volcanic eruptions on wader productivity. Ibis, doi: 10.1111/ibi.12449

Paper IV: Jóhannesdóttir, L., Gill, J. A., Alves, J. A., & Gunnarsson, T. G. (201X). Interacting effects of agriculture and landscape structure on breeding wader populations in Iceland. Manuscript.

Paper V: Jóhannesdóttir, L., Alves, J. A., Gill, J. A., & Gunnarsson, T. G. (2017). Reconciling biodiversity conservation and agricultural expansion in the sub-arctic environment of Iceland. Ecology and Society, doi: 10.5751/es-08956-220116

Papers I and **III, V** are reproduced with kind permission from the publishers. In addition, some unpublished data are presented.

Other publications included as an appendix in the doctoral thesis (with permission from the publisher):

Jóhannesdóttir, L., Arnalds, Ó., Brink, S., & Gunnarsson, T. G. (2014). Identifying important bird habitats in a sub-arctic area undergoing rapid land-use change. Bird Study, 61(4), 544-552. doi: 10.1080/00063657.2014.962481

Author's contribution

Paper I. Lilja Jóhannesdóttir collated the data for this paper, was the leading author in collaboration with co-authors and is the corresponding author.

Paper II. Lilja Jóhannesdóttir, in collaboration with co-authors, designed the methods and was responsible for all data collection. Lilja Jóhannesdóttir analysed and interpreted the results, wrote the paper together with co-authors and is the corresponding author.

Paper III. Lilja Jóhannesdóttir helped with design of the methods, data analysis, writing, and is the second author on this paper.

Paper IV. Lilja Jóhannesdóttir designed the methods, together with co-authors, and collected all the bird data. Sigmundur H. Brink extracted land cover information. Lilja Jóhannesdóttir analysed and interpreted results, wrote the paper together with co-authors and will be the corresponding author.

Paper V. Lilja Jóhannesdóttir designed the questionnaire, in collaboration with co-authors, and carried out all of the interviews with farmers. She analysed and interpreted the results, wrote the paper together with co-authors and is the corresponding author.

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Here I go again
–Whitesnake

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Every lyric out there
–All the bands

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Waka Waka
–Shakira

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1 Introduction

One of the most urgent challenges facing humankind is to balance nature conservation with the extraction and usage of resources such as food and water. These resource demands by humans have grown rapidly and extensively over the last century (Millennium Ecosystem Assessment 2005) and, with a fast-growing human population, the demand for resources is likely to grow even further in the near future (Green et al. 2005). It has been predicted that the human population growth will plateau around the mid-21st century but a deceleration in human population growth has been correlated with increased wealth, which will result in more consumption, so even when human population growth stops, the demand will continue to increase, adding more pressure to Earth's ecosystems (Godfray et al. 2010). Integrating conservation and increased resource demand is therefore likely to be increasingly challenging in the coming decades (Godfray et al. 2010, Rands et al. 2010). The Anthropocene has been characterised by overexploitation of resources and has driven biodiversity loss through direct (e.g. habitat destruction, over fishing and hunting) and indirect (e.g. global warming, sea level rise) environmental changes (Jackson 2008). Despite clear knowledge of the intrinsic value of species and their importance for ecosystem services, despite being highly valued by humans and despite widespread information on the scale of biodiversity decline, there is currently no sign of reduction in large-scale extinction rates (Millennium Ecosystem Assessment 2005, Butchart et al. 2010). Understanding biodiversity responses to environmental change is therefore one of the biggest issues facing human societies.

1.1 Agriculture

Agriculture is one of the most influential forms of land use in the world and agricultural land expanded by ~466% from the year 1700 until 1980 (Meyer & Turner 1992). After 1980 this expansion slowed down but, by then, approximately 40% of all terrestrial land in the World was already being used for agriculture (World Bank 2014), with much of the remaining areas being mostly comprised of land unsuitable for agriculture such as deserts, urban areas, mountains etc. (Ramankutty et al. 2002). It is estimated that 70% of the grasslands, 50% of the savannah, 45% of the temperate deciduous forests and 27% of the tropical forests have been cleared for agriculture globally (Foley et al. 2005). Even though rates of agricultural expansion are decreasing overall they are still expanding in some regions of the World, such as Sub-Saharan Africa and Latin America (World Bank 2014).

1.1.1 Intensification of agriculture

Even though the rate of expansion of agricultural land decreased late in the 20th century, the increase in production has been extensive (Figure 1) and has even outpaced global human population growth (Matson et al. 1997). This has primarily been achieved by increasing yield through intensification of management on land already used for agriculture, for example through the use of better crop varieties, increased usage of chemical fertilizers and pesticides, powerful irrigation mechanisms and mechanization of agricultural operations (Naylor 1996, Matson et al. 1997).
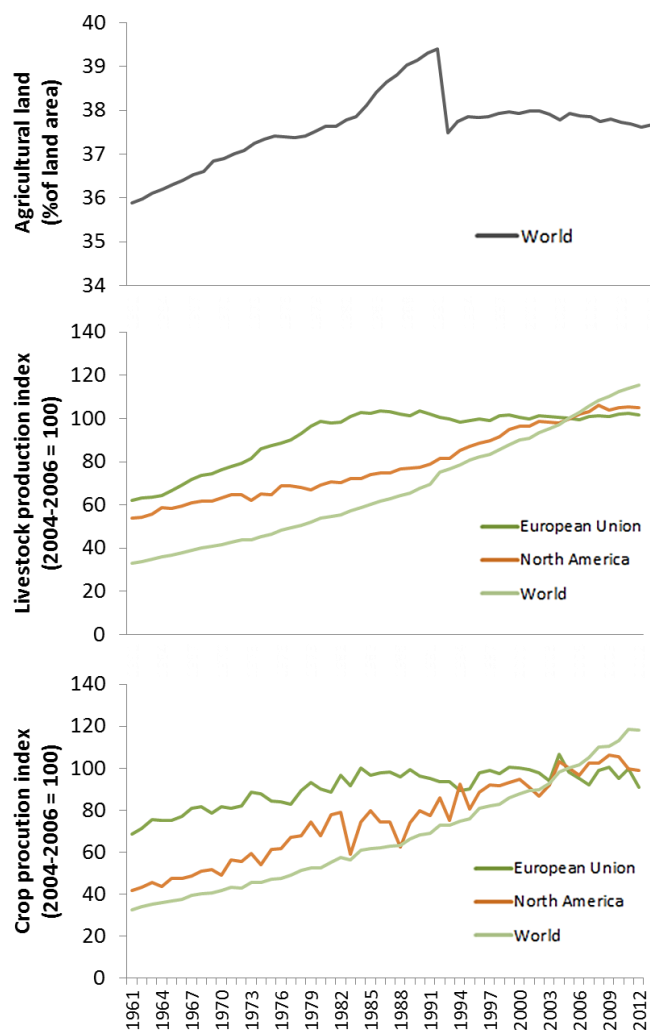
Figure 1 – Development of global agricultural production from 1961 to 2012 (World Bank 2014).

1.1.2 Consequences of agricultural intensification

During recent decades, extreme losses of biodiversity have occurred worldwide at an unprecedented scale, and agricultural expansion and intensification have been key drivers of this global change (Matson et al. 1997; Tilman et al. 2001). The increase in agricultural intensification has had major impacts all around the globe and on all ecosystems of the planet, by direct and/or indirect influences operating at different scales. Detrimental local effects include increased erosion and reduced soil fertility; at the regional level negative consequences have also been recorded, such as pollution of ground water and eutrophication of rivers and lakes; and negative global consequences include impacts on climate and the global carbon cycle (Zeng et al. 2014). This intensification of agriculture in recent decades has directly resulted in widespread declines in biodiversity across many different taxa, including birds (Donald et al., 2001, Fuller et al., 1995), mammals (Flowerdew, 1997), arthropods and flowers (Sotherton and Self, 2000). This decline in

biodiversity is driven by different mechanisms of agricultural intensification which can range from large-scale land conversion to more fine-scale processes such as changes in vegetation structure due to livestock grazing (Table 1).

1.1.3 Birds and agriculture

Agricultural expansion and intensification has caused declines in many bird populations across the world (Fuller et al. 1995, Voříšek et al. 2010, Donald et al. 2001, Millennium Ecosystem Assessment 2005). These declines have occurred as a result of many different changes in landscape and vegetation structure and associated consequences for resource availability and demography, particularly loss of key habitat features and resources and homogenization of landscapes (Table 1).

Table 1 - Common mechanisms through which conversion of natural land to agriculture and agricultural practices have been shown to impact bird populations.

Habitat/structure change	Impact	Example of references
Habitat loss	Loss of suitable habitat	Wilcove et al. 1998, Donald et al. 2001, Schmiegelow & Mönkkönen 2002
Homogenization of landscapes	Loss of resource diversity	Benton et al. 2003, Wilson et al. 2005
Abandoned farmland	Habitat change/loss	Radovic et al. 2013, Sanderson et al. 2013, Zakkak et al. 2015, Lasanta et al. 2017
Drainage, pond removal and water level change	Habitat change/loss of key resources	Cumming et al. 2001, Newton 2004, Gunnarsson et al. 2005b
Habitat fragmentation	Habitat loss, increased predation risk	Watson et al. 2005, Knight et al. 2016
Increase in field size	Habitat loss and increased homogenisation	Benton et al. 2003
Timing and frequency of harvesting/mowing	Increased risk of egg or chick mortality through agricultural operations, loss of food resources. More frequent events of abrupt vegetation structure changes	Hole et al. 2002, Newton 2004, Schekkerman et al. 2008
Fertilizer and pesticide	Reduced seed and insect food supplies	Wilson et al. 1999, Newton 2004
Livestock	Changes vegetation structure, trampling and predation of eggs and chicks	Wakeham-Dawson et al. 1998, Soderstrom et al. 2001, Fondell & Ball 2004

1.2 Icelandic agriculture

Agriculture in Iceland is, in many ways, different from agriculture in other Western countries, as climatic conditions and volcanic activity make agricultural production precarious (Jóhannesson 2010). These conditions also influence the slow rate of human population growth (inhospitable circumstances making life conditions strenuous), so the country remained sparsely populated and still today has only 330 000 people, with a population density of 3.1 inhabitants/km^2, compared to 112 inhabitants/km^2 in the EU and an order of a magnitude lower than the Scandinavian countries with 15-22 inhabitants/km^2 (Helgadóttir et al. 2013). Agricultural practices in Iceland were mostly of subsistence scale

until the mid-20th Century, (see below), with expansion rate being relatively low since then, in comparison with other Western countries.

1.2.1 Location, landscape and climatic conditions

Iceland lies just south of the Arctic Circle, between latitudes 63-66°N and 13-24°W, in the North-Atlantic Ocean (Einarsson 1984). Despite its northern latitudes, the climate is relatively mild, with average temperatures of approximately -1°C in January and 10°C in July, due to the Gulf Stream bringing warm sea currents from the south (Icelandic Meteorological Office 2015). Consequently the lowlands experience sub-arctic climates, while conditions in the highlands are closer to arctic climates, with glacial icecaps covering about 10% of the country (National Land Survey of Iceland 2013, Arnalds 2015). Annual rainfall ranges from 400 to 3000 mm (Icelandic Meteorological Office 2015) and the growing season is about 4 months, but agricultural potential is considerably limited by the low average summer temperatures.

Iceland is mountainous with an average altitude of 500 m a.s.l. and only a quarter of land lies below 200 m (Einarsson 1984), the area defined as suitable for cultivation in Iceland, and 90% of farms are located below 200 m (National Land Survey of Iceland 2013). Consequently, most of the centre of Iceland is uninhabited highland, and settlement and farming occur along the lowlands of the coastline and the southern lowlands (Jóhannesson 2010). Volcanic activity is frequent in Iceland, causing severe erosion and leaving large areas vulnerable to soil degradation (Arnalds 1987). So, taken together, climate and soil conditions impose quite severe limitations on farming in Iceland.

1.2.2 Natural hazards and agriculture

The most common natural hazards for agriculture in Iceland are extreme weather events, as temperatures below zero can be expected in summer months every few years (Icelandic Meteorological Office 2015), and have repeatedly caused damage to harvests. Flooding of rivers also occasionally occurs, but the effects are usually limited to relatively few farms. Volcanic eruptions and earthquakes pose a serious threat to Icelandic agriculture; threats from volcanos include ash fall, lava, flooding of glacial rivers and earthquakes can cause serious damage to houses and even threaten livestock. Through the history of Icelandic agriculture, eruptions and earthquakes have repeatedly caused great damage (Jóhannesson 2010).

These events vary regionally in frequency because both weather conditions, such as temperature and rainfall, and geological activity vary around the country. Iceland is located on the mid-Atlantic ridge, which runs through the island from south-west to north-east, causing frequent seismic activity along the ridge, making areas closer to the ridge more likely to be impacted (Arnalds 2015). The landscape of the south and north-east coasts has been highly impacted by catastrophic flooding, with large areas of barren land. Proximity to the mid-Atlantic ridge is also beneficial for soil fertility, because of nutritional inputs from volcanic events (Arnalds 2015, Gunnarsson et al. 2015).

1.2.3 History of Icelandic agriculture

Iceland was settled in the 9th century and the settlers brought with them Scandinavian agricultural habits of cereal production, animal husbandry and fishing and, for the first

1000 years of inhabitation, Icelandic agriculture was self-sufficient and almost entirely based on sheep husbandry (Helgadóttir & Sveinsson 2006, Helgadóttir et al. 2013). Alongside urbanization at the beginning of the 20th century, markets for agricultural products developed and agriculture grew beyond subsistence, as farmers adopted new (still quite primitive) technologies in hay production involving improvements of hay fields and artificial fertilizers (Júlíusson & Ísberg 2005). It was not until after the end of World War II that there was real progress in Icelandic agriculture when the rural population decreased rapidly and a subsidy system was set up to reward increased production. Moreover, farmers started using technological advances such as mechanical diggers to greatly increase drainage of wetlands, which played a fundamental part in the expansion of cropland although the most extensive drainage of wetlands occurred in the second half of the 20th century (when ~70% of inland wetlands were impacted (Arnalds et al. 2016)). From 1950 until the 1990s, cultivated land in Iceland grew rapidly in extent (Figure 2). In the last two decades of 20th century, overproduction resulted in calls for revision of the extensive subsidy system. A quota system was introduced and farmers had to adapt to production limitations (Helgadóttir et al. 2013). In the last two decades, food habits have been changing and the proportion of local agricultural products in the total food budget is declining. The drive is now towards maintaining profit by reducing inputs as well as by increasing outputs (Helgadóttir & Sveinsson 2006).
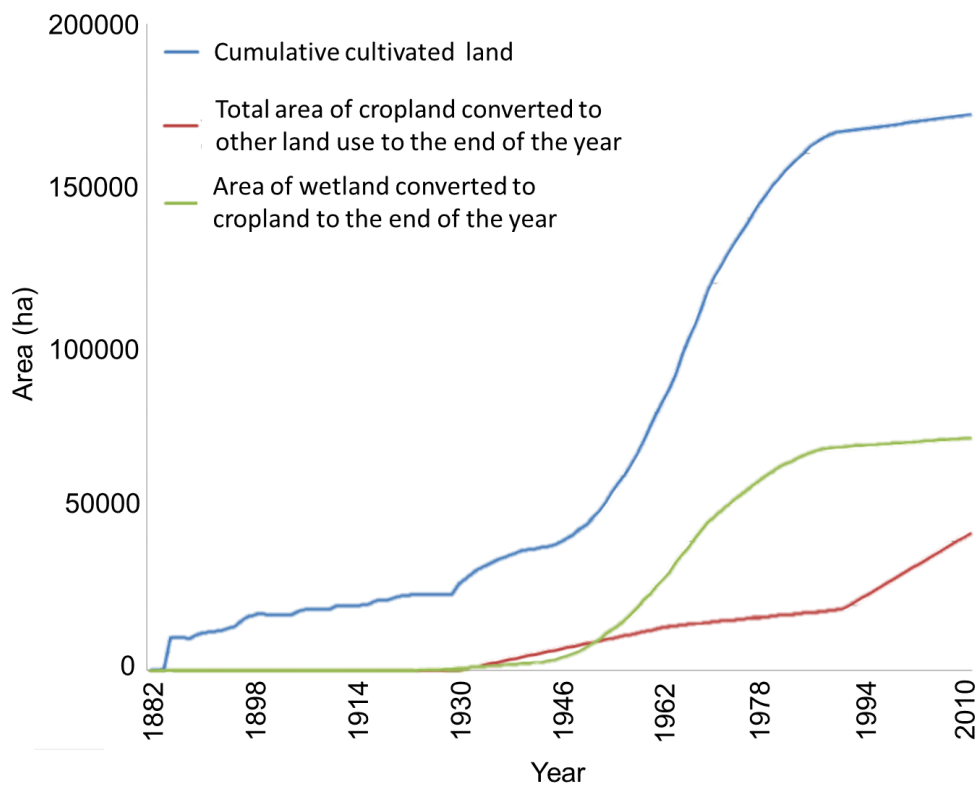
Figure 2 - Time series of agricultural expansion in Iceland. The cumulative area (blue line) represents changes in the total area of cultivated land. Area of wetland converted to cropland (green line) represents the organic soil part of that area. Total area converted to other land uses (red line) represents the estimated area of abandoned cultivated land (adapted from (Snorrason et al. 2015).

1.2.4 Agriculture in Iceland at present

Icelandic agriculture still remains of relatively low intensity despite rapid growth in recent decades and large patches of semi-natural habitats (e.g., marshes, bogs, heaths, and river plains) are still present in most agricultural areas. Unlike many other countries of Europe and in the US where more than 20% of the land is cultivated (Nickerson et al. 2011, Eurostat 2016), agriculture in Iceland does not yet dominate the landscape, with only ~2% of land currently cultivated in the country (~7% of the area below 200 m a.s.l., which is the area suitable for agriculture) (The Farmland Database 2013). Agricultural expansion is ongoing and Icelandic farmers own or manage the majority of land below 400 m a.s.l. (Kristófersson et al. 2007) and currently there are few regulations that restrict land management. The land that is best suited for cultivation is also land that is of high value for biodiversity, so the interests of landowners and biodiversity are likely to conflict (Jóhannesdóttir et al. 2014).

Overall, Icelandic agriculture is primarily pastoral, with arable crop production in Iceland being limited due to a cold climate and short growing season. Cultivated land consists mainly of hayfields (90%), but barley and rapeseed are grown on limited areas (Jóhannesson 2010).

1.2.5 Birdlife in agricultural areas in Iceland

Birdlife in Iceland is characterized by low species diversity as only around 80 species breed in the country, but also by the great abundance of these breeding species. Iceland supports internationally important populations of 21 breeding bird species (Einarsson et al. 2002), and is responsible for a large proportion of the world population of several of them (Figure 3) (Wetlands International 2006). Iceland is also an important staging area for birds migrating across the Atlantic Ocean on their way between wintering and breeding areas (e.g. Red Knot (*Calidris canutus*), Sanderling (*Calidris alba*), and Greater White-fronted Goose (*Anser albifrons*)) (Einarsson et al., 2002). Nearly half of Iceland's internationally important species are waders, but wader populations have been declining worldwide in recent years (International Wader Study Group 2003, Piersma et al. 2016, Pearce-Higgins et al. 2017).

The most common birds in agricultural areas in Iceland during breeding season are seven wader species; Oystercatcher (*Haematopus ostralegus)*, Golden Plover (*Pluvialis apricaria*), Dunlin (*Calidris alpina*), Snipe (*Gallinago gallinago*), Whimbrel (*Numenius phaeopus*), Black-tailed Godwit (*Limosa limosa*), Redshank (*Tringa totanus*) and one passerine species, the Meadow Pipit (*Anthus pratensis*) (Figure 3). All these species occur in high densities across lowland areas (Jóhannesdóttir et al. 2014) and have very large breeding populations in Iceland (Guðmundsson 2002). Iceland has been identified as the second most important breeding area for waders in Europe, following the vastly larger Russia (Thorup 2004). All these species, excluding the Oystercatcher, are found in high densities in wetlands (Jóhannesdóttir et al. 2014) reflecting their importance for birdlife in these landscapes (Figure 3), however a large amount of wetlands have been drained for agricultural purposes and currently ~50% of hayfields are on drained wetland soils (Wöll et al. 2014). Potential expansion of agricultural land therefore poses a further threat to this important habitat.

Species	Subspecies	Population (pairs)	Data quality	% of world population	Year of protection	Species proportional distribution in different habitats
Oystercatcher	(Haematopus ostralegus ostralegus)	20 000	0	3	1914	
Golden Plover	(Pluvialis apricaria altifrons)	310 000	2	34	1914	
Dunlin	(Calidris alpina schinzii)	270 000	2	10	1914	
Snipe	(Gallinago gallinago faeroeensis)	180 000	1	3	1914	
Whimbrel	(Numenius phaeopus islandicus)	250 000	2	27	1954	
Black-tailed Godwit	(Limosa limosa islandica)	25 000	2	7	1904	
Redshank	(Tringa totanus robusta)	140 000	2	12	1914	

Legend: Wetland, Semi-wetland, Grassland, Cultivated land, Rich heathland, Poor heathland

Figure 3 - Population estimates of breeding wader species in lowland Iceland, and estimates of data quality (ranging from 0 (guesses) to 5 (full coverage);Thorup 2004); the percentage of the world population that breeds in Iceland (Delany & Scott 2002); the year each species was protected by Icelandic law (Schmalensee et al. 2013); and the proportional distribution of each species across the six main vegetated habitats in lowland Iceland (from Jóhannesdóttir et al. 2014).

1.3 Bird conservation

Conservation of bird populations typically involves two key methods; protect the species and protect their habitats, which for example are the key pillars of the EU Birds and Habitats Directives (Birdlife International 2017). Species protection involves e.g. protecting birds from hunting and persecution and predator control, while habitat protection involves ensuring the quality and extent of habitat, and its ability to provide sufficient resources for the species occurring in those sites, remains intact.

1.3.1 Agri-environmental schemes

One response to the biodiversity declines caused by the intensification of agriculture has been the implementation of agri-environmental schemes. These schemes provide funding to farmers and land managers who manage their land in ways that supports biodiversity, enhances the landscape, and improves the quality of water, air and soil (Kleijn & Sutherland 2003). Many agri-environmental schemes have been designed to aid farmland bird conservation, in order to reverse widespread declines of these species. The success of these schemes has been debated, with many studies failing to find benefits to wildlife (Kleijn et al. 2001). However, where appropriately designed and targeted, these schemes have proved to be useful in halting declines in some species (Donald & Evans 2006).

1.3.2 Bird conservation in Iceland

Iceland is a member of several international agreements which confer protection status to birds and their habitats. Iceland ratified the Convention on Wetlands (Ramsar Convention)

in 1977, the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) in 1993, the Convention on Biological Diversity in 1994 and became a member of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) in 2013 (Schmalensee et al. 2013). Within Iceland, six areas are designated as Wetlands of International Importance (Ramsar 2014) and 33 other areas are protected through Icelandic law due to their importance for birds. Many of these areas are only a few hectares and the choice of protected areas has been somewhat haphazard, and currently a holistic network of protected habitats is missing (Schmalensee et al. 2013).

1.3.3 Importance of stakeholders

Protected areas are often of great importance for conservation of bird species with restricted and patchy distributions, but protection of bird species that are widespread across the wider countryside is typically much harder to achieve. In order to protect species that range across areas of multiple ownership, collaboration with stakeholders becomes vital. One key feature in successful conservation management in such cases is to consolidate the different interests of conservation and stakeholders (Young et al. 2005, Redpath et al. 2013).

In Iceland, almost all land in lowland areas is either privately owned or state property managed by farmers (Kristófersson et al. 2007), so their actions can have decisive impacts on the species occupying these landscapes. Currently there are very few restrictions on land management in Iceland (Alþingi 2015). In order to protect species, a legal framework and close collaboration and active communication with stakeholders is therefore required in order to reconcile potential conflicts and ensure that different interests are appreciated from the outset, as well as having all parties involved working together toward mutually agreed goals (Redpath et al. 2013).

1.4 Aims of the thesis

The main objective of this thesis is to explore the relationship between breeding waders and agriculture in Iceland, in order to understand the current status and possible consequences of agricultural intensification and associated fragmentation of natural habitats in different landscape contexts.

1.4.1 Current status of Icelandic waders and agriculture (paper I)

This paper contributed to a symposium organized by the International Wader Study Group on the status of meadow breeding waders across Europe. In this paper I give an overview, based on the information available, of the population status, trends, threats and challenges of conserving breeding wader species that are most commonly found in agricultural areas in Iceland. It also includes an overview of Icelandic agriculture, its history and current extent.

1.4.2 Distribution and abundance of waders (paper II)

In this paper I quantify the distribution and abundance of breeding waders in areas of varying intensity of agricultural management throughout lowland Iceland (south, west and north regions), as these encompass a wide range of soil types and agricultural activity, in order to understand the influence of current levels and structure of agricultural management in Iceland on the important wader populations that breed in these areas.

1.4.3 Effects of environment on breeding waders (papers III and IV)

Different environmental conditions can have important impacts both on breeding waders and conditions for agriculture. The volcanic nature of Iceland and the sometimes harsh weather conditions can potentially impact the abundance and demography of breeding waders, but little is known about these relationships. In **paper III** I quantify annual variation in Black-tailed Godwit productivity to assess the effect of variable spring temperatures and how these relationships are impacted by volcanic eruptions. This study also provides information on the magnitude and duration of volcanic activity effects on Black-tailed Godwit productivity. The impacts of these environmental factors are likely to be similar across the focal wader species in the thesis, which use the same breeding habitats as the Black-tailed Godwit and rely on the same food resources.

Following on from **paper III**, which explores temporal variation in demography, I continue exploring spatial variation in the effects of environmental conditions on biodiversity, by addressing how landscape structure and habitat heterogeneity influences breeding bird densities. In **paper IV**, I specifically use the variation in extent of agriculture in lowland Iceland to explore how wader densities on different semi-natural habitats vary in relation to the amount of agriculture and wetland in the surrounding landscape, and how this varies across an altitudinal gradient that reflects variation in underlying productivity, as a consequence of the volcanic nature (historical Aeolian dust deposition) of the land.

1.4.4 First steps towards wader conservation (paper V)

There are currently no conservation efforts aimed at protecting breeding waders in Iceland, despite populations of international importance being supported by Icelandic landscapes. Icelandic farmers own and manage the majority of Icelandic lowlands so their land management decision can have considerable impacts on waders. In **paper V** I use questionnaire surveys to understand farmer's intentions regarding expansion of agricultural land on their properties and how they value birdlife. Then I explore the potential for collaboration with farmers, and which actions they would be willing to undertake in order to maintain the breeding wader populations in farming regions.

2 Methods

2.1 Study area

Field data collection for this study focused on the three regions of Iceland where the majority of agricultural production in Iceland takes place: the north, south and west (Figure 4). In the summers of 2013 and 2014, a total of 64 farms were visited across these regions, with farms being chosen in a stratified random structure in order to capture existing variation in farm types and size, surrounding landscapes and type of livestock (Figure 4) (**papers II and V**).
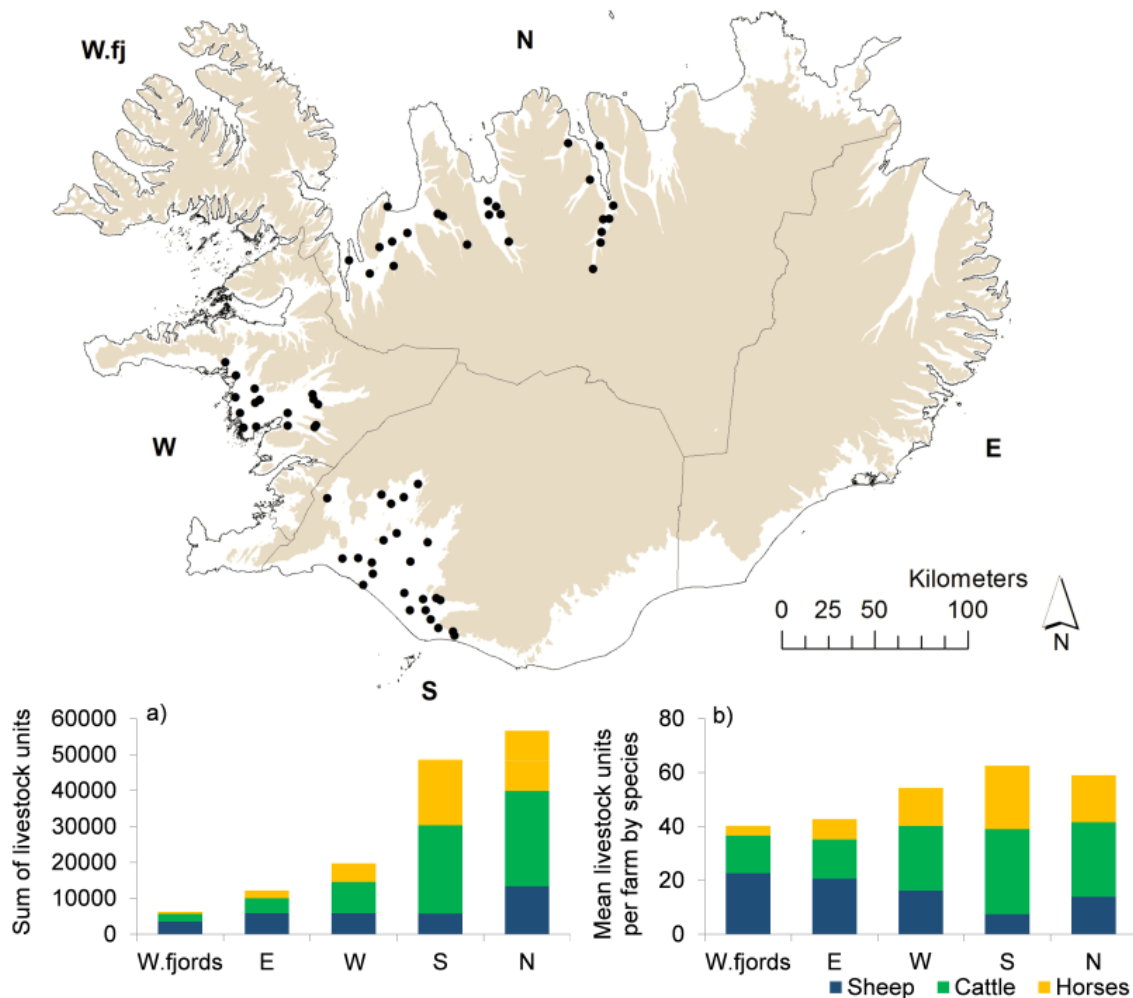

Figure 4 - Map of Iceland (top) showing areas below 400 meters above sea level (in white) and the locations of surveyed farms (filled circles) in each of the regions (indicated by lines). Regional variation in (a) total livestock units (LU: cattle = 0.9; horses = 0.8; sheep = 0.1) and (b) composition of livestock units per farm (Statistics Iceland 2015a).

2.2 Bird surveys

Surveys were carried out to quantify the abundance of breeding birds within areas subject to similar management. Two types of transects are most commonly used in bird surveying, line transects and point transects, and the method used typically depends on the landscape and species involved (Gregory et al. 2004). In this thesis, all bird survey data was acquired using line transects, given the extensive, open, and uniform habitats covered. Line transects are also best suited for mobile, large or conspicuous species and those that easily flush in response to human presence. Using line transects makes birds less likely to be attracted to the observer and enables rapid coverage of large areas of ground and efficient recording of the abundance of many species (Gregory et al. 2004).

At each farm, three different locations were selected, representing different levels of agricultural management (intensive, moderate, light), and bird surveys were carried out at each of these managements (**paper II**). Given that the spatial distribution of these species is likely to change at different stages of the breeding cycle, due to seasonal differences in adult and chick resource requirements, each farm was surveyed twice during the season: *early*, from mid-May till mid-June - encompassing most egg-laying and incubation (peak nest initiation for the main species concerned is late May); and *late*, from mid-June to mid-July - the period that primarily encompasses chick rearing (Gunnarsson; 2010). At each location, all birds were counted along one line transect per management level (average transect length ($\pm$ SD) = 253 $\pm$ 75 m; width = 92 $\pm$ 24 m, corresponding to an average survey area ($\pm$ SD) of 2.3 $\pm$ 0.8 ha) (Bibby et al. 2000, Jóhannesdóttir et al. 2014).

In order to estimate breeding bird abundance and density on large areas of semi-natural habitat that varied in the surrounding landscape composition, and to quantify the effects of amount of agricultural land and wetland in surrounding landscapes on bird density, a previously existing dataset was used (appendix, **paper IV**). Fieldwork for that dataset was carried out (by Lilja Jóhannesdóttir) in the summers of 2011 and 2012, when bird surveys were done in the lowlands of South Iceland in areas below 200 m a.s.l. (Figure 5). The land cover information used in the study was extracted from the Icelandic Farmland Database (see details below). Survey sites within the five most common vegetated natural habitats (wetland, semi-wetland, grassland, rich heathland and poor heathland) were selected using a stratified random system, implemented in ArcGis 10.1 GIS software. Sites were selected so they covered at least 20 ha of a single habitat type to reduce effects of adjacent habitats. For practical reasons, sites were selected so they these had no more than 2 km from roads and distanced by more than 0.5 km from each other, in order to secure independence between survey points. Previous studies have shown that the distribution of habitat types in lowland Iceland is not strongly related to distance from roads (Gunnarsson et al. 2006). In total, 200 sites were surveyed, 40 of each habitat (Figure 5).
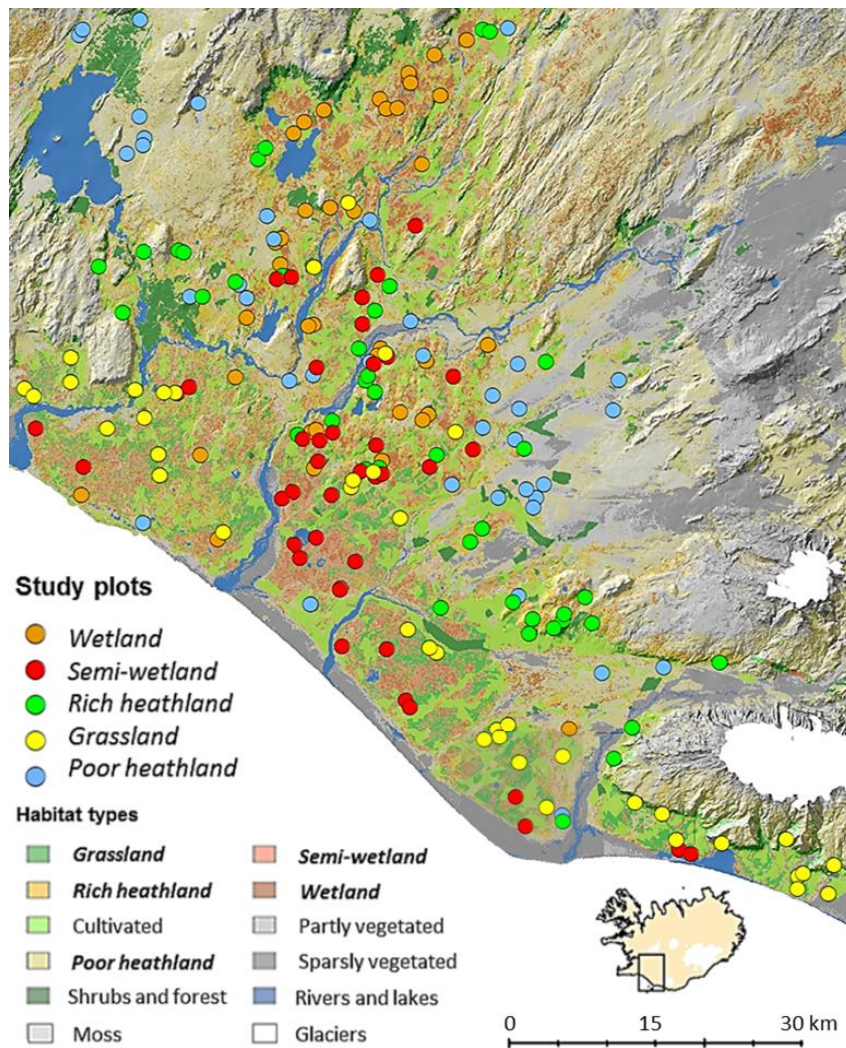
*Figure 5 - Map of South Iceland, including the study area of **paper IV**, showing the position of study plots and respective dominant habitat, where bird abundance was surveyed. Sampling was restricted to areas below 200 m a.s.l. (from Jóhannesdóttir et al, 2014).*

2.2.1 Estimating timing of laying and large-scale productivity

In order to estimate annual variation in productivity over large spatial scales, one wader species, the Black-tailed godwit, was selected as a model due to the very agonistic behaviour of adults when caring for young (Gunnarsson et al. 2005a). During the last 10 days of June 2011–2016, road-based surveys were carried out in the lowlands of southern Iceland and, along these transects (totalling 198 km), the presence of all alarming adult Godwits within 100 m of the car was recorded (**paper III**). Each strongly alarming individual or pair was taken to indicate the presence of a brood. In each case the perpendicular distance from the road transect to the chicks (when seen) or adults was recorded with a laser rangefinder to ensure only broods within 100 m of the road were included, along with a GPS position of the car on the road. The number of broods recorded along the transects was used as an estimate of annual productivity.

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Given that the surveys all took place at a fixed time in late June, the number of broods observed in each year could be influenced by the timing of egg-laying. As part of long-term studies on Black-tailed Godwit breeding ecology in southern Iceland, the timing of egg laying has been monitored most years since 2001 (Alves et al. submitted), by locating as many nests as possible and floating the eggs to hind cast the date of laying of the first egg (Liebezeit et al. 2007). During the period used in this thesis (2011-2016) between 14 and 28 Godwit nests (mean=20.6 ± 5.5 sd) were monitored each year in the southern lowlands. As the surveys all took place in late June, the number of broods observed in each year could be influenced by the timing of egg laying.

2.2.2   Weather data

To assess the influence of spring temperature on large-scale productivity, we extracted the mean daily temperature during May of each year (2011–2016) from the weather station of the Icelandic Meteorological Institute (www.vedur.is) nearest to the surveyed area (Eyrarbakki 63°520N, 21°090W) (**paper III**).

2.3 Extraction of spatial data

The land cover information used to explore the effects of landscape structure on breeding bird densities was extracted from the Icelandic Farmland Database which uses satellite images with extensive ground truth verification to classify the surface of Iceland into 12 different classes (**paper III and IV**) (Arnalds & Barkarson 2003). The classification represents variables that reflect productivity, mostly vegetation cover, soil and drainage. The Icelandic Farmland Database classifies land down to the scale of 196 m2 (pixel size 14 × 14 m). Around each transect (**paper IV**), four different sized buffers were extracted (500, 1000, 1500 and 2500 m radius) and the area of each habitat type was recorded from within the buffers.

2.4 Questionnaire survey

In **paper V,** I was seeking to understand farmer's intentions regarding future farming practices, their views on bird conservation, the importance of birdlife to them, and their willingness to participate in different actions aimed at bird conservation. Questionnaires are a useful tool to gather and quantify information about human characteristics, attitude and behaviour (McLafferty 2003). In order to compare farmer responses between different regions and across farmer characteristics, I used a five point Likert scale questionnaire (Likert 1932) so that respondents results could be compared statistically.

2.5 Statistical analyses

Throughout the thesis, general or generalized linear models have been used to explore the variation in the data. On several occasions, mixed models were used with random effects in order to account for non-independence; for example, because the bird surveys included counts of a range of species, models of the overall variation in bird abundance included species as a random factor to account for sites having different bird community composition and for differences in the behaviour of individual species. Where appropriate, non-parametric tests such as Mann-Whitney, Fisher's and G-tests, were also used. All statistical analyses were carried out in the programs R and SPSS.

3 Results

3.1 Paper I

Icelandic meadow breeding waders: status, threats and conservation challenges

Iceland hosts vast populations of breeding meadow birds, with estimated proportions of the world population ranging from 3 to 34%, highlighting Iceland's importance for these species. These species are found in all regions of the country with high but varying densities and similar species compositions, highlighting the need for concerted effort to conserve them. There is little information on trends and demography of most species but survey programs have been implemented in recent years, therefore availability of information is likely to improve in the near future.

3.2 Paper II

Importance of agricultural and semi-natural habitats for breeding waders in low-intensity farming landscapes

Measurements of bird density in areas of varying intensity of agricultural management, where birds have a range of agricultural and semi-natural habitats available, shows that all these habitats are used extensively by breeding birds, but the patterns of use vary regionally, seasonally and between species. The current landscape structure in lowland Iceland, with agricultural land embedded within semi-natural land in mosaic-like manner, may therefore be benefitting the breeding bird community, while a more homogenous landscape comprising primarily agricultural or semi-natural land may be less able to sustain the current variety and abundance of breeding waders.

3.3 Paper III

Effects of spring temperature and volcanic eruptions on wader productivity

Along with spatial information on bird distribution, temporal variation in productivity can be a major driver of population abundance. Annual variation in the numbers of Black-tailed Godwits broods along a 198 km transect between 2012 and 2016 was very closely and positively related to mean May temperatures. However, during a relatively warm spring, (2011) when a volcanic eruption impacted the study area, Godwit productivity fell to exceptionally low values. The study provides a rare example of the magnitude of impact that extreme events such as a volcanic eruption may have on bird productivity, but also highlights the likely short-term duration of such an event.

3.4 Paper IV

Effects of agriculture and landscape structure on breeding wader populations in Iceland

Icelandic lowlands are a fine-scale mosaic of different open natural habitats and agriculture, and the landscape is currently very heterogeneous. The heterogeneity remains constant at different spatial scales throughout the southern lowlands, though the abundance of different habitat types varies with altitude. The amount of both cultivated land and wetland in surrounding landscapes significantly influences the density of waders on semi-natural habitats. Increasing amounts of wetland in the surrounding area generally result in higher densities of waders, but the effect of amount of cultivated land in the landscape on wader density varies with altitude: at lower altitudes densities decline with increasing amounts of cultivated land, while the opposite occurs at higher altitudes.

3.5 Paper V

Reconciling biodiversity conservation and agricultural expansion in the sub-arctic environment of Iceland

Questionnaire surveys throughout lowland Iceland revealed that farmer attitudes towards breeding waders on their land are generally positive, and most consider it important to have rich birdlife on their farm. Although most farmers indicated that they are likely to expand their agricultural land, not many farmers reported that they currently take breeding waders into consideration in their land management. However, they were generally positive towards participating in the different conservation measures I proposed in the questionnaire.

4 Conclusions

Agriculture has driven widespread declines in bird populations around the globe (Donald et al. 2001, Millennium Ecosystem Assessment 2005) but, in some areas, the current extent of agriculture is such that negative effects on wildlife are not yet apparent and positive effects might be occurring (Tscharntke et al. 2005, Wright et al. 2012). In Iceland, the landscapes in which most agricultural production occurs also support exceptionally high densities of several wader species (Jóhannesdóttir et al. 2014). These landscapes are of huge international importance as this it is the second most important wader breeding area in Europe, following the vastly larger Russian wader breeding grounds (Thorup 2004).

Here I have shown that the most common species in the Icelandic agricultural landscapes occur in high densities right across the agricultural management gradient that characterises much of lowland Iceland, from semi-natural land to more intensely managed land such as frequently cut hayfields, but densities are generally lower in more intensely managed areas. This suggests that, if the area of cultivated land in Iceland expands, declines in breeding wader populations are likely. This pattern has already been described in many other countries in Western Europe, where birdlife has declined severely following increased agricultural development (Donald et al. 2001, Green et al. 2005). The most likely scenario in Iceland is increased demand for agricultural production in the near future, followed by expanding area of agriculture. Throughout the last decade there has been an exponential growth in tourism in Iceland (Óladóttir 2015), as well as growth in the Icelandic population, which is estimated to increase by ~30% in the next 50 years (Statistics Iceland 2015b). Because of Iceland´s northern location, farmers are faced with cultivation restrictions as opportunities to increase yield on land currently used for cultivation are limited, so in order to meet the growing demand they are likely to increase production through expansion of cultivated land. Indeed the majority of farmers surveyed in this study reported a clear intention to increase the area of cultivated land in the coming years, and this has clear potential to impact breeding wader populations. Fortunately, Icelandic farmers were also generally positive towards participating in conservation action aimed at protecting the still large wader populations that breed in Iceland, and this may offer opportunities to work with farmers towards reducing the impacts of agricultural expansion on Icelandic breeding wader populations.

This current situation in Iceland, where large breeding wader populations are still present but are threatened by potentially large and rapid land use changes looming on the horizon, provides a unique opportunity to understand and identify the landscape structure that needs to be maintained in order to sustain wader populations. The information presented in this study will hopefully prove useful for other countries or regions that currently struggle to preserve their breeding wader populations in the face of anthropogenic changes. The existing landscape in lowland Iceland, the fine scale mosaic of cultivated land and semi-natural land, provides conditions and resources which seem to be highly suitable for waders and could be used as an example of the type of landscape needed to recover wader populations that have suffered from agricultural development. Many agri-environmental schemes implemented to provide resources for breeding birds have not been successful at boosting declining populations (Kleijn et al. 2001, Malpas et al. 2013), and one of the

problem has been identified is focusing conservation efforts on small patches of land, which might only fulfil a part of birds requirements, rather than providing lower numbers of larger patches which might be more likely to provide the suite of required resources (Whittingham 2007, Butler 2013).

The results presented here therefore highlight the urgent need to protect these sorts of landscapes, which still sustain important wader populations. The work will also hopefully provide complementary information regarding the similar issues of anthropogenic land use change that breeding waders may be faced with in areas at similar latitudes around the globe, where agriculture does not yet dominate landscapes, but where only very limited information on both the status of wader population and the effects of land use is currently available. Protecting these landscapes from further land use change is likely to be a key component of maintaining migratory wader populations throughout the world.

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Icelandic meadow breeding waders: status, threats and conservation challenges

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Abstract

Populations of many migratory wader species around the world are in serious decline, largely caused by anthropogenic activities. Throughout the developed world, agricultural expansion and intensification have been identified as among the main drivers of these declines. However, not everywhere have agricultural activities reached levels where noticeable negative impacts on breeding waders are apparent. Since settlement, Icelandic farmers have largely been self-sufficient in agricultural productivity, and substantial expansion of agricultural land only began after the 1940s'. Agricultural expansion has continued since then and today around 7% of area below 200 m a.s.l. (areas at higher altitudes are typically unsuitable) are used for cultivation. Large areas of natural or semi-natural habitats are therefore still common and widespread in Iceland, and the current mosaic-like landscape created by areas of agricultural land within these habitats may help to provide the resources needed by the very large populations of waders that breed in the country. Wader species have all been protected from hunting and egg-collecting by law since the 20th century. However, lowland landscapes in Iceland are changing quite rapidly, as a result of agricultural expansion, afforestation and widespread construction of summer cottages, and all of these developments pose potential threats to these species. Predictions of the potential impact of current and future land use changes on these species is hampered by limited information on population dynamics, and no specific conservation efforts are currently aimed at meadow breeding waders in Iceland.

Keywords

Shorebird conservation, sub-arctic habitats, lowland ecosystems, land use changes, agricultural expansion, breeding distribution.

Introduction

Migratory waders are declining in many parts of the world (International Wader Study Group 2003, Bart et al. 2007, Piersma et al. 2016) and evidence suggests that changing environmental conditions during the breeding season contribute to these declines in many cases (Zockler et al. 2003, Wilson et al. 2004). Agricultural developments are a major cause of these changing conditions, largely because the resulting landscape and vegetation structure fails to provide the necessary resources for breeding waders (Vickery et al. 2001, Smart et al. 2006). However, rates of agricultural development vary around the world.

Development and intensity of agriculture in Iceland

Icelandic agriculture is highly influenced by the country's geographic location, just south of the Arctic Circle (between 63° and 66° North). The interior of Iceland consists mostly of highland areas rising from 400 m elevation to more than 2000 m (57% of the area of Iceland is above 400 m a.s.l.; National Land Survey of Iceland 2013), and lowland areas

are primarily along the coastline and river plains. Despite its high latitude, the temperature in Iceland is relatively mild in winter due to the Gulf Stream bringing warm sea currents from the south. Consequently the lowlands experience sub-arctic climates, while conditions in the highlands are closer to arctic climate (Arnalds 2015). Iceland was settled in the 9th century and since then Icelandic agriculture has been characterised by long periods of self-sufficiency and little cultivation, harsh weather and soil conditions and modest levels of foreign trade (Jóhannesson 2010). It was only at the beginning of 20th century that agriculture grew beyond subsistence, and cultivation developed alongside urbanization following the Second World War (Júlíusson & Ísberg 2005). In 1900, the most common land cover type in the lowlands of South Iceland was natural wetland (Wald 2012) and wetlands were also very common in other regions (Danish General Staff 1905). In the 1940s, the Icelandic government implemented a programme of subsidised drainage of wetlands encouraging farmers to increase both the area under cultivation and the grazing potential of their land. During the following four decades, extensive drainage took place in the lowlands, with 29,700 km of ditches being excavated (Gísladóttir et al. 2009). There were no legislative constraints on the extent of the drainage and many drained areas were never subsequently used for agriculture. During the 20th century, an estimated 55 to 75% of Icelandic wetlands were drained to some extent (Óskarsson 1998) and nearly 97% of the wetlands in South Iceland were disturbed by drainage (Þórhallsdóttir et al. 1998), totalling 4200 km^2 of which only 570 km^2 are used for cultivation (Barkarson et al. 2016). During this period, the area of cultivated land in Iceland grew considerably, expanding from 400 km^2 in 1940 to 1650 km^2 in 1980 and has continued to increase to present levels of ~1750 km^2 (7% of the area below 200 m a.s.l.) (National Land Survey of Iceland 2013, Snorrason et al. 2015). These cultivated areas are constrained to the lowlands while the highlands, which are mostly sparsely vegetated or barren land, are used for grazing of sheep and horses. Cultivated areas in Iceland are mostly hayfields that are used for grazing or fodder production for livestock for meat and dairy production, as agriculture in the country is almost entirely animal based (pastoral). Arable production is small-scale and mostly comprises barley grown for fodder on the farm where it is grown, although most grain fodder is imported (Jóhannesson 2010).

Agriculture in Iceland is not as widespread and intense as in many other countries where agriculture dominates the rural landscape (Figure 1). Large areas of semi-natural land, on which only low intensity grazing tends to occur, still remain in Iceland at present. The 7% of lowland area that is cultivated contrasts sharply with many other countries in Europe in which ~80% of land is either used for production system, settlement or infrastructure (European Environment Agency 2016). However, estimates suggest that >60% of the remaining semi-natural areas in Iceland could potentially be converted to cultivated land (The Farmers Association of Iceland 2010, The Farmland Database 2013). At present, Icelandic lowlands are characterised by a fine scale mosaic mixture of semi-natural habitats and agriculture (Figure 1).
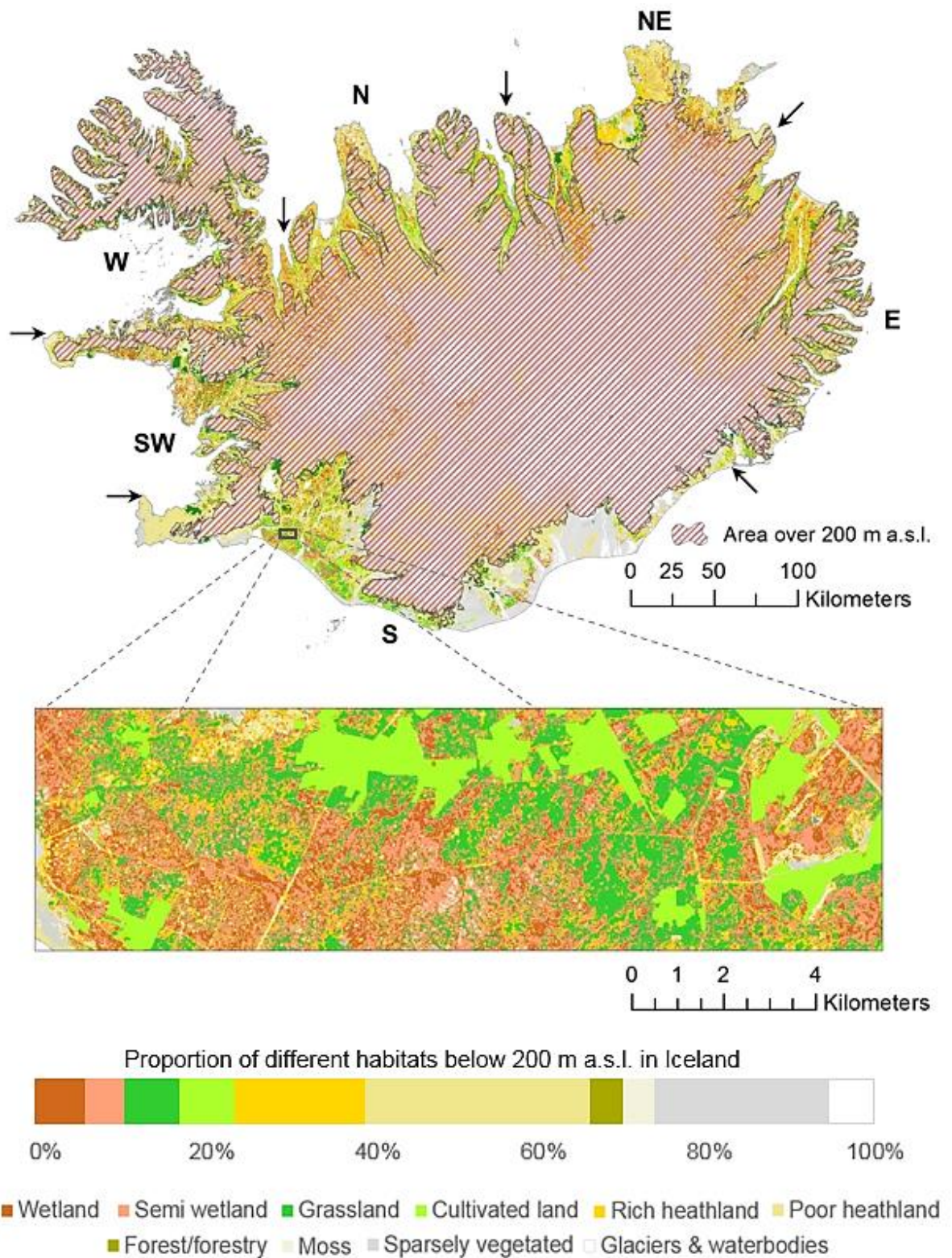
Figure 1 -Composition and proportion of different habitats in Iceland below 200 m a.s.l. (striped areas are above that level). The central inset shows an example of the small scale mosaic of habitats typical of the agricultural areas in south Iceland. The arrows show borders between regions of the country.

Species	Subspecies	Population (pairs)	Data quality	% of world population	Year of protection	Species proportional distribution in different habitats
Oystercatcher	(Haematopus ostralegus ostralegus)	20 000	0	3	1914	
Golden Plover	(Pluvialis apricaria altifrons)	310 000	2	34	1914	
Dunlin	(Calidris alpina schinzii)	270 000	2	10	1914	
Snipe	(Gallinago gallinago faeroeensis)	180 000	1	3	1914	
Whimbrel	(Numenius phaeopus islandicus)	250 000	2	27	1954	
Black-tailed Godwit	(Limosa limosa islandica)	25 000	2	7	1904	
Redshank	(Tringa totanus robusta)	140 000	2	12	1914	

Wetland ■ Semi-wetland ■ Grassland ■ Cultivated land ■ Rich heathland ■ Poor heathland ■

Figure 2 - Population estimates of breeding wader species in lowland Iceland, and estimates of data quality (ranging from 0 (guesses) to 5 (full coverage)(Thorup 2004); the percentage of the world population that breeds in Iceland (Delany & Scott 2002); the year each species was protected by Icelandic law (Schmalensee et al. 2013); and the proportional distribution of each species across the six main habitats they use in lowland Iceland (from Jóhannesdóttir et al. 2014 - see Figure 1 for habitat distribution).

Legal status

Seven wader species breed in meadow-like habitats in lowland Iceland (as well as breeding in other habitats); Oystercatcher *Haematopus ostralegus ostralegus*, Golden Plover *Pluvialis apricaria altifrons*, Dunlin *Calidris alpina schinzii*, Snipe *Gallinago gallinago faeroeensis*, Whimbrel *Numenius phaeopus islandicus*, Black-tailed Godwit *Limosa limosa islandica* and Redshank *Tringa totanus robusta*. All these species, and their eggs, became protected by Icelandic law early in the 20th century, excluding Whimbrel which only became protected in 1954 (Figure 2), but there is no evidence to suggest that hunting of these species was common before protection. Iceland is a member of several international agreements which confer protection status to waders and their habitats. Iceland ratified the Convention on Wetlands (Ramsar Convention) in 1977, the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) in 1993, the Convention on Biological Diversity in 1994 and became a member of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) in 2013 (Schmalensee et al. 2013). Iceland is also part of the Arctic Council which has a biodiversity working group, the Conservation of Arctic Flora and Fauna (CAFF) which, among other current projects, is working specifically towards encouraging flyway-wide protection for migratory species breeding at Arctic latitudes. For the African-Eurasian Flyway, one of CAFF's priority conservation issues and proposed actions is to secure the breeding habitat of waders in Iceland by ensuring that national programmes of afforestation, and other land use policies and practices, are sustainable. CAFF aims to cooperate with Icelandic authorities to avoid changes in land use in the Icelandic lowlands that may impact breeding water birds, particularly regarding the national afforestation

policy (CAFF 2016). Plans for large-scale state-subsidised afforestation of Icelandic lowlands have raised considerable concern for several years, especially because of the threats it poses to breeding waders, such as loss of breeding habitat and potential avoidance of areas close to forests (Wilson et al. 2014). The Standing Committee of the Bern Convention mandated an on-the-spot appraisal of the Icelandic afforestation situation in 2001 which confirmed the threat to migratory waders. The Standing Committee urged the Icelandic Government to undertake seven specific actions, including impact assessment, habitat protection and strategic planning. To date, limited progress has been made in response to these recommendations (BirdLife Iceland 2014).

Numbers, trends and distribution of meadow birds in Iceland

Breeding population sizes in Iceland of the seven meadow wader species range from 20000 to 310000 pairs, and the estimated proportions of the world population range from 3 to 34% (Figure 2), highlighting Iceland's importance for these species (Guðmundsson 2002).

Trends

Unfortunately, systematic efforts to monitor breeding wader populations in Iceland have only recently started (first began in 2006), so no long-term population trends are currently available. Sufficient data should be available to track trends over the short term in a few regions in the near future. The exception to this gap in knowledge is the Icelandic Black-tailed Godwit population which overlaps little with other subspecies on its wintering grounds in W-Europe (Alves et al. 2010), and so monitoring schemes (Crowe et al. 2012, Frost et al. 2016) from other countries are useful for assessing the size of the Icelandic breeding population. Throughout the 20th century the Icelandic Black-tailed Godwit population has increased and the breeding range has expanded across lowland Iceland (Gunnarsson et al. 2005b). There is also some evidence to suggest that the population of oystercatchers may have increased in recent decades, since their range has expanded into more northerly parts of Iceland (Jóhannsson & Guðjónsdóttir 2009).

Demographic parameters

Demographic studies have only been conducted on a few meadow breeding species in Iceland. These have been short term and provide only snapshots of the variation in demographic rates. And although these provide some evidence for spatial and annual variation in current demographic rates, estimating longer term demographic changes require systematic long-term studies which are not in operation. Nesting success has been studied in Black-tailed Godwit, Snipe and Whimbrel, and can vary across habitats and between years. In a study of Black-tailed Godwits on 12 study sites in South Iceland in 2001-2003, between 50 and 75% of nests hatched each year (Mayfield adjusted success rate) and hatching success was generally higher in marshes than on dwarf-birch bog (Gill et al. 2007). Similarly, comparisons of nest survival of Whimbrels in South Iceland in 1997 and 1999 showed that, on a riverplain site, 61-100% (Mayfield-adjusted) of nests survived each year but only 1-19% of nests survived on a heathland site (Gunnarsson 2000). A later

study of Whimbrel nesting success in 2009-2010 found 15-17% nest survival on a grassland site but 19-29% on a river plain site (Katrínardóttir et al. 2015). Finally, a recent study of Snipe nest success in different habitats in South Iceland in 2015 recorded Mayfield-adjusted nest survival rates of 3-18%, with survival being higher in marshes and a mosaic of lupin (*Lupinus nootkatensis*) and birch (*Betula pubescens*) habitat than in lupin fields (Wentworth 2015).

Less is known about fledging success of waders in Iceland but, on the 12 Black-tailed Godwit study sites mentioned previously, 20-80% of pairs which attempted to breed fledged one or more chicks with, on average, ~30% of pairs fledging one or more chicks on dwarf-birch bog sites and ~ 55% on marsh sites (Gunnarsson et al. 2005a). Variation in fledging success among habitats was also apparent in whimbrels in South Iceland between 1997 and 1999, where chick survival from hatching to fledging ranged from 50-55% on a river plain site (1.5-2.0 fledglings/pair) and from 36-40% (0.0-0.7 fledglings/pair) on a heathland site (Gunnarsson 2000). Similarly, whimbrel chick survival in 2009-2010 was 21% (0.36 fledglings/pair) on a river plain site and 32% (0.50 fledglings/pair) on a grassland site (Katrínardóttir et al. 2015).

Very little is known about survival rates of Iceland breeding waders but estimates of annual survival rates of Icelandic Black-tailed godwits from colour-ring resightings range from 87-99% (Gill et al. 2007), while return rates of colour-ringed whimbrels to their breeding grounds (minimum survival) has ranged from 60-81% in two studies (Gunnarsson et al. 2005a, Katrínardóttir et al. 2015).

Distribution

All seven meadow-breeding wader species can be found in every region of Iceland (Figure 3) and in all of the most common vegetated habitats (Gunnarsson et al. 2006), but their densities vary between habitats (Jóhannesdóttir et al. 2014). Oystercatchers and Redshanks are generally more frequently found in grasslands and on cultivated land, while Dunlin, Snipe, Whimbrel and Black-tailed Godwits are more often found on wetlands and semi-wetlands, and Golden Plover is most frequently found in the drier heath-habitats (Figure 2). As all of these habitats are patchily distributed throughout the lowlands (Figure 1), the species are generally widely distributed and not concentrated in specific areas. Although all seven species are most common in the lowlands, Golden Plover, Dunlin and Whimbrel also breed in the highlands (Guðmundsson 2002). The density of waders differs between regions in lowland Iceland, with up to three times more waders in the South than in the West (Gunnarsson et al. 2006). The divergent tectonic plate boundary that crosses Iceland along the North-Atlantic ridge, originates frequent volcanic eruptions (Arnalds 2015), and patterns of spatial variation in wader density are positively correlated with the amount of volcanic dust deposition. Deposition rates vary on a SW-NE axis through Iceland and regional variation in wader abundance is apparent along this axis, likely caused by the fertilizing effect of the dust input, particularly in wetlands (Gunnarsson et al. 2015). Volcanic activity can have extreme effects on ecosystems as a whole, altering landscapes and even changing average temperatures. Short-term effects of volcanic activity have been shown to negatively affect breeding of Whimbrels in Iceland (Katrínardóttir et al. 2015), whereas long-term effects may be beneficial across broad geographical regions, as shown

by the positive association between wader density and ash deposition rates across the country (Gunnarsson et al. 2015).
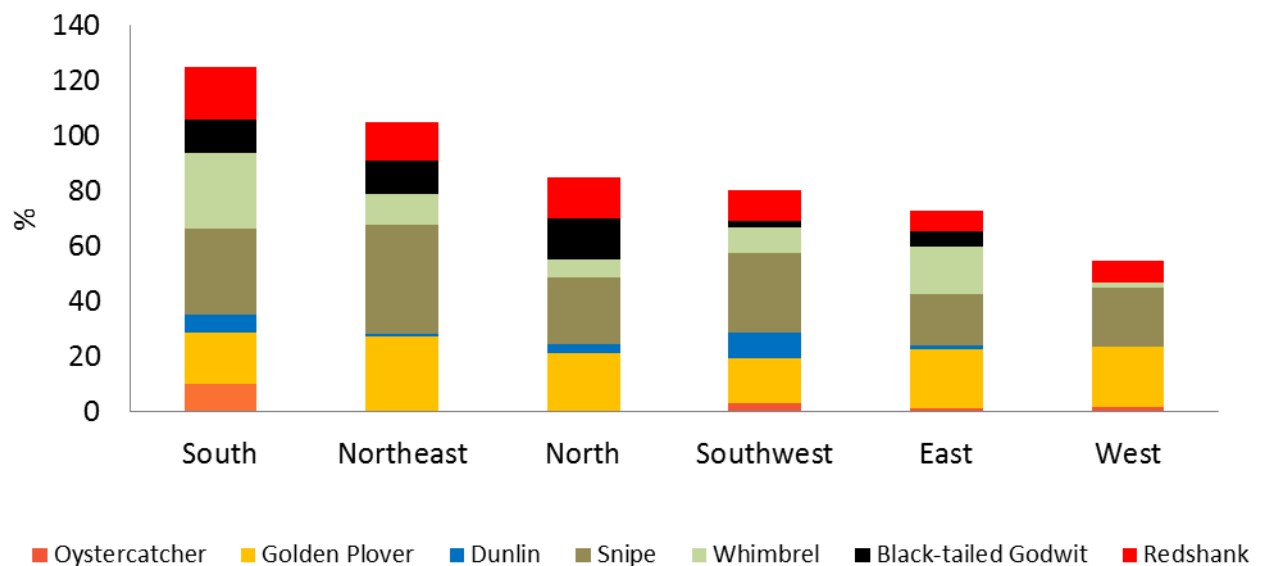
Figure 3 – Regional variation in Icelandic meadow-breeding wader species throughout lowland Iceland, measured as percentage of survey points in each region at which each species was recorded (adapted from Gunnarsson et al, 2006). As each survey point can have more than one species, each region can total more than 100% (see Figure 1 for regions).

Threats and conservation

Land use changes are likely to be the most serious threat for meadow-breeding waders in Iceland (Sutherland et al. 2012), as a consequence of the resulting habitat loss, fragmentation and homogenisation. In the first decade of the 21th century, rapid land use changes occurred in Iceland, with conversion of natural landscapes into man-made surfaces (e.g. for settlement, infrastructure, recreation and agriculture) increasing by ~20% overall between 2000 and 2006, and by over 30% in South Iceland (Wald 2012), where the density of breeding waders is highest (Gunnarsson et al. 2006). The three most prominent land use changes in Iceland at present are commercial afforestation, the construction of new summer cottages and expansion of agricultural land (Wald 2012).

Afforestation

The Icelandic government plans to afforest 5% of the land below 400 m a.s.l. (Alþingi 2006), where waders are most common and where 2.7% of the area already has forest cover (The Farmland Database 2013). Afforestation poses a threat to waders through loss of breeding and foraging habitats. The resulting change in vegetation structure makes the

habitat unsuitable as ground-nesting species typically prefer non-forested, open habitats which offer good visibility, probably to reduce the risk of predation (Stroud et al. 1990, Gunnarsson et al. 2006, Vliet et al. 2010).

Summer cottages

There are currently ~15000 summer cottages in Iceland but the area over which permission for construction has been agreed could equate to up to 60000 cottages (Skipulagsstofnun 2014). These are mostly concentrated in the lowland areas where waders are most abundant. In addition to the loss of habitat that results from the construction of buildings, the accompanying infrastructure, such as paths, roads, associated tree planting around houses and the presence of domestic cats in areas with breeding waders, can negatively impact the attractiveness of these areas to breeding waders and could increase levels of nest and chick predation (Loss et al. 2013, Wilson et al. 2014).

Agriculture

Agricultural expansion in Iceland is ongoing and, in a recent questionnaire study, the majority of Icelandic farmers surveyed reported that they are likely to expand their agricultural land within the next five years (Jóhannesdóttir et al. 2017). To what extent that proposed expansion will be carried out remains uncertain, but Icelandic farmers own the majority of land below 400 m a.s.l. (Kristófersson et al. 2007, Arnalds 2015), thus their land management decisions have the potential to greatly influence meadow breeding waders. Currently there are few regulations that restrict landowner action; this freedom to manage land independently means that farmers are the key decision-makers regarding wader conservation In Iceland. Expansion of agricultural land by means of conversion of natural or semi-natural land into areas that are cultivated or intensively grazed can lead to fragmentation and loss of wader breeding habitat. The land that is best suited for cultivation is in flat low-lying areas which are also preferred by waders, and important habitat types for breeding waders, such as partially drained wetlands are often targeted for agricultural expansion (Guðmundsson 2002, Gunnarsson et al. 2006, Jóhannesdóttir et al. 2014, Arnalds 2015). Water level management is important in agriculture but the presence of pools and other wet features is very important for waders, as the invertebrate prey on which they forage are typically most abundant around these wet features (Eglington et al. 2010). Changes in water tables can thus seriously impact the suitability of habitats for breeding waders (Gunnarsson et al. 2005b, Smart et al. 2006, Eglington et al. 2008). Mowing of crops can destroy nests and kill both chicks and adults, so the frequency and timing of mowing activities within the breeding season are also important factors for waders (Schekkerman & Beintema 2007, Kleijn et al. 2010, Schroeder et al. 2012). The timing of hayfield mowing in Iceland has been advancing, mostly because of increased demand for good hay quality (Helgadóttir et al. 2013). However, with rising global temperatures, mowing time in Iceland could occur even earlier in the season, which is likely to increase the frequency with which mowing coincides with wader nesting and thus the destruction of eggs or young chicks may become more common. Icelandic agriculture is mostly livestock-based and livestock grazing is common throughout the lowlands and throughout the year as horses are kept outside all year around. Livestock grazing can impact ground-nesting birds directly through trampling and egg eating, and indirectly by

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changing vegetation structure such that areas are either unsuitable for nesting or more vulnerable to nest predators (Vickery et al. 2001, Tichit et al. 2005, Smart et al. 2006, Katrínardóttir et al. 2015, Laidlaw et al. 2015). Low levels of grazing can be beneficial for waders, for example by reducing encroachment of native bush species such as birch (*Betula spp.*) and willows (*Salix spp.*), but overgrazed habitats typically do not provide the necessary shelter for nests, chicks and adults, and shorter vegetation is likely to have lower prey abundance (Jóhannesdóttir et al. 2014).

Conservation measures and their effectiveness

There are no specific conservation measures aimed at meadow breeding waders in Iceland. About 9% of the land area in the country is protected, but most of these areas are in the highlands (The Environment Agency of Iceland 2016) and, as the largest proportion of meadow-breeding waders occurs on privately-owned land in the lowlands, this has little impact on them. National legislation is not well developed to deal with the cumulative impacts of the current rapid changes in land use on biodiversity, or with selective habitat protection at the scale of individual farms. Nevertheless, a recent study shows that farmers consider it important to have diverse birdlife on their land, and many report that they would be willing to participate in land management actions aimed at protecting and conserving birdlife (Jóhannesdóttir et al.2017). One management action that is currently available to farmers is funding to restore wetlands, but its implementation has been slow (7 km^2 have been restored in the last two decades), although farmers have been increasingly interested in restoration options (Barkarson et al. 2016). Restoration of wetlands in lowland Iceland has the potential to be highly beneficial for breeding waders and with farmer willingness to participate in land management actions, given the right support this can potentially become an important conservation action in the future.

Future perspectives

Icelandic habitats sustain wader populations of international importance (Delany & Scott 2002, Thorup 2004) but land use changes offer an imminent threat to these populations. The loss and fragmentation of breeding habitats that is resulting from afforestation, construction of summer cottages and agricultural expansion, will erode the value of Icelandic landscapes for these species. It is hard to predict the speed and extent of these land use changes but they certainly have potential to seriously impact these internationally important populations. Unlike many other European countries, the landscape of Iceland has not yet been altered to such an extent that population declines are apparent, but lessons can clearly be learnt from other countries before irreversible damage occurs. Farmers play a key role in land management in the lowland areas of the country where most meadow breeding waders occur and their willingness to participate in conservation actions may be crucial for the preservation of these species.

Acknowledgement

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Use of agricultural land by breeding waders in low-intensity farming landscapes

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Abstract

Agriculture is one of the primary threats to biodiversity but agricultural land can also provide key resources for many species and, in some parts of the world, agricultural land supports important populations of species of conservation concern. In these cases, it is important to understand species' use of farmed land before further expansion or intensification of agricultural activities occurs. Agriculture in Iceland is still relatively low in intensity and extent, and internationally important populations of several breeding bird species are abundant in farmed regions. In these high latitude landscapes, agricultural land could provide resources that help to support these species, and the consequences of future agricultural expansion will depend on the nature of these relationships. To address these issues, we conducted surveys of bird abundance at 64 farms in areas of Iceland that vary in underlying productivity, and quantified (a) levels of breeding bird use of farmed land managed at differing intensities, from cultivated fields to semi-natural land and (b) changes in patterns of use throughout the breeding season, for a suite of species. Breeding birds use all three land management types in large numbers but, overall, bird abundance is lower in more intensively managed farm land. However, more intensively managed agricultural land supports higher densities of birds than semi-natural habitats in areas with lower underlying productivity. This suggests that in landscapes in which agricultural land does not yet dominate, conservation and commercial production can co-exist, especially in areas of low productivity. Areas like Iceland, in which agricultural land still supports large populations of internationally important species, are rare and this study highlights the need to protect these systems from the agricultural development that has led to widespread biodiversity loss throughout most of the world.

Introduction

The development and expansion of agriculture throughout the world has been a major driver of biodiversity loss (Green et al. 2005, Foley et al. 2005, Millennium Ecosystem Assessment 2005), primarily because the resulting landscapes do not provide the resources needed by many species at the appropriate spatial and temporal scales (Robinson & Sutherland 2002, Tscharntke et al. 2005). However, there can be circumstances in which farmed land can provide important resources, and may even provide resources not available elsewhere in the local landscape (Tscharntke et al. 2005). For example, in landscapes in which agricultural land occurs alongside natural habitats, the resulting spatial and temporal heterogeneity in vegetation structure may provide suitable conditions for a wider range of species than would otherwise be supported. Farmed land can provide important resources to support birds and other taxa (Dunning et al. 1992), but this is highly dependent on the extent and intensity of agricultural management (Gill et al. 2007). Areas in which agriculture is managed at low intensity are often of value for biodiversity (Bignal & McCracken 1996) and can provide key resources for species (Evans-Ogden et al. 2008), including highly threatened species (Wright et al. 2012). Agricultural management can also

result in the creation of open areas, drainage of wetlands and associated creation of ditches, all of which can potentially provide habitat that might be suitable for nesting birds, and cultivated fields can provide abundant and accessible invertebrate prey resources. However, such positive effects of agriculture can be compromised by expansion and/or intensification of land management. When agricultural management intensity increases and expands over large areas, the loss of landscape heterogeneity is typically associated with severe reductions in biodiversity (Benton et al. 2003, Tscharntke et al. 2005). These processes have occurred consistently throughout many areas of the world, fuelled by increased demands for food by a rapidly growing human population and a dietary change towards more meat-based consumption (Keyzer et al. 2005, Tilman et al. 2011). Fulfilling the ever-growing food demand while reducing effects of agriculture on wildlife has become a key challenge for conservation, opportunities for management that can sustain wildlife within agricultural landscapes are increasingly rare. A key issue in this context is how farmed land is used by species of conservation concern, and how this varies with management intensity. However, acquiring such information can be difficult in areas in which agricultural management already dominates landscapes. Consequently, areas with lower agricultural intensity and in which gradients from intensely-managed to natural land still remain, are of particular importance. These allow identification of the conditions in which species of conservation concern can occur within agricultural landscapes, and the landscapes in which these species can persist.

Icelandic agriculture is still of relatively low intensity and does not yet dominate the landscape, with only ~2% of land cultivated in the country (~7% of the area below 200 m a.s.l. which is area suitable for agriculture) (The Farmland Database 2013). This contrasts sharply with the US, in which ~20% of land is farmed (Nickerson et al. 2011), and many countries in the EU which, on average, use ~25% of their land for cultivation (Eurostat 2016). In Iceland, large patches of moderately grazed, semi-natural habitats are still present and surround the hay- and arable fields that occur on farms, thus creating gradients of agricultural intensity from the farm into the surrounding natural land (Figure 1) which are repeated throughout the lowland landscape. The current mosaic of habitat structure in Iceland provides a unique opportunity to assess how different agricultural management regimes can influence the presence and distribution of internationally important breeding bird populations which inhabit these landscapes.

The use of farmed land by wildlife might vary in relation to underlying productivity but, in Iceland, productivity varies significantly between regions due to the volcanic nature of the island and the resulting intense but geographically variable aeolian deposition (Arnalds 2015). This influences soil fertility and has been shown to influence bird density, which declines with distance from the volcanically active Mid-Atlantic ridge that runs from south-west to north-east Iceland (Gunnarsson et al. 2015). Icelandic lowlands support internationally important breeding populations of 21 bird species (Einarsson et al. 2002) and host a large part of the world population for several species (Wetlands International 2006). Iceland is especially important for breeding waders (Charadrii) (Gunnarsson et al. 2006). It sustains very high densities of several species (Jóhannesdóttir et al. 2014) and is one of the most important breeding areas for waders in Europe (Thorup 2004). These high densities are likely a product of large areas of open, vegetated landscapes (Figure 1) (Gunnarsson et al. 2006, Pickett & Siriwardena 2011).

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Fulfilling the requirements of breeding waders on farmed land has both a spatial and a temporal component, as the suitability of the habitat matrix will depend both on the scale over which individual species move, and on the different seasonal needs of those species. For example, the use of agricultural land may vary seasonally as adult mobility during egg-laying and incubation is likely to be constrained to the nesting area but, as the broods of these precocial species become more mobile, they may move between areas subject to different levels of agricultural management, particularly if these areas differ in abundance of prey resources, ease of movement through the vegetation and/or opportunities to hide from predators.

Figure 1 – An example from South Iceland showing the typical spatial structure of Icelandic agricultural areas. The most intensively managed areas (arable and hayfields; dark green) are close to the farm houses (black circles); areas with moderate management (e.g. fertilized grazing areas and old hayfields rarely mown; green) are more distant; and natural or semi-natural areas surround the farms (light green). Most lowland area in Iceland is privately owned and managed by farmers.

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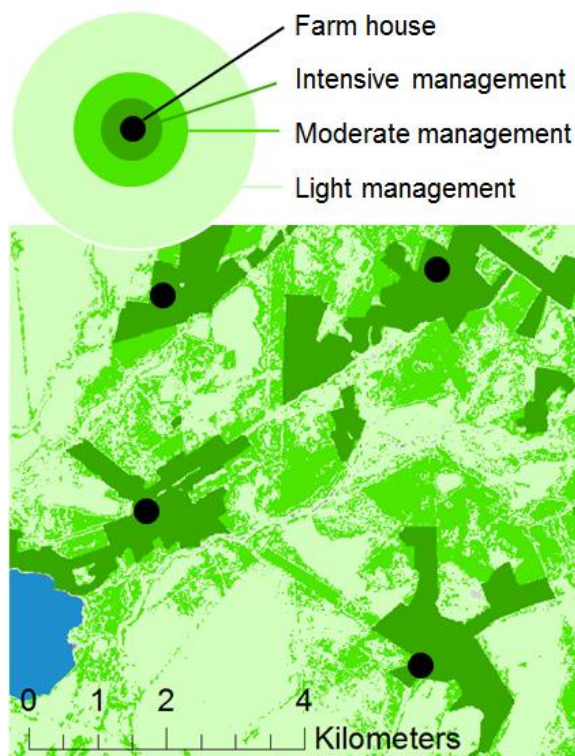
The aim of this study was to quantify (a) levels of breeding bird habitat use along a gradient from heavily managed agricultural land to semi-natural land; (b) seasonal changes in patterns of habitat use during the breeding season; and to explore the consistency of these patterns between (c) regions with varying underlying productivity and (d) species, in order to understand the influence of current levels and structure of agricultural management in Iceland on the important ground-nesting bird populations that breed in these areas, and the implications for declining wader populations in intensively managed agricultural regions elsewhere.

Methods

Study locations

This study was undertaken in Iceland, a volcanic island in the North-Atlantic Ocean located between 63° and 66° North latitude and 13° to 24° longitude. Average temperatures ranges from approximately -1°C in January and 10°C in July, annual rainfall ranges from 400 to 3000 mm (Icelandic Meteorological Office 2015), and the growing season is about 4 months. Frequent volcanic activity in Iceland causes severe erosion and leaves large areas vulnerable to soil degradation (Arnalds 1987). Areas suitable for cultivation in Iceland are mostly below 200 m a.s.l., which cover ~15% of Iceland (and where 90% of farms are located) (National Land Survey of Iceland 2013).

In the summers of 2013 and 2014, 64 farms (2.5% of the total number of farms in Iceland; (Statistics Iceland 2012) were visited in three main agricultural regions (24 each in the north and south and 16 in the west; Figure 2) which encompass the majority of agricultural production in Iceland (Statistics Iceland 2015). Farms were selected to capture geographical variation in farming practices, landscapes and biodiversity, as well as a range of farm types regarding production capacity and livestock composition (See (Jóhannesdóttir et al. 2017) for detailed information on farms). To avoid spatial clustering,

farms were selected to be >5 km apart. However, in some areas, lower levels of participation by farmers resulted in eight occasions where farms were closer than the desired level (minimum distance = 2 km).
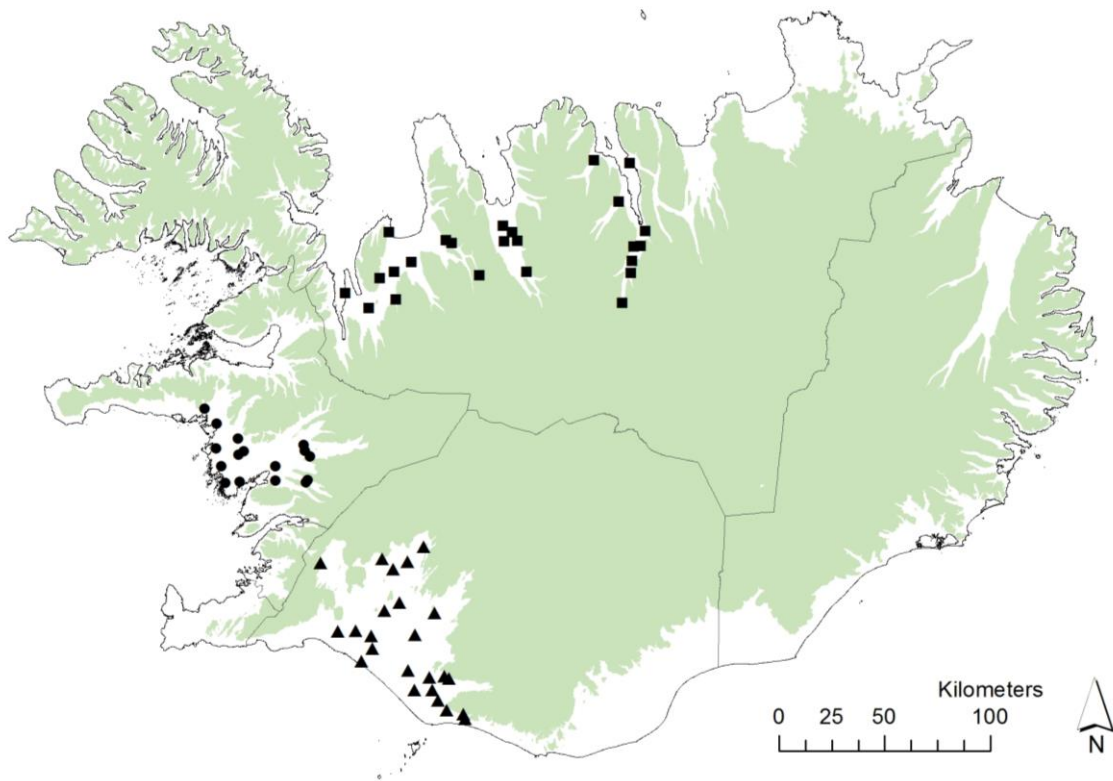
Figure 2 – Locations of the 64 surveyed farms in lowland Iceland, across three different regions: south (triangles), west (circles) and north (squares). Area above 200 m a.s.l. is shaded. Large unsurveyed lowland areas towards the SE are barren glacial outwash plains not suitable for agriculture.

Bird surveys

At each farm, three survey locations were selected representing different levels of agricultural management (intensive, moderate, light; Table 1), with the exception of two farms; one missing moderate management and the other light management land. Each farm was surveyed twice: early, from mid-May till mid-June, encompassing most egg-laying and incubation (peak nest initiation for the main species concerned is late May); and late, from mid-June to mid-July, the period that primarily encompasses chick rearing (Gunnarsson 2010). At each location, all birds were counted along one line transect per management level (Bibby et al. 2000, Jóhannesdóttir et al. 2014). As size and shape of agricultural fields can vary substantially, transect length and width were limited by field size but the single observer (LJ) aimed to keep the surveyed area similar to ensure constant survey effort (average transect length ($\pm$ SD) = 253 $\pm$ 75 m; width = 92 $\pm$ 24 m, corresponding to an average survey area ($\pm$ SD) of 2.3 $\pm$ 0.8 ha). Due to constraints on access to agricultural fields, all transects were conducted along field edges, with the observer counting all visible birds on the field side only.

Table 1 – Classification and definition of the three different agricultural management types surveyed on farms throughout lowland Iceland

Management type	Description
Intensive	Hay (85%) and arable (15%) fields (~90% of fields in Iceland are hayfields). Most hayfields are mown twice per year.
Moderate	Old hayfields that are rarely or never mown but used for grazing, or fertilized grasslands used for livestock grazing.
Light	Semi- natural or natural areas under little (low intensity grazing, usually by sheep or horses) or no agricultural influence

Data analysis

We used generalized linear mixed models (GLMMs) with a Poisson error distribution and log-link function to analyse the variation in the total number of birds (all species) on each transect, and the number of each of the eight most common species, with transect area (natural log-scale) as an offset. Management type (intensive, moderate or light), region (north, south or west) and survey round (early or late) and interactions between management and region, management and round, and management, region and round were used as fixed factors, while farm identity was included as a random factor to control for the non-independence of the multiple surveys on each farm. The model including all species also had an additional random factor of species. In the single-species models, three species Oystercatcher (Haematopus ostralegus ostralegus), Black-tailed Godwit (Limosa limosa islandica) and Redshank (Tringa totanus robusta) had too few observations to test for all the interactions (see Table 3 - grey blocks represent missing interactions). Meadow Pipit (Anthus pratensis) was excluded from the multi-species model, as this passerine species has different resource requirements to the wader species which were the primary focus. Statistical analyses were performed in the program SPSS Statistics 22.0.

Results

A total of 3282 birds of 29 species were recorded on 190 transects surveyed across the 64 farms over two rounds (380 transects in total). Most of the species were not commonly seen and eight species dominated; Oystercatcher, Golden Plover (Pluvialis apricaria altifrons), Dunlin (Calidris alpina schinzii), Snipe (Gallinago gallinago faeroeensis), Whimbrel (Numenius phaeopus islandicus), Black-tailed Godwit, Redshank and Meadow Pipit comprised 84% of the total number of individuals recorded (Meadow Pipit alone accounted for 39% of all birds recorded).

Table 2 - Results of a generalized linear mixed model (GLMM) of the variation in the total number of individuals of the seven most common wader species (Oystercatcher, Golden Plover, Dunlin, Snipe, Whimbrel, Black-tailed Godwit and Redshank), in relation to management type (Intensive, Moderate, Light), region (south, west or north) and round (early or late season). Transect area was included as an offset and farm identity and species as random factors. Significant factors are shown in bold.

Wader species	F	DF	Sig.
Corrected model intercept	10.859	17	**<0.001**
Management	58.828	2	**<0.001**
Region	1.300	2	0.273
Round	25.332	1	**<0.001**
Management*Region	62.939	4	**<0.001**
Management*Round	18.747	2	**<0.001**
Management*Region*Round	28.591	6	**<0.001**

Large numbers of waders were recorded on all transects in all regions, but wader density varied significantly across the three management types, with the greatest densities occurring in areas with light management, but this pattern was more evident in early than late season (Table 2, Figure 3). Wader density was significantly greater in late than early season, but this increase occurred in intensive and moderate management and not in light management (Table 2, Figure 3). Overall, densities did not vary significantly between regions but there was a significant interaction with management type, with lower densities occurring in intensive management in the south and north while, in the west, densities were highest in the intensive management category in both seasons (Table 2, Figure 3). The seasonal differences in density on the three management types also differed significantly between regions (Table 2; three-way interaction), with seasonal declines in density on all three management types in the south, but seasonal increases on intensive and moderate management in the west and moderate management in the north (Figure 3).
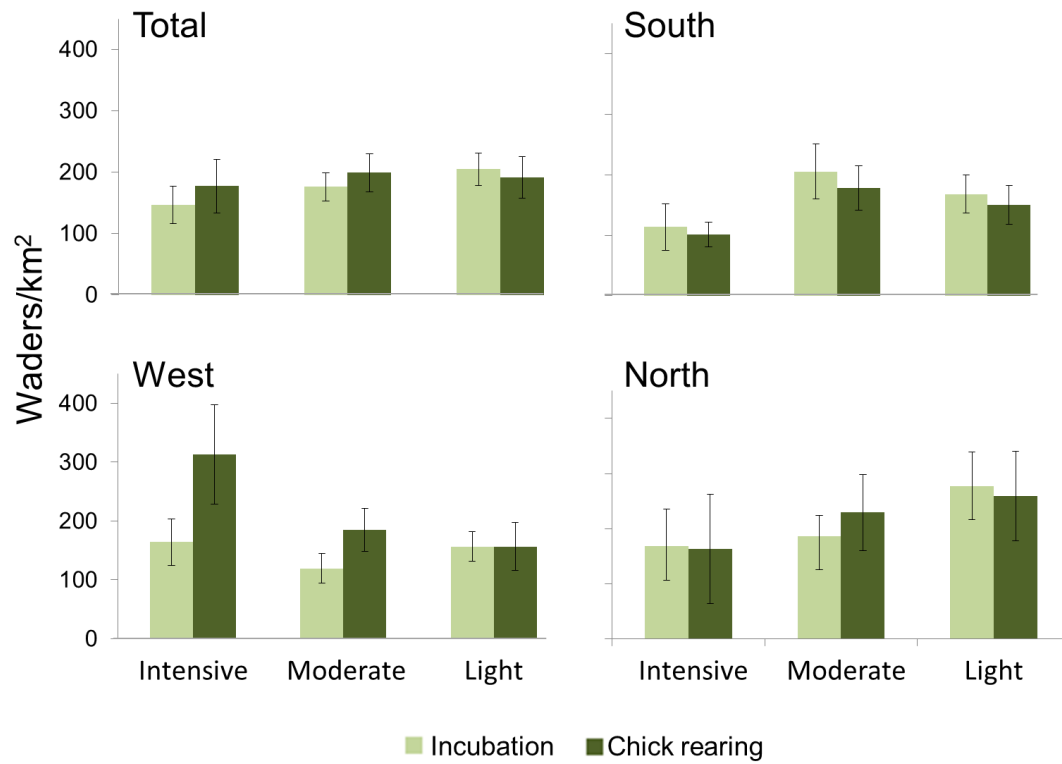
Figure 3 - Mean (±SE) densities of the seven most common wader species on the three different management types in the early (light green) and late (dark green) season surveys across all survey sites (total) and in each of the three regions (see Figure 1 for regions).

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Table 3 - Results of generalized linear mixed models (GLMMs) of the variation in the number of individuals of each of the eight most common species (offset by transect area), in relation to management type (Intensive, Moderate, Light), region (south, west or north) and round (early or late), having farm as a random factor. Grey box indicates when a species had too few observations to test for the interactions. Significant factors are shown in bold.

Dunlin (n=117)	F	DF	Sig.	Snipe (n=289)	F	DF	Sig.
Corrected model	3.368	17	**<0.001**	Corrected model	4.011	17	**<0.001**
Management	9.219	2	**<0.001**	Management	2.347	2	0.097
Region	0.28	2	0.756	Region	5.252	2	**0.006**
Round	3.655	1	0.057	Round	16.934	1	**<0.001**
Management*Region	2.320	4	0.057	Management*Region	7.271	4	**<0.001**
Management*Round	5.398	2	**0.005**	Management*Round	1.186	2	0.307
Management*Region*Round	2.373	6	**0.029**	Management*Region*Round	2.907	6	**0.009**

Black-tailed Godwit (n=111)	F	DF	Sig.	Redshank (n=300)	F	DF	Sig.
Corrected model	3.938	9	**<0.001**	Corrected model	7.635	17	**<0.001**
Management	4.155	2	**0.016**	Management	19.901	2	**<0.001**
Region	0.206	2	0.814	Region	0.985	2	0.374
Round	2.583	1	0.109	Round	23.661	1	**<0.001**
Management*Region	2.731	4	**0.029**	Management*Region	5.882	4	**<0.001**
Management*Round				Management*Round			
Management*Region*Round				Management*Region*Round	2.059	8	**0.039**

Whimbrel (n=226)	F	DF	Sig.	Golden Plover (n=326)	F	DF	Sig.
Corrected model	5.000	17	**<0.001**	Corrected model	3.668	17	**<0.001**
Management	3.925	2	**0.021**	Management	9.469	2	**<0.001**
Region	0.009	2	0.991	Region	2.322	2	0.100
Round	0.003	1	0.955	Round	5.697	1	**0.018**
Management*Region	3.423	4	**0.009**	Management*Region	4.740	4	**0.001**
Management*Round	0.063	2	0.939	Management*Round	1.842	2	0.160
Management*Region*Round	0.579	6	0.747	Management*Region*Round	4.200	6	**<0.001**

Meadow Pipit (n=1287)	F	DF	Sig.	Oystercatcher (n=89)	F	DF	Sig.
Corrected model	10.326	17	**<0.001**	Corrected model	8.004	5	**<0.001**
Management	51.919	2	**<0.001**	Management	7.252	2	**0.001**
Region	12.428	2	**<0.001**	Region	12.884	2	**<0.001**
Round	5.837	1	**0.016**	Round	0.101	1	0.751
Management*Region	12.856	4	**<0.001**	Management*Region			
Management*Round	0.518	2	0.596	Management*Round			
Management*Region*Round	0.718	6	0.635	Management*Region*Round			
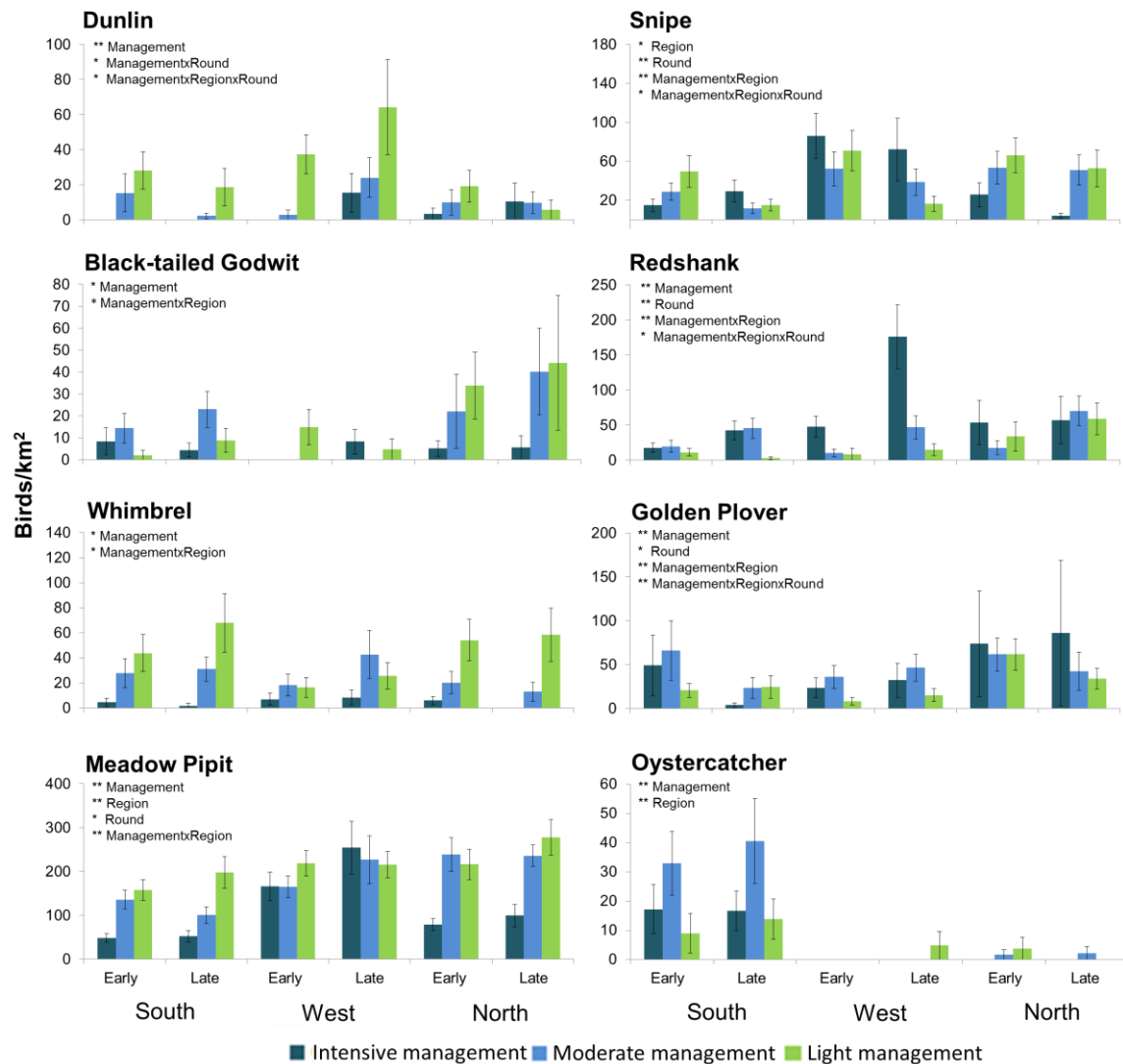
Figure 4 - Mean (± SE) densities of the seven most common wader species and one passerine (Meadow Pipit) between transects with differing management (Table 1), in early and late breeding season and in different regions of Iceland. Asterisks and terms indicate significant differences from generalized linear mixed models (see Table 3) with *p<0.05, **p<0.005. Note different scales on each plot.

Factors influencing density of individual species

Dunlin, Black-tailed godwit, Whimbrel and Meadow Pipit all showed similar variation in density across management types, with lower densities generally occurring in intensive management and higher densities in light management (Figure 4). By contrast, densities of Snipe and Redshank were higher in intensive management, but only in the west (Figure 4). Regional variation in densities was apparent in many species, the most extreme being Oystercatcher, which was very rare on farms in the north and west but was common in the south, and densities in this region were greatest in moderate management. For several species (Snipe, Redshank, Black-tailed godwit, Whimbrel, Meadow pipit), relative use of

intensive management was greater in the west than in the other two regions, particularly in the late season (Figure 4).

Discussion

Agriculture is generally thought to depress biodiversity but in some cases it can be beneficial, especially low intensity agriculture (Bignal & McCracken 1996, Tscharntke et al. 2005). Icelandic agriculture is still at low intensity and lowland agricultural areas are characterized by a heterogeneous mosaic of farmed and semi-natural habitats, with a management gradient ranging from frequently mowed (2-3 times per year) hayfields or arable fields (primarily barley), to semi-natural areas with light or no management (although most of this land is under some sort of grazing management). Measurements of bird density along this gradient, where birds have a selection of agricultural and semi-natural habitats, show that all these habitats are used extensively by breeding birds, but the patterns of use vary regionally, seasonally and between species. Agricultural land in Iceland therefore appears to provide important resources for breeding birds but this varies across species, with some, such as Oystercatcher and Redshank, extensively using more intensively managed agricultural land, while others (e.g. Dunlin and Whimbrel) only occur at very low densities. The current landscape structure in lowland Iceland, with agricultural land embedded within semi-natural land, may therefore be benefitting the breeding bird community, while a more homogenous landscape comprising primarily agricultural or semi-natural land would likely be less able to sustain the current variety and abundance of breeding waders (Benton et al. 2003, Tscharntke et al. 2005). In other more intensively managed agricultural systems; wader populations have declined sharply because of agricultural intensification (Donald et al. 2001, Newton 2004, Roodbergen et al. 2012).

Effects of agricultural management type on breeding bird density

Wader density varied significantly along the management gradient, with lower densities tending to occur in more intensively managed areas, particularly in the early (nest-laying and incubation) season. This suggests that further expansion of frequently-cut hayfields and arable fields would be likely to result in reduced overall densities, as has been widely reported in other countries (Taylor & Grant 2004, Amar et al. 2011, Ławicki et al. 2011). However, these differences in density with management varied between regions and species. Three wader species (Dunlin, Black-tailed Godwit and Whimbrel) and the one passerine (Meadow Pipit) tended to occur in the highest densities in the least intensively managed areas, but the densities of Snipe, Redshank, Golden Plover and Oystercatcher showed quite different patterns. This illustrates how different species can respond to agriculture land use in different ways, and thus how the impacts of agricultural expansion might vary between species. The regional variation in relationships between density and management type also shows how the same species can respond differently to different environmental conditions.

Regional variation in bird densities on agricultural land

Although there is no strong regional difference in wader density, the regional variation in relative use of different management intensities indicates an important influence of underlying productivity on the use of agricultural land. Wader densities are generally lower on more intensively managed land, except in the west during the chick rearing period when the highest densities occur in the intensive management areas. The likely reason for this regional variation is the underlying difference in primary productivity caused by the active tectonic plate boundary that crosses Iceland along the North-Atlantic ridge. Frequent volcanic eruptions have resulted in the dispersal of large amounts of volcanic dust over many thousands of years (Arnalds 2015), with greater deposition closer to the plate boundary. The dust has an important fertilizing effect and, as the western part of Iceland is further from the plate boundary than the north and the south, the soils in the west receive less volcanic dust and are therefore less productive (Arnalds 2015). This variation in underlying productivity has previously been shown to influence wader density in Iceland, with higher densities occurring in areas with higher volcanic dust input (Gunnarsson et al. 2006, 2015). Interestingly this regional difference in bird density was not apparent on the agricultural land that was the focus of the present study (Table 2), suggesting that agricultural activities (e.g. fertilizer application) may mask the lower underlying productivity of semi-natural areas in the west. The higher densities of birds in the more intensively managed agricultural land in the west might therefore also reflect effects of agricultural activities, such as the fertilization and liming of the soil, improving the productivity of these sites relative to the surrounding land. Previous studies show that the use of synthetic and organic fertilizer in Iceland can positively affect earthworm density, which are an important prey for waders, though the benefits vary between species (Sigurðardóttir & Þorvaldsson 1994). Liming is also beneficial for earthworms, as most earthworm species in temperate agricultural soils prefer a pH of around 7 and liming has often been shown to increase earthworm numbers (Haynes & Naidu 1998). The seasonal increase in bird density on intensively managed sites in the west (Figure 3) suggests that adults may be moving broods into cultivated land (e.g. densities of Redshank in the west were threefold higher during the chick rearing period than during incubation (Figure 4)), and thus that resources for chicks may be relatively more abundant or accessible in these areas.

In the south and north regions, the density of Snipe follows the overall pattern of higher density in areas with light management, but interestingly that pattern is reversed in the west (Figure 4). Most snipe found in intensively managed sites were foraging in the drainage ditches surrounding fields, and wet features such as these can be beneficial for many taxa (Herzon & Helenius 2008). Drainage ditches around agricultural land might therefore provide important resources for snipe, particularly in the west where productivity on semi-natural land is lower (Gunnarsson et al. 2015).

The pronounced regional difference in the density of Oystercatchers is likely to reflect the largely coastal distribution of this species in regions other than the south (Jóhannsson & Guðjónsdóttir 2009).

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Seasonal difference in bird densities on agricultural land

The temporal difference in density might be explained by a change in detectability caused by different behaviour between the species and their changing requirements during the season. The seven wader species include three species (dunlin, golden plover and snipe) which tend to show cryptic behaviour during chick rearing, and hide themselves and their chicks from any threats, while four species (redshank, whimbrel, black-tailed godwit, oystercatcher) defend their chicks and mob intruders during chick rearing (Jónsson & Gunnarsson 2010). The cryptic species generally tended to occur in lower numbers in the later round, which could reflect lower detectability, a tendency to leave agricultural habitat during chick-rearing or lower breeding success (leading to adults leaving the area).

The variation in the use of different management categories between seasons possibly reflects birds specifically choosing habitats based on different requirements as the breeding period progresses. For example, in the west, Dunlin, Black-tailed godwit, Meadow Pipit, Redshank and Golden Plover all show a trend in which densities in the intense management increase later in the breeding period, which might suggest that the adults are moving onto cultivated land with their chicks. This pattern might be driven by the fertilizing effect of cultivated land suggesting that, in the west, agriculture might be particularly beneficial to these species.

Current situation and future developments in Iceland

Although the density of birds in these landscapes tends to be higher in lightly managed than intensively managed agricultural land, densities in the areas under the most intense agricultural management are still very high, suggesting that agricultural habitats provide important resources within these landscapes. These density estimates are typically much higher than those recorded in other countries in which these species breed. For example density estimates on grasslands in the Netherlands (for Oystercatcher, Snipe, Black-tailed Godwit and Redshank), are ~40% of the density recorded in Iceland (Jóhannesdóttir et al. 2014), and on grazing marshes in south-east England the density of breeding Redshank is only ~1% of the density of waders in cultivated fields in Iceland (Smart et al. 2006).

The current complex landscape structure of agricultural land and semi-natural land in lowland Iceland seems to be highly suitable for these species, given the large populations that the Icelandic landscape supports. However, this favourable habitat composition is likely to change, as a recent study shows that farmers in Iceland intend to expand their cultivated land in the coming years in response to increasing demand for agricultural production (Jóhannesdóttir et al. 2017). Understanding spatial and temporal variation the use of agricultural and semi-natural land by these species will be key in designing strategies to reduce the impact of this increase in agricultural production. Currently there are very few restrictions on land management in Iceland (Alþingi 2015) and there are no conservation efforts focussed on these species, even though Iceland is of international importance for breeding waders and almost all of these species are declining globally (International Wader Study Group 2003). Integrating conservation measures into land

management in Iceland will therefore be crucial in order to sustain these populations. The role of farmers in the conservation of these species is especially important both because agriculture provides important resources for these species at present and because most of lowland Iceland is either privately owned or state property managed by farmers (Kristófersson et al. 2007). However, questionnaire surveys suggest that Icelandic farmers are interested in having rich birdlife on their estate, and are willing to participate in different management strategies aimed at sustaining these populations (Jóhannesdóttir et al. 2017). Iceland is one of an increasingly rare group of countries in which agricultural landscapes still support large numbers of species of conservation concern, but evidence from other countries throughout the world has shown how fragile this situation can be, and how rapidly biodiversity can be lost in response to agricultural expansion and intensification. Protecting these landscapes from further development is therefore crucial, both to maintain the species that they support and to aid the design of restoration and recovery strategies in locations in which widespread declines have already occurred.

Acknowledgements

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Effects of spring temperature and volcanic eruptions on wader productivity

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Abstract

Key demographic parameters often show substantial annual variation that can have important consequences for rates of population growth. Since 2011 we have conducted annual estimates of the productivity of Icelandic Black-tailed Godwits *(Limosa limosa islandica)* over a large part of their breeding range. During this period, a volcanic eruption resulted in extensive dust deposition across the region. We show that Godwit productivity varies with spring temperatures but in the year of the volcanic eruption, productivity was reduced to almost zero. This rare but extreme event is likely to have had only a short-term influence, whereas ongoing warming of sub-Arctic regions is potentially a more substantial driver of the continued growth of this population.

Keywords:

Introduction

A major driver of population growth rates is the temporal variation in recruitment (Sæther et al. 2016). However, identifying temporal drivers of demography may require information collected over sufficiently large spatial scales to encompass the influence of variation in local factors such as habitat quality, density and predation rates, which can also influence demography (Jonsson et al. 2013, Stojanovic et al. 2014). To develop the population-wide demographic models needed in a rapidly changing world (Robinson et al. 2014), long-term, large-scale studies of temporal variation in demography are therefore needed. In particular, extreme but rare events may have important effects on demography, but are inevitably difficult to identify (Katrinardottir et al. 2015, Senner et al. 2015).

Many populations of waders (Charadrii) breed intemperate or Arctic regions, undertake long migrations to their wintering grounds, and currently have declining global populations (Thomas et al. 2007, Delany et al. 2009, Sutherland et al. 2012). It is therefore necessary to identify drivers of variation in demographic rates of waders in order to manage their impacts. Migratory wader populations, particularly those breeding in Arctic latitudes, often show high levels of annual variation in productivity over large spatial scales. For example, the proportion of juveniles in flocks of high Arctic-nesting species on the non-breeding grounds has been shown to fluctuate annually, in association with population abundance cycles of lemmings (*Lemmus spp., Dicrostonyx spp.*) in the Arctic (Summers & Underhill 1987, Aharon-Rotman et al. 2015), and the proportion of juveniles in non-breeding wader flocks has also been shown to vary annually with weather conditions during the breeding season (Schekkerman et al. 1998, Beale et al. 2006).

Iceland hosts internationally important breeding populations of several wader species (Gunnarsson et al. 2006), including almost the entire population of the islandica subspecies of Black-tailed Godwit (*Limosa limosa islandica*) (Gunnarsson et al .2005a). Godwits are restricted to breeding in lowland basins around the country, with the southern lowlands of Iceland containing the largest breeding area and hosting around half of the breeding population (Gunnarsson et al. 2006, Jóhannesdóttir et al. 2014). In 2011, a monitoring programme was initiated for Godwits (and for more species from 2012), in which brood counts are used to estimate annual variation in breeding success in the southern lowlands. In 2010 and 2011, two volcanoes erupted in southern Iceland: Eyjafjallajokull (63°38.00N, 19°37.00W) in 2010 (14 April–23 May) and Grımsvotn (64°25.120N, 17°19.480W) in 2011 (21–28 May) (Sigmundsson et al. 2010, Petersen et al. 2012). Both these eruptions emitted large amounts of volcanic dust and, although much of the ash from Eyjafjallajokull went out to sea, Grimsvotn ash was widely distributed in southern Iceland (Gudmundsson et al. 2012). During the field season of 2011, volcanic ash was wide spread in the study area but its daily prevalence was highly dependent on local weather conditions. On dry days, fieldworkers used face masks to protect their lungs, as simply walking through vegetation disturbed large amounts of ash into the air. The ash was further redistributed by wind and often formed piles in depressions. A layer of ash was frequently observed covering pools in wetlands and traps for invertebrate sampling frequently became clogged with ash. Short-term negative effects of volcanic dust on birds have been reported previously and are probably mediated through increased invertebrate mortality (Dalsgaard

et al. 2007, Marskeet al. 2007). For example, a pronounced reduction in breeding success of Icelandic Whimbrels (*Numenius phaeopus*) breeding close to the eruption site was recorded in 2011 (Katrinardottiret al. 2015). However, the duration of impact of the eruption on breeding waders and the spatial scale over which these effects may be apparent are unknown, as the opportunities to explore the effects of volcanic eruptions on bird demography are exceedingly rare. At high latitudes, timing of breeding and breeding success can also vary in relation to spring temperatures, probably as a consequence of temperature-driven variation in vegetation growth and invertebrate emergence and abundance (Tulp & Schekkerman 2008, J.A. Alves et al. unpubl. data). The volcanic activity that coincided with our monitoring programme provided a unique opportunity to explore the effects of both spring temperature and stochastic extreme events on large-scale productivity of a wader population on the sub-Arctic breeding grounds. Here we quantify annual variation in Godwit productivity to assess whether productivity increases with spring temperatures but is negatively impacted by volcanic eruptions, and to assess the magnitude and duration of any effects of volcanic activity.

Methods

Estimating large-scale productivity

During the last 10 days of June 2011–2016, road-based surveys were carried out over a large part of the low-lands of southern Iceland (Figure 1). The car was driven at a maximum speed of 40 km/h, with open windows. Surveying was only conducted in dry conditions and at wind speeds below 7 m/s. Along transects which totalled 198 km (Figure 1), the presence of all alarming adult Godwits within 100 m of the car was recorded. All habitats along the transect were surveyed irrespective of their suitability for Godwits. Godwits (and many other waders) perform noisy and conspicuous alarm behaviour near their chicks (Gunnarsson et al.2005b) and previous studies have shown that strongly alarming adults are a robust indicator of the presence of one or more chicks (Gunnarsson et al. 2005b). Each strongly alarming individual or pair was taken to indicate the presence of a brood. In each case the perpendicular distance from the road transect to the chicks (when seen) was recorded with a laser rangefinder to ensure only chicks within 100 m of the road were included, along with a GPS position of the car on the road. In those cases when chicks were not observed, the distance to the alarming adult or, for pairs, the midpoint between the two adults was recorded. The number of broods recorded along the transect was used as an estimate of annual productivity. The conspicuous alarming behaviour of adults means that detectability of broods is very unlikely to vary within 100 m of the vehicle.
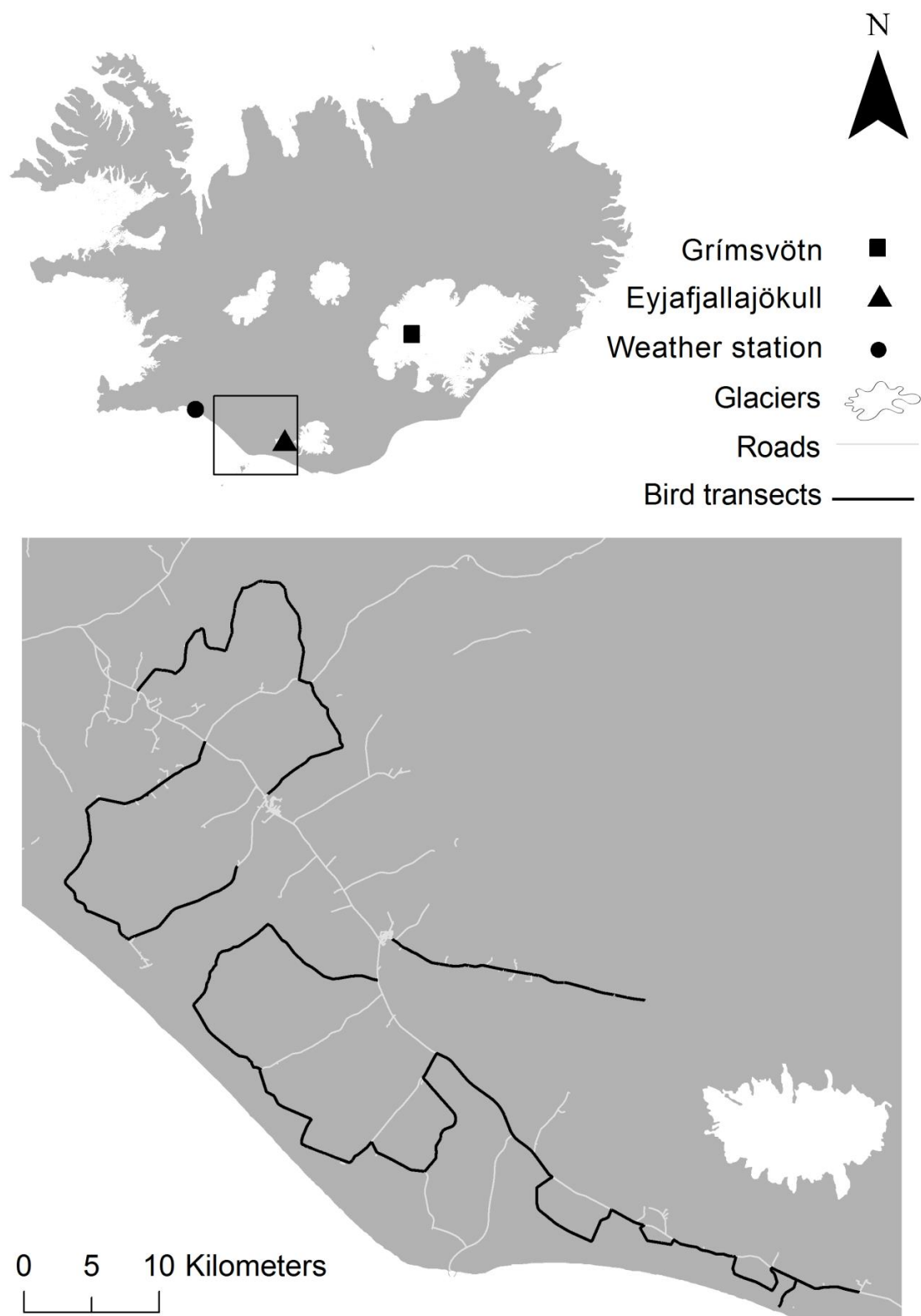
Figure 1 - Map of Iceland and the location of the 198 km road transect along which Godwit broods were surveyed in late June 2011-2016.

Weather data

To assess the influence of spring temperature on large-scale productivity, we extracted the mean daily temperature during May of each year (2011–2016) from the weather station of the Icelandic Meteorological Institute (www.vedur.is) nearest to the transect (Eyrarbakki 63°520N, 21°090W). The relationship between spring temperature (mean May temperature) and annual Godwit productivity was assessed using a GLM with a normal error structure, with and without the year in which the volcanic eruption took place (2011).

Timing of laying

As part of long-term studies of Godwit breeding ecology in southern Iceland, the timing of egg laying has been monitored each year since 2001 (J.A. Alves et al. unpubl. data) by locating as many nests as possible and floating the eggs to hind cast the date of laying of the first egg (Liebezeit et al. 2007). In each year from 2011 to 2016, between 14 and 28 Godwit nests (mean=20.6 ± 5.5 sd) were monitored in the southern lowlands. As the surveys all took place in late June, the number of broods observed in each year could be influenced by the timing of egg-laying. To assess whether our annual estimates of productivity varied in relation to timing of egg laying, a GLM with annual productivity as the dependent variable and mean nest initiation date as the predictor and a normal error structure was used.

Statistics were performed in R 3.2.2 (R Development Core Team 2008).

Results

The mean number of broods recorded within 100 m along the 198-km transect between 2011 and 2016 was 17.8 (± 10.1 sd) but the variation between years was extremely high (range 2–31 broods per year; Figure 2a).

The number of broods along the transect was strongly positively related to mean May temperature in each year between 2012 and 2016 but not when 2011was included (Figure 2b). In 2011, when the region was largely covered by volcanic ash, only two broods were recorded along the transect. This is only 7.5% of the value (26.7 broods) that would be predicted by the relationship with mean May temperature for non-eruption years (7.2°C, the second highest May temperature in 2011–2016) (Figure 2b).

The overall mean start of laying in 2011–2016 was 26 May (range 21–28 May), and the mean timing of nest initiation in each year was not significantly related to the number of broods present in late June (R^2= 0.399, P=0.18).
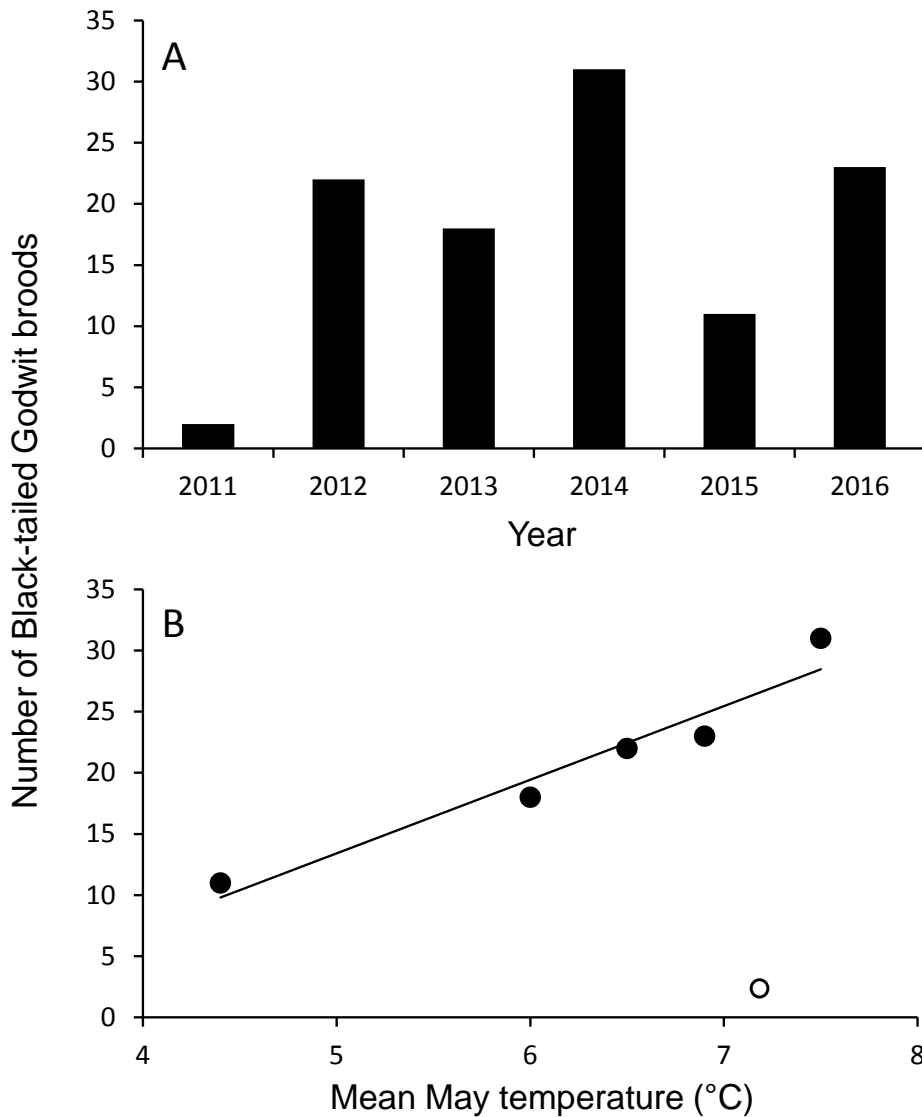
Figure 2 - (a) Annual variation in productivity of Black-tailed Godwits and (b) the relationship between mean May temperature and large-scale productivity. Productivity is measured as the number of broods recorded along a fixed road transect in Southern Iceland each year. The line is fitted through years 2012-2016 but 2011, which was the only year with a volcanic eruption, is noted by an open circle. Linear model without eruption year: $R^2 = 0.94$, $P = 0.007$; Linear model including eruption year: $R^2 = 0.11$, $P = 0.53$).

Discussion

During a 6-year period in which spring temperatures varied greatly and a major volcanic eruption took place in southern Iceland, we recorded substantial variation in the productivity of Godwits. The variation in productivity between 2012 and 2016 was very closely and positively related to mean May temperatures. However, during a relatively warm spring (2011) when a volcanic eruption impacted the study area, productivity of the

Godwit population fell to almost nothing. The study provides a rare example of the magnitude of impact that extreme events such as a volcanic eruption may have on bird productivity but also highlights the likely short-term duration of such an event. Godwits are long lived (median lifespan c. 10 years; Gillet al. 2001) and events of this type are rare in comparison with their typical lifespan. A large part of the Icelandic Godwit population winters on the estuaries of Britain, and annual censuses on these areas have shown sustained increases in the Godwit population (Frost et al.2016). Intriguingly, the population index for 2011/12 (immediately following the eruption) decreased slightly before increasing quite substantially the following winter (Frost et al.2016), potentially reflecting the reduction and subsequent increase in productivity recorded in our surveys on the breeding grounds.

The rapid recovery of productivity in the year following the volcanic eruption (2012) indicates that the negative effects of the volcanic eruption seem to be short induration. A similar effect has been observed in Whimbrels in the same region, where large-scale breeding success was temporarily negatively impacted during the 2011 eruption (Katrinardottir et al.2015). In the long-term, the effects of volcanism on waders in Iceland are most likely to be positive, as volcanic dust recharges vegetated land with nutrients and buffers pH, and densities of waders across Iceland are generally higher where volcanic dust inputs are higher (Gunnarsson et al.2015).The negative short-term effects of volcanic eruptions are likely to be due to the effects of the high volume of volcanic dust on invertebrate prey populations. Previous studies have suggested that the brittle volcanic dust can cause mortality of invertebrates through blocking of the spiracles and increased rates of abrasion and desiccation (Marske et al.2007, Elizalde 2015). Volcanic eruptions may also influence water and air quality (Horwell & Baxter 2006, Stewart et al.2006), and the presence of large amounts of ash covering the ground could encourage adults to defer breeding attempts in that year.

The process by which higher spring temperatures promote higher productivity is not yet fully understood but is likely to be a combination of factors. It is worth noting that even though May and June temperatures were not correlated for the set of years considered here, temperature in these months is correlated in longer time series (J.A. Alves et al. unpubl. data) so temperature links with productivity may well operate over longer or different periods than for the May correlate explored here. The timing of emergence of the invertebrate prey of waders can vary strongly with temperature (Tulp & Schekkerman 2008, Pearce-Higgins et al. 2010), and the resulting variation in food abundance can potentially affect both adult body condition and the growth and survival of young (Schekkerman et al.1998, Pearce-Higgins et al.2010). The timing of laying of Godwits in Iceland is earlier in warmer springs (Gill et al.2014, J.A. Alves et al. unpubl. data) and thus variation in the number of broods counted in late June could result from differences in hatch dates (with fewer broods having hatched by late June in colder years). However, the annual variation in productivity that we recorded was unrelated to timing of laying in these years. Another potential driver of a relationship between spring weather and productivity in waders is the proportion of adults which defer breeding attempts or do not re-nest upon early failure each year, but this may be more common in colder springs, when adults are in poorer body condition. Our relationship with pre-breeding temperature (May) may point to the potential of this process to influence large-scale productivity. However, little is known about how common deferral of breeding may be in these species.

This study shows how annual variation in productivity of a wild bird population over large areas can vary greatly in response to both rare, extreme events and moderate but persistent effects of temperature on environmental conditions. As expected for a long-lived species, effects of a single year of very low productivity were short in duration and probably had a limited effect on population growth rate. The pronounced effect that spring temperature has on annual variation in productivity is, however, likely to be crucial for the future population trajectory of Godwits and related species, given the ongoing and rapid warming of Arctic and sub-Arctic regions.

Acknowledgements

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Interacting effects of agriculture and landscape structure on breeding wader populations in Iceland

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Abstract

The capacity of different landscapes to sustain viable populations depends on the spatial and temporal availability of key population-specific resources within those landscapes. Heterogeneous landscapes generally sustain higher levels of biodiversity than homogenous ones as those provide a wider range of resources. Agricultural expansion has resulted in large-scale homogenisation of landscapes with associated declines in many taxa. However, during the early stages of agricultural development, increased landscape heterogeneity and changes in local productivity through fertilizer inputs can potentially increase resource availability for some species. Agriculture in Iceland is not yet highly intensive or extensive, and primarily occurs as hayfields embedded within a mosaic of semi-natural wetlands and heaths. These landscapes also support internationally important breeding populations of several wader species but the role of agricultural land in promoting or constraining breeding waders densities is currently unknown. Understanding the effect of agriculture land on these wader populations is important as the area of cultivated land is likely to expand in Iceland during the coming years, in big part through conversion of the remaining wetlands. Here we quantify the relationships between breeding wader densities in lowland Iceland and the amount of cultivated land in the surrounding landscape, in order to assess the extent to which cultivated land affects wader populations in these landscapes, and the potential implications on wader density of future expansion of cultivated land at the expense of wetlands. Densities of waders on transects through wetlands were greater in landscapes with larger amounts of wetland, indicating the importance of more wetland availability for these species. The amount of cultivated land in the surrounding landscape interacts with altitude, as wader numbers decline with increasing amounts of cultivated land at lower latitudes but the inverse pattern occurs at higher latitudes, suggesting that the additional resources provided by cultivated land may be more important in the less fertile uplands. Further conversion of wetlands into cultivated land in low-lying areas of Iceland is likely to be detrimental for breeding waders, but such effects may be reduced or even reversed in less fertile areas.

Introduction

Landscapes vary in their ability to sustain viable populations of species through the different types and levels of resources that they may provide. Resource availability is often a function of habitat heterogeneity, with more heterogeneous landscapes typically providing more diverse resources and opportunities for individuals exploiting those (Roth 1976, Benton et al. 2003, Tscharntke et al. 2005). Habitat heterogeneity influences species diversity and density, and ecosystem function, at different spatial scales (Roth 1976, Pickett & Cadenasso 1995, Christensen 1997). Landscape and habitat heterogeneity can stem, for example, from variability in vegetation structure, composition, density and biomass which are partly driven by the underlying productivity of ecosystems (Pickett & Cadenasso 1995, Forman 2014, Gunnarsson et al. 2015) and also by anthropogenic actions. Agricultural land has become one of the largest terrestrial biomes, occupying ~40% of all land on the planet (Foley et al. 2005). The expansion of agriculture has altered landscapes unlike any other anthropogenic activity and has had an immense effect on biodiversity in these landscapes (Flowerdew 1997, Sotherton & Self 1999, Donald et al. 2001, Foley et al. 2005, Ellis et al. 2010). Populations of numerous species, particularly specialist species, have declined as agriculture has expanded, while generalist species have often thrived in agricultural habitats (Wright et al. 2012).

Agriculture is a major driving force in changing both the heterogeneity and the productivity of landscapes, with associated effects on biodiversity (Benton et al. 2003, Tscharntke et al. 2005). The relationship between agricultural intensification and biodiversity can be unimodal in some landscapes, with the onset of agricultural development increasing heterogeneity and fertiliser inputs increasing local productivity, but increasing agricultural intensification resulting in landscape homogenization with associated reductions in resource diversity having negative effects on biodiversity (Figure 1) (Donald et al. 2001, Flowerdew 1997, Sotherton & Self 1999). The processes and mechanisms that drive the relationship between agriculture and biodiversity will vary between farming systems but the most important factor is typically the change in landscape structure (Benton et al., 2003). The effect of increases in agricultural area on landscape heterogeneity can be mediated differently depending on the underlying habitat structure and fertility. For example, in nutritionally impoverished areas, the input of synthetic fertilisers to cultivated fields may be beneficial for some species (Gunnarsson et al. 2015), whereas in fertile areas, fertiliser inputs may have little or no effect on productivity. Information on the relative impacts of agriculture in different landscapes is therefore key in order to understand and ultimately predict the consequences of further agricultural expansion in such landscapes.
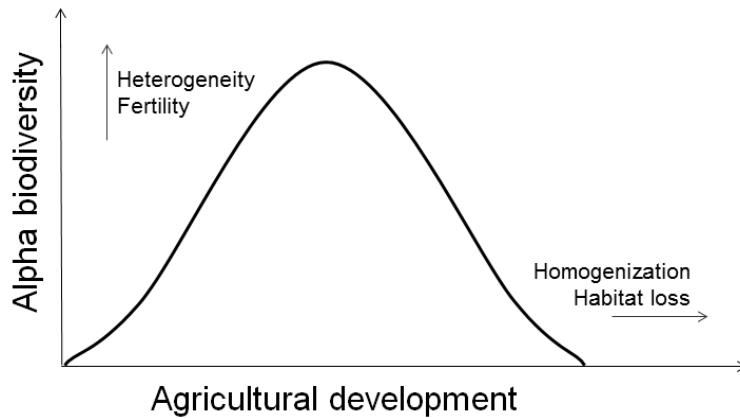
Figure 1 – A likely relationship between agricultural development and alpha biodiversity. Initially, agricultural development may increase habitat and resource heterogeneity in the landscape and soil fertility may increase in some conditions, with potentially positive effects on alpha biodiversity. However, as agricultural intensity and extent increase, homogenization and habitat loss start to negatively affect alpha biodiversity.

There is great variation in the extent to which agriculture has developed across regions and countries and the disturbance it causes (Alexandratos & Bruinsma 2012). In areas suitable for cultivation, agriculture is often very intense and many taxa have declined in abundance (Robinson & Sutherland 2002, Benton et al. 2003, Pe'er et al. 2014). However, in more marginal areas for production and in less developed countries, agriculture is often less intensive and widespread, and has less impact on the environment and can even benefit biodiversity (Loos et al. 2014, Sutcliffe et al. 2015). In Iceland, agricultural development started late and only grew beyond domestic subsistence at the beginning of the 20th century (Júlíusson & Ísberg 2005). Icelandic agriculture is somewhat restricted by the northern location of the island, just south of the Arctic Circle, and agriculture today does not dominate the landscape; only 7% of the area below 200 m a.s.l. (the area which is suitable for agriculture) is used for cultivation (National Land Survey of Iceland 2013, Snorrason et al. 2015). Icelandic lowlands currently comprise a fine-scale mosaic of open natural habitats and agriculture (primarily hayfields), making the landscape highly heterogeneous. For example, Iceland has over one million wetland patches smaller than one hectare, which together comprise 30% of the 9000 km2 of inland wetlands (50% are >5 ha), and inland wetlands cover about 20% of all vegetated surfaces of Iceland (Arnalds et al. 2016). These wetlands are of high value for biodiversity and they support several internationally important bird populations (Einarsson et al. 2002), particularly of waders (Charadrii) and wildfowl (Anatidae) (Gunnarsson et al. 2006, Jóhannesdóttir et al. 2014). However, wetlands in Iceland have undergone extensive drainage in recent decades, and an estimated 47% of inland wetlands have now been affected by drainage (Arnalds et al. 2016). This drainage was primarily undertaken to create suitable agriculture land and currently approximately half of cultivated land in Iceland is on drained wetland soils (Wöll et al. 2014). Furthermore, a recent study showed more than half of farmers intend to increase their cultivated land in the coming years in Iceland (Jóhannesdóttir et al. 2017). This expansion is likely to further increase drainage of wetlands, with potentially serious impacts on the breeding bird populations in these areas as a consequence of habitat loss and reductions in landscape heterogeneity. Despite the importance of Icelandic wetlands

for biodiversity, there is currently no mechanism for protection of wetlands less than 2 ha under the current law (Alþingi 2015) and many of the remaining patches are smaller than 2 ha.

Iceland is a volcanic island with very diverse landscapes, from flat floodplains and river valleys in the lowlands to mountainous and desert areas in the highlands, and more than half of Iceland lies above 400 m a.s.l. (National Land Survey of Iceland 2013). Frequent volcanic events result in intense aeolian deposition that is geographically variable depending on distance from the Mid-Atlantic ridge (where most volcanic activity occurs), which runs from south-west to north-east Iceland (Arnalds 2015). This deposition strongly influences soil fertility (due to the resulting high pH and favourable nutrient availability). This gradient of aeolian deposition has been shown to influence the distribution of breeding birds, with densities in wetland areas in particular being greater in areas of higher Aeolian deposition (Gunnarsson et al. 2015). These diverse landscapes with abundant remaining semi-natural land, offer a unique opportunity to quantify breeding bird distribution in relation to the extent of agriculture, and to identify factors that influence the shape of these relationships. Expansion of agriculture inevitably means loss of other habitats, and in Iceland wetlands have historically been the most common habitat converted for production. In this study, we make use of the variation in extent of agriculture in lowland Iceland to explore how densities of internationally important breeding wader populations on different semi-natural habitats vary in relation to the amount of agriculture in the surrounding landscape, and how this varies across an altitudinal gradient that reflects variation in underlying productivity as a consequence of historical Aeolian dust deposition. We also explore how breeding waders densities vary in relation to the amount of wetland in surrounding landscapes, and estimate how both factors (amount of wetland and agricultural area) interacting with altitude will likely influence breeding wader densities with increasing agricultural conversion of natural wetlands.

Methods

This study was undertaken in Iceland, an island in the North-Atlantic Ocean located between 63° and 66° North on the mid Atlantic ridge. Agriculture in Iceland is still of relatively low intensity and large patches of semi-natural habitats (e.g. marshes, bogs, heathland and river- plains) are present in most agricultural areas (Figure 2).
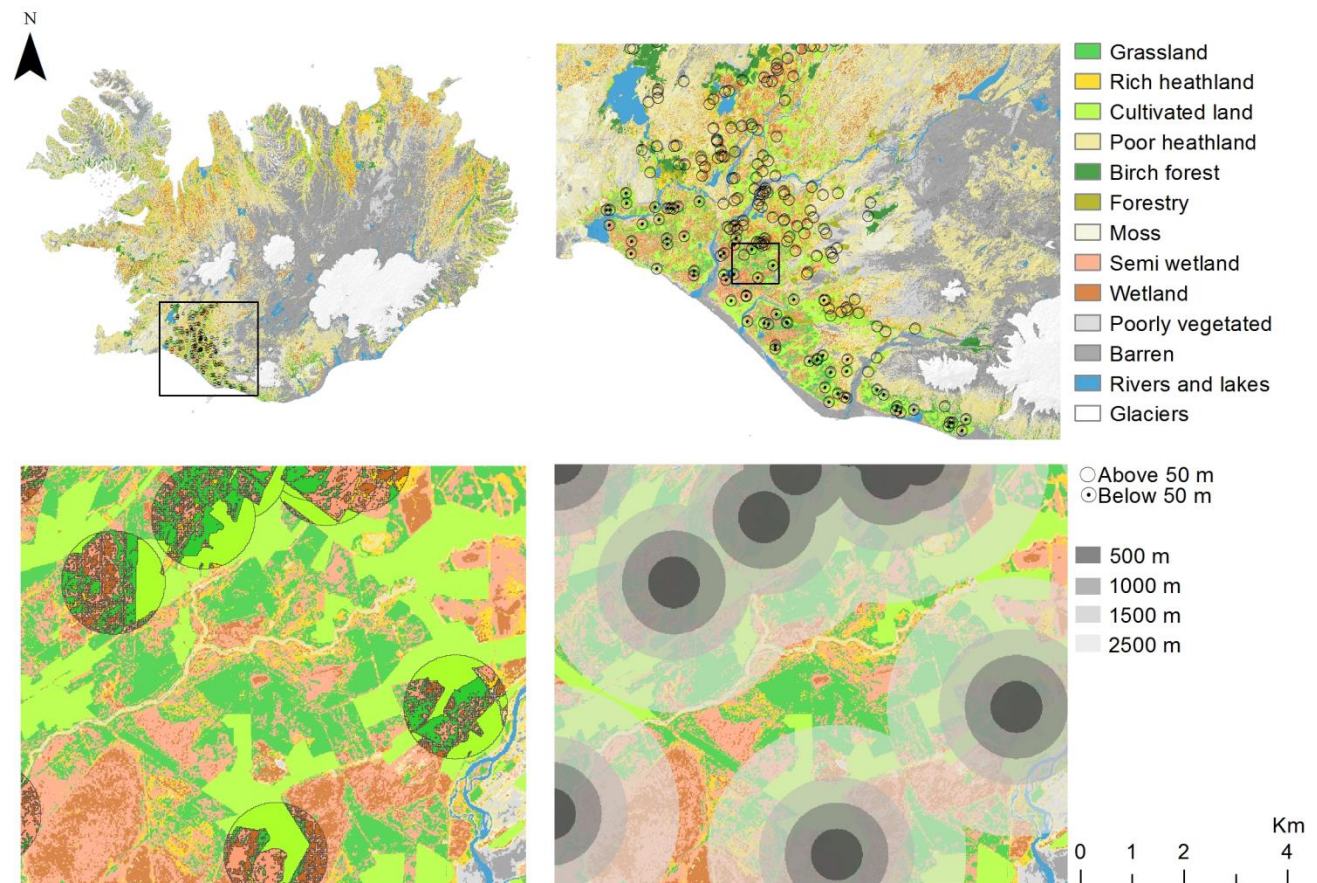
Figure 2 - The location of the 200 bird survey transects (top left), and how these are distributed above and below 50 m a.s.l (top right). The two lower images display the area within the rectangle in the top right panel, and portray the fine-scale mosaic of habitats in the southern lowlands (lower left, circles are 1000 m buffers around example survey locations) and the four different buffers within which areas of agriculture and wetland were calculated (lower right).

Survey locations

Surveys of breeding birds were carried out at 200 locations in the lowlands of South Iceland, in areas below 200 m a.s.l. (Figure 2). The area is one of the most important agricultural regions in Iceland, providing 36% of annual agricultural GDP in the year 2010 (FAI 2010) and about 10% of land below 400 m a.s.l.in the area is cultivated land (Wald 2012). Cultivated areas in Iceland are mostly hayfields that are used for grazing and fodder production (winter feed) for livestock for meat and dairy production, as agriculture in the country is almost entirely livestock-based (pastoral). Arable production is small-scale and mostly comprises barley grown for fodder on the farm where it is grown, although most grain fodder is imported (Helgadóttir et al. 2013). Land cover data for this study were extracted from the Icelandic Farmland Database, which uses satellite images with extensive ground truth verification to classify the surface of Iceland into 12 different classes (Arnalds & Barkarson 2003, Gisladottir et al. 2014). Survey sites within the five most common vegetated habitats (40 each of wetland, semi wetland, grassland, rich heathland, poor

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heathland, Figure 2) were selected by a stratified random method, employing ArcGis 10.1 GIS software. The selected sites had to cover at least 20 ha of a single habitat type and to be at least 0.5 km apart. In addition, for practical reasons of access, survey sites were selected so that they were no more than 2 km from roads and tracks (Jóhannesdóttir et al. 2014). Previous studies have shown that the distribution of habitat types in lowland Iceland varies little with respect to distance from roads and tracks (Gunnarsson et al. 2006).

Bird censuses

Breeding bird surveys were conducted in 2011 and 2012, from the middle of May until the end of June, a period which encompasses the majority of the breeding season. Counts were performed during periods of greatest bird activity, in the morning from 06:00 to 13:00 and in the afternoon from 17:00 to 22:00 (Davíðsdóttir 2010). Surveys were only conducted during suitable weather conditions (wind speed lower than 6 m/s and in dry weather) to avoid conditions of low bird detectability (Bibby et al. 2000). At each survey site, birds were counted along a line transect, where every bird within 100 m to each side of the observer was recorded (Bibby et al. 2000). Average length of the transects were 511 m (sd = 69.4 m, range 216-685 m), and their total length was 101 km (Jóhannesdóttir et al. 2014).

Extraction of spatial data

The land cover information used in the study was extracted from the Icelandic Farmland Database which uses satellite images with extensive ground truth verification to classify the surface of Iceland into 12 different classes (Arnalds & Barkarson 2003, Gisladottir et al. 2014). The classification represents variables that reflect productivity, mostly vegetation cover, soil and drainage. Around each transect, four different sized buffers were extracted (500, 1000, 1500 and 2500 m radius) and the amount of each habitat was recorded from within the buffers.

Data analysis

Models were constructed at two levels: first a multispecies model was used to explore the landscape drivers of the overall abundance of waders; second, individual species models were used to explore species-specific responses to landscape variables. For the multispecies model we used a generalized linear mixed model (GLMM) with a Poisson error distribution and a log-link function to analyse the variation in the total number of waders on each transect, with transect area (natural log-scale) as an offset. Separate models were run for each buffer, with the amount of cultivated land and wetland within the buffer, altitude of transect and interactions between altitude and area of cultivated land, and altitude and wetland area as fixed factors, and species as a random factor to control for differences in community composition at each site. For the single-species models, which were constructed for the six most common wader species (Golden Plover (Pluvialis apricaria), Dunlin (Calidris alpine), Snipe (Gallinago gallinago), Whimbrel (Numenius phaeopus), Black-tailed Godwit (Limosa limosa) and Redshank (Tringa totanus)), generalized linear models (GLM) with a Poisson error distribution and log-link function were constructed with the same fixed effects and with transect area (natural log-scale) as an

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offset, but with no random effects. For data presentation altitude was split into above and below 50 m a.s.l. (Figure 2) for there is a compositional change in the landscape at approximately that altitude where it changes from flat coastal plains to higher altitude inlands (Figure 3). Density predictions are only plotted for species which showed a significant relationship, density is predicted for 25, 50 and 100 m, these altitudes were chosen to ca. represent an average for the different altitudes. For simplicity, species-specific models are only presented for the 1000 m buffer (see results), but models from different buffer sizes showed a similar result. All statistical analyses were performed using RStudio (Version 0.98.1091).

Results

Landscape structure

Icelandic lowland landscapes are characterized by a small-scale mosaic of different semi-natural habitats and agricultural land (Figure 2). The habitat composition around each of the 200 survey locations was similar for buffers ranging from 500 m to 2500 m radius (Figure 3). Areas around survey locations below 50 m a.s.l. had slightly less heathland and more semi-natural wetland and grassland than areas above 50 m, but the overall habitat composition varied little with each buffer (Figure 3 b,c).
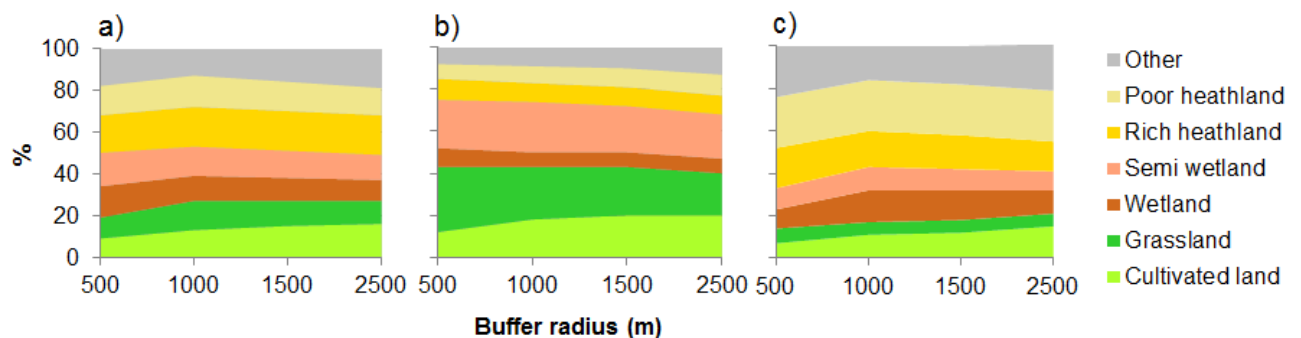
Figure 3 – Mean proportional distribution of different habitats within the four different-sized buffers around: (a) the 200 survey locations, (b) the 67 survey locations below and (c) the 133 locations above 50 m a.s.l. (other = forests, sparsely vegetated and barren land, and streams and lakes).

Factors influencing breeding wader density

There was substantial variation in the density of all the six most common wader species recorded on the transects, ranging from 0 up to 300 birds/km2 (Figure 4); however most common density was below 50 birds/km2.
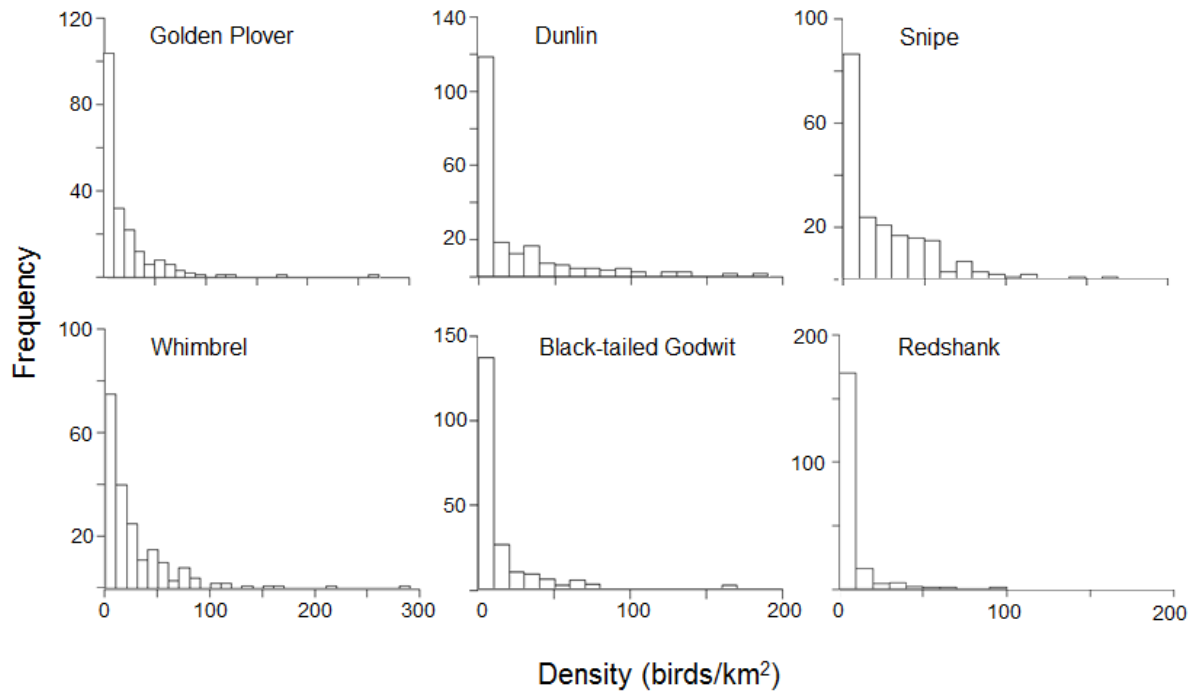
Figure 4 - Frequency distribution of the density of the six most common wader species in the lowlands of South-Iceland on the 200 transects (note variable axis).

Wader densities varied significantly with the area of cultivated land in the surrounding landscape within some buffer areas, but a significant interaction between area of cultivated land and altitude was apparent at all buffer sizes (Table 1). Wader densities declined with increasing area of cultivated land below 50 m but increased with area of cultivated land above 50 m (Figure 4). Wader densities also varied significantly with altitude, with higher densities occurring at lower altitudes. The amount of wetland within the buffer was also significantly related to the density of waders, with higher densities occurring in areas with more wetland in all buffer sizes. The effect of amount of wetland also differed with altitude, but only at the smallest buffer size (500 m) and this interaction was much weaker than the altitudinal variation in the effect of area of cultivated land (Table 1).

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Table 1 - Results of a generalized linear mixed model (GLMM) on the variation in the total number of individuals of the six most common wader species (Golden Plover, Dunlin, Snipe, Whimbrel, Black-tailed Godwit and Redshank) on 200 survey locations, in relation to amount of cultivated land and wetland (within the surrounding 500, 1000, 1500 and 2500 m), and the altitude of the survey location. Transect area was included as an offset and species as a random effect. Significant factors are shown in bold.

Fixed effect	500 m			1000 m			1500 m			2500 m		
	Est.	z	p	Est.	z	p	Est.	z	p	Est.	z	p
Intercept	-11.00	-47.19	**<0.001**	-10.98	-47.12	**<0.001**	-10.99	-47.12	**<0.001**	-11.00	-47.20	**<0.001**
Cultivated land	0.03	1.16	0.246	6.32e-2	2.66	**0.008**	1.26e-2	0.52	0.603	-0.07	-2.88	**0.004**
Wetland	0.10	4.43	**<0.001**	1.14e-1	4.93	**<0.001**	9.52e-2	4.02	**<0.001**	0.06	2.42	**0.016**
Altitude	-0.10	-4.27	**<0.001**	-1.17e-1	-4.79	**<0.001**	-1.22e-1	-4.88	**<0.001**	-0.12	-5.11	**<0.001**
Cultivated * Altitude	0.14	6.32	**<0.001**	2.14e-1	8.73	**<0.001**	1.42e-1	6.12	**<0.001**	0.10	4.79	**<0.001**
Wetland * Altitude	0.06	2.29	**0.022**	-4.92e-4	-0.02	0.988	1.61e-4	0.01	0.996	0.05	1.90	0.058

Figure 5 - Predicted wader densities (from the GLMM in Table 1) in relation to the area of cultivated land within the 1000 m radius buffer (size 3.13 km2) at three different altitudes (dotted lines = SE).

Factors influencing density of each breeding wader species

Densities of three wader species (Golden Plover, Dunlin and Whimbrel) declined significantly with increasing area of cultivated land within 1000 m (Table 2). However, these effects varied significantly with alti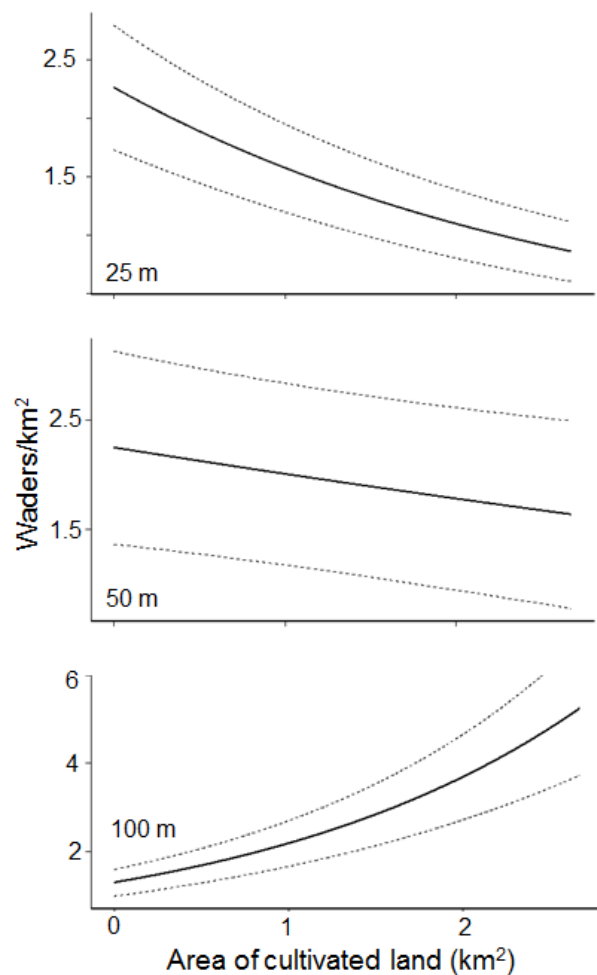tude (range: 0-200 m a.s.l.); densities increased with amount of cultivated at higher altitudes but decreased at lower altitudes (Figure 6). Densities of Dunlin, Snipe and Black-tailed Godwit increased with area of wetland in surrounding 1000 m area but densities of Whimbrel and Redshank decreased whilst Golden Plover densities were unrelated to wetland area (Table 2). Snipe and Whimbrel densities were also influenced by an interaction of wetland area and altitude but the direction of the relationship varied between them; at lower altitudes an increase in wetland area was associated with higher densities of Snipe but lower densities of Whimbrel, while the reverse occurred at higher altitudes (Figure 7). Densities of three species were significantly lower at higher altitudes (Dunlin, Whimbrel and Redshank).

Table 2 – Results of generalized linear models (GLMs) on the variation in numbers of the six most common wader species in relation to amount of cultivated land and wetland (within the surrounding 1000 m) and the altitude of the survey transects. Transect area was included as an offset. Significant factors are shown in bold.

Fixed effect	Golden Plover			Dunlin			Snipe		
	Est.	z	p	Est.	z	p	Est.	z	p
Intercept	-10.54	-54.42	**<0.001**	-10.25	-52.13	**<0.001**	-10.61	-60.03	**<0.001**
Cultivated land	-1.07e-6	-3.92	**<0.001**	-1.13e-6	-4.28	**<0.001**	-2.06e-7	-0.96	0.338
Wetland	-5.02e-7	-1.23	0.217	1.33e-6	4.44	**<0.001**	9.81e-7	3.17	**0.002**
Altitude	2.51e-4	0.14	0.893	-1.51e-2	-5.69	**<0.001**	-2.43e-3	-1.27	0.206
Cultivated * Altitude	1.14e-8	3.88	**<0.001**	1.97e-8	5.45	**<0.001**	4.89e-9	1.70	0.089
Wetland * Altitude	1.59e-9	0.33	0.742	-6.35e-9	-1.84	0.066	-8.07e-9	-2.31	**0.021**

| Fixed effect	Whimbrel			Black-tailed Godwit			Redshank		
	Est.	z	p	Est.	z	p	Est.	z	p
Intercept	-9.34	-62.18	**<0.001**	-11.77	-42.77	**<0.001**	-10.92	-34.551	**<0.001**
Cultivated land	-.1.13e-6	-5.69	**<0.001**	2.71e-7	0.93	0.353	-4.9e-7	-1.231	0.218
Wetland	-1.31e-6	-4.22	**<0.001**	1.19e-6	2.53	**0.012**	-1.67e-6	-2.229	**0.026**
Altitude	-1.9e-2	-9.30	**<0.001**	-2.35e-3	-0.77	0.441	-1.67e-2	-3.78	**<0.001**
Cultivated * Altitude	2.25e-8	8.57	**<0.001**	2.95e-9	0.73	0.468	1.02e-8	1.61	0.107
Wetland * Altitude	1.85e-8	5.30	**<0.001**	-5.41e-9	-1.05	0.293	1.5-e8	1.659	0.097
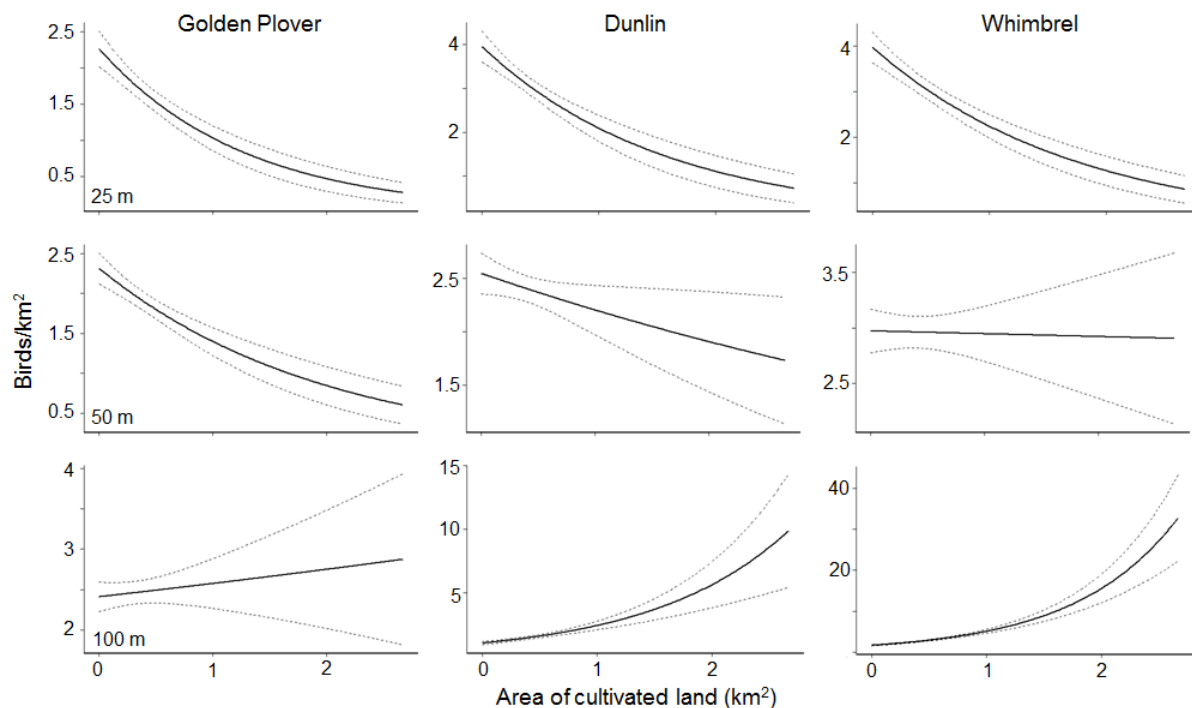
Figure 6 – Predicted wader densities (from the GLMs in Table 2) in relation to the area of cultivated land within the surrounding 1000 m at three different altitudes (dotted lines = SE)
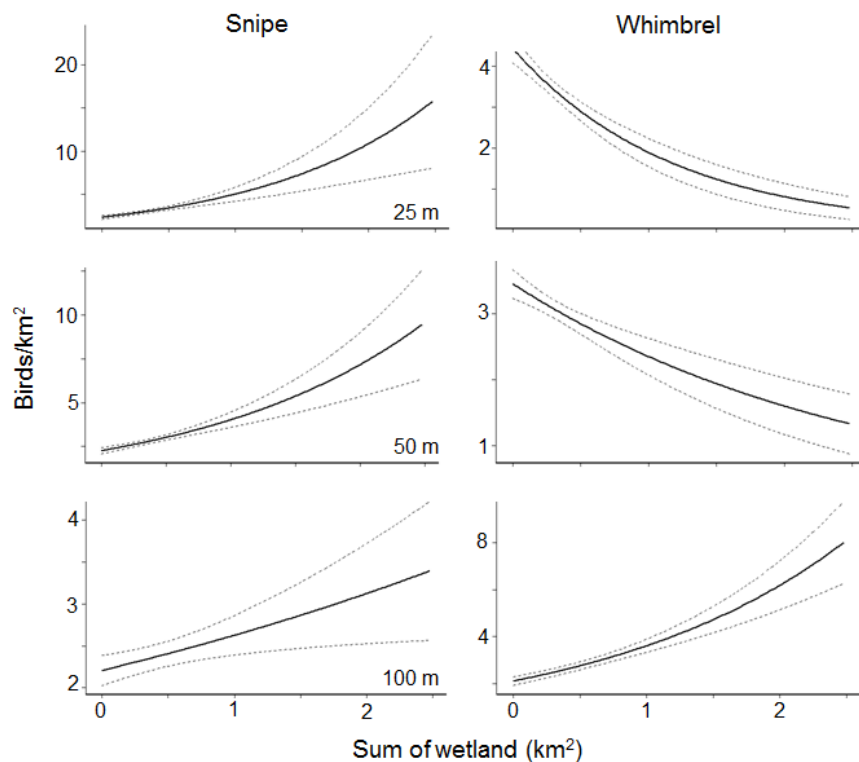

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Figure 7 – Predicted wader densities (from the GLMs in Table 2) in relation to the area of wetland within the surrounding 1000 m at three different altitudes (dotted lines = SE).

Discussion

Heterogeneity of landscapes has a decisive impact on resource availability and therefore influences the density and diversity of species using those landscapes. Heterogeneity can either stem from ongoing natural processes or abrupt anthropogenic actions (Pickett & Cadenasso 1995, Forman 2014, Gunnarsson et al. 2015). Agricultural intensification has been identified as a key driver in replacing heterogeneous landscapes with homogeneity with the associated loss of biodiversity in many parts of the world (Matson et al. 1997, Benton et al. 2003, Kentie 2015).

However, Icelandic lowlands are composed by a heterogeneous fine-scale mosaic of different open natural habitats and agriculture. The heterogeneity remains constant at different radius buffer sizes (500-2500m) throughout the lowlands, though the extent of different habitats varies between altitudes. However, this complex landscape structure is threatened as Icelandic farmers intend to expand their cultivated land in coming years (Jóhannesdóttir et al. 2017), which will likely result in landscape homogenization and associated potential impacts on the biodiversity it currently supports (Būhning-Gaese 1997). Here we quantified the effects of the amount of both cultivated land, which is likely to expand, and wetland, which is likely to be lost, on wader densities on semi-natural land in south Iceland. The amount of both cultivated land and wetland in surrounding landscapes significantly influences the density of waders. Larger total area of wetland are generally associated with higher densities of waders but the effect of cultivated land on density varies with altitude; wader densities decline with increasing area of cultivated land at lower altitudes where wetland, grassland and cultivated land are abundant. However, density increases with increasing area of cultivated land at higher altitudes (although all sites are below 200 m a.s.l.) where wetland, grassland and cultivated land is less abundant.

Species-specific response to different landscapes

Interestingly, three species (Golden Plover, Dunlin and Whimbrel) showed a contrasting response to the amount of cultivated land in relation to altitude - all three species were predicted to decline if amount of cultivated land increased at altitudes below 50 m but at 100 m altitude an increase in cultivated land would result in higher densities. All these three species mostly breed in dryer heath habitats whilst the other three species (Snipe, Black-tailed Godwit and Redshank) are more commonly found breeding in wetter habitats (Jóhannesdóttir et al. 2014). Therefore, an increase of cultivated land at higher altitudes would likely allow an increase in nutrients in drier areas favoured by Golden Plover, Dunlin and Whimbrel.

Agriculture in the higher altitudes of the southern lowlands is positively affecting these wader densities but as described in the introduction (Figure 1) this is not an unlikely scenario as the early stages of agricultural development can locally improve resources for birds. However, this is not a linear relationship and potential tipping points remain undetermined. If, as intended by farmers (Jóhannesdóttir et al. 2017), agricultural expansion continues with conversion of natural wetlands without considering landscape heterogeneity, then most abundant species will likely decline, particularly in lowland areas (Figure 6).

Difference in underlying productivity and habitat composition

The altitudinal variation in the influence of amount of cultivated land on breeding wader densities suggests that the locations in which future expansion of cultivation might occur will be an important factor in how it will affect wader populations. Further expansion at lower altitudes is likely to negatively affect wader densities, whilst at higher altitudes the effects of agricultural expansion will likely be positive, at least in the short term. We have previously shown (Jóhannesdóttir et al. in review) that the relative importance of agricultural land for breeding waders in lowland Iceland varies regionally, with larger numbers of waders using agricultural land in the West than in the North and the South. This difference was linked to an underlying gradient of soil fertility which varies across Iceland due to volcanic activity being mostly restricted to the divergent tectonic plate boundary that crosses Iceland on a SW-NE axis along the North-Atlantic ridge. As a consequence, areas in the South and North receive larger quantities of volcanic dust whereas areas in the west receive less (Arnalds 2015). The volcanic dust deposition influences the fertility of the land through raising nutrient and pH levels. This has also been shown to influence bird density on all habitats throughout lowland areas (not only on agricultural land) which declines with distance from volcanic hotspots, therefore creating regional density differences (Gunnarsson et al. 2015). These processes are likely to influence the consequences of expansion of cultivated land based on where the expansion occurs.

The altitudinal variation of wader density in response to the amount of cultivated land can partly be explained by the different composition and amounts of habitats present at different altitudes. Habitats vary in their fertility and amount of water present which are important for breeding waders (Smart et al. 2006) and the habitat composition varies between altitudes. At lower altitudes more fertile and wetter habitats, such as grasslands and wetlands, dominate the landscape (~75%) but at higher altitudes the heathland habitats and the combined habitat group of other habitats, which are mostly unsuitable for waders, comprise ~60% of the area within the buffers (Figure 3). Thus the dominant habitats above 50 m a.s.l. are generally dryer and less fertile, which is likely to make the agricultural land relatively more beneficial as a foraging habitat than at lower altitudes, where more fertile habitats are abundant (O´Connell et al. 1996).

Conservation implications

Changes of Icelandic landscapes are to be expected in the coming years as most farmers intend to increase their area of cultivated land (Jóhannesdóttir et al. 2017). This expansion will inevitably impact the internationally important breeding wader populations of Iceland, but the level of such impact will also depend on where the expansion will occur. The results presented here highlight that an increase of cultivated land at lower altitudes is more likely to negatively impact wader density than at higher altitude, within the lowlands.

The data presented here should be considered in land management, as it highlights that the implications of land use changes for biodiversity are context dependent. It is clear that national land management policy or legislation should be in place in order to protect the species that have a wide distribution on a range of habitats in the wider countryside. Also is

collaboration with stakeholders crucial to identify landscapes and management strategies that allow international important breeding wader species to persist.

Acknowledgements

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Reconciling biodiversity conservation and agricultural expansion in the sub-arctic environment of Iceland

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Abstract

Intensified agricultural practices have driven biodiversity loss throughout the world, and although many actions aimed at halting and reversing these declines have been developed, their effectiveness depends greatly on the willingness of stakeholders to take part in conservation management. Knowledge of the willingness and capacity of landowners to engage with conservation can therefore be key to designing successful management strategies in agricultural land. In Iceland, agriculture is currently at a relatively low intensity but is very likely to expand in the near future. At the same time, Iceland supports internationally important breeding populations of many ground-nesting birds that could be seriously impacted by further expansion of agricultural activities. To understand the views of Icelandic farmers toward bird conservation, given the current potential for agricultural expansion, 62 farms across Iceland were visited and farmers were interviewed, using a structured questionnaire survey in which respondents indicated of a series of future actions. Most farmers intend to increase the area of cultivated land in the near future, and despite considering having rich birdlife on their land to be very important, most also report they are unlikely to specifically consider bird conservation in their management, even if financial compensation were available. However, as no agri-environment schemes are currently in place in Iceland, this concept is highly unfamiliar to Icelandic farmers. Nearly all respondents were unwilling, and thought it would be impossible, to delay harvest, but many were willing to consider sparing important patches of land and/or maintaining existing pools within fields (a key habitat feature for breeding waders). Farmers' views on the importance of having rich birdlife on their land and their willingness to participate in bird conservation provide a potential platform for the co-design of conservation management with landowners before further substantial changes in the extent of agriculture take place in this sub-arctic landscape.

Keywords

Introduction

Combining commercially efficient agricultural land use with biodiversity conservation is one of the major challenges of modern times. Agricultural landscapes are complex socioecological systems, and achieving conservation objectives within these landscapes requires the integration of resource uses, landowner perspectives, and governance frameworks. As such, agricultural systems are similar to many other socioecological systems in which successful management or sustainable preservation of resources relies heavily on stakeholder involvement and suitable regulation that take complex feedback processes into account (Ostrom 2009). One key feature in successful conservation management is to consolidate the different interests of conservation and agriculture (Young et al. 2005, Redpath et al. 2013). This requires active communication to reconcile potential conflicts and ensure that different interests are appreciated from the outset, as well as

having all parties involved working together toward mutually agreed goals (Redpath et al. 2013). Increases in agricultural extent and efficiency have driven widespread declines in biodiversity throughout the world (Donald et al. 2001, Foley et al. 2005, Millennium Ecosystem Assessment 2005), and as the human population increases, the demand for agricultural products will likely continue to grow. The increased demand for agricultural production has been met with both expansion of agricultural land and the intensification of land already used for agriculture, both of which have been shown to substantially impact biodiversity (Flowerdew 1997, Sotherton and Self 2000, Benton et al. 2003, Donald et al. 2006, Katayama et al. 2015). Different conservation approaches have been used to reduce the impact of agricultural expansion and intensification on farmland biodiversity. Two fundamentally different approaches have received a lot of attention: constrain the land area used for agriculture by maximizing its yield, even with high costs for local biodiversity, but sparing other areas for conservation, often referred to as "land sparing"; and maintain agricultural intensification at lower levels that may spread the impacts on biodiversity, often referred to as "land sharing" (Green et al. 2005). In either approach, the involvement of stakeholders is likely to be an important factor determining the success of conservation projects. Evidence suggests that farmers who participate in developing conservation schemes experience an increase in their commitment and satisfaction (Emery and Franks 2012). However, a fundamental step toward their early involvement is to understand their views on biodiversity conservation and their expectations of potential changes in future land management.

In areas where agriculture is restricted by environmental conditions, such as at high latitudes or altitudes, factors such as short growing seasons, extreme rainfall, or lack of soils can limit the opportunities for agricultural intensification. In these cases, increasing agricultural production usually requires expansion of agricultural land. At the sub-arctic latitude of Iceland (63°-66° North) the growing season is very short, which limits opportunities to intensify agricultural production, and increased demands for agricultural products are therefore likely to be met by expanding the area of cultivated land. However, the potential impact of such expansion on the species that occur in lowland Iceland is unknown. Icelandic biodiversity is characterized by relatively low species diversity but great abundance of many of those species. Iceland supports internationally important breeding populations of 21 bird species (Einarsson et al. 2002) and hosts a large part of the world population for several bird species (Wetlands International 2006). Iceland is especially important for northern hemisphere breeding waders (Charadrii; Gunnarsson et al. 2006). It sustains very high densities of several species (Jóhannesdóttir et al. 2014) and is one of the most important breeding areas for waders in Europe (Thorup 2004). Iceland sustains such high densities in part because of large areas of open landscape with small-scale mosaics of suitable habitats that fulfil different breeding wader requirements (Gunnarsson et al. 2006, Pickett and Siriwardena 2011). This landscape has been shaped through the centuries by livestock grazing and deforestation, which, together with frequent volcanic activity (Arnalds 1987), have resulted in large areas of forest-free open landscapes. In the 20th century, extensive drainage projects were subsidized by the Icelandic government to increase agricultural opportunities and productivity. At that time ~55%-75% of Icelandic wetlands were drained to some extent (Óskarsson 1998), which caused radical changes to habitats and landscape. For some breeding wader species, these changes might have initially been favourable, because some drainage may have increased the mosaic of available breeding habitats. Following the widespread drainage, the area of

hayfields quadrupled in 30 years, slowing down in the 1980s but maintaining an increasing trend (Snorrason et al. 2015). Currently, 6% of the area below 200 meters above sea level (m a. s.l.) is cultivated, but estimates suggest that >60% of that area could potentially be converted to cultivated land (The Farmers Association of Iceland 2010, The Farmland Database 2013). This rate of conversion of semi-natural habitats to farmland is alarming given the potential for both direct loss of breeding habitat for waders and degradation of the remaining habitat as a result of drainage of pools and advances in timing of harvest (Eglington et al. 2008).

The Icelandic government has recently placed more emphasis on limiting development (other than agriculture) on land that could be used for agriculture, (Alþingi 2015a), in anticipation of future increased demand for agriculture products driven by huge increases in tourism (the numbers of tourists visiting Iceland have increased by 185% since 2005, going from 350,000 to 1 million; Óladóttir 2015), as well as growth in the Icelandic population, which is estimated to increase by ~30% in the next 50 years (from 330,000 to 440,000; Statistics Iceland 2015a). Given projections for global increases in the human population (United Nations 2015), current forecasts predict a required ~60%-110% increase in worldwide agricultural production (from levels in 2005) to meet the increased demand for produce (FAO 2009, Tilman et al. 2011).

Icelandic agriculture is limited by both geographical and geological factors. The oceanic climate results in prolonged periods with temperatures close to 0°C in winter and cool summers, with average temperatures being approximately -1°C in January and 10°C in July (Icelandic Meteorological Office 2015). The lowlands, where almost all agriculture occurs (generally defined as areas below 300-400 m a.s.l.), are characterized by a sub-arctic climate; while the highlands, covering much of the country, have low arctic to arctic conditions, with glacial icecaps covering about 10% of the country. Areas suitable for cultivation are mostly below 200 m a.s.l., which cover ~15% of Iceland and where ~90% of farms are located (National Land Survey of Iceland 2013). Annual rainfall ranges from 400 to 3000 mm (Icelandic Meteorological Office 2015), and the growing season is about 4 months. Volcanic activity is frequent in Iceland and causes severe erosion, leaving large areas vulnerable to soil degradation (Arnalds 2015). Agricultural production in Iceland is heavily subsidized (OECD 2015), accounting for ~1% of annual GDP, and its production fulfils most dairy and meat demand in the domestic market (Jóhannesson 2010). Cultivated areas in Iceland are mostly hayfields that are both used for grazing and fodder production for livestock grown for meat and dairy production. The total area of hayfields at present is ~120,000 ha (The Farmers Association of Iceland 2010), with arable production being small-scale and mostly comprising barley grown for fodder on the farm where it is grown. Barley production is increasing, and barley is currently grown on ~4000 ha, yielding about 15,000-16,000 tons and accounting for 10%-12% of the cereal used for livestock production (Tómasson et al. 2011). Icelandic agriculture consists of mostly three types of livestock: sheep, cattle, and horses. Sheep are kept indoors during winter and are grazed close to the farms in spring and autumn but during summer most are grazed in the highlands, so lowland farmland has few sheep during summer. Cattle are mostly kept indoors, but most dairy cows do roam in fields close to the farm during daytime in summer. Horses can stay outside the whole year and most do, though some are kept inside for riding and training purposes. Generally the density of livestock in Iceland is low. Livestock can impose a direct threat to breeding birds through trampling and predation of nests

(Katrínardóttir et al. 2015), but grazing by livestock also helps to maintain the open landscape that provides conditions suitable for breeding (Durant et al. 2008).

The remaining areas of semi-natural habitats in lowland Iceland currently sustain very high densities of breeding waders, particularly the remaining wetter habitats (e.g., marshes and bogs; (Jóhannesdóttir et al. 2014). The effect of the expansion of agriculture into areas of semi-natural habitats could potentially be reduced by integrating conservation measures into land management, but currently there are very few restrictions on land management in Iceland (Alþingi 2015*b*). Given that almost all land in lowland Iceland where farming occurs is either privately owned or state property managed by farmers (Kristófersson et al. 2007), it is important to understand farmers' views and attitudes toward bird conservation on their land.

To explore the potential for collaboration with landowners, and which actions they would be willing to undertake for bird conservation, we visited farms across the main agricultural regions of lowland Iceland. We asked farmers a series of questions about their future land management and their attitudes toward birds and bird conservation, focusing on four specific conservation measures that are likely to be key in maintaining large breeding wader populations in farming regions (Table 1).

Table 1 – Details of the four agricultural land management issues likely to be of specific importance for breeding waders in lowland Iceland, and the mechanisms through which they can influence breeding wader distribution and demography.

Conservation management	Impact on waders	References
Grazing intensity	Shapes vegetation height and heterogeneity. High levels of grazing creates short, homogeneous swards that can be unsuitable for foraging, sheltering and nesting Livestock trampling of nests and chicks Occasional egg and chick predation by livestock	(Vickery et al. 2001, Smart et al. 2006, Tichit et al. 2005, Katrínardóttir et al. 2015)
Harvest timing	Agricultural machinery can destroy clutches and chicks, when timing of harvest coincides with nesting and chick-rearing Can alter invertebrate food availability through changes in vegetation structure	(Kleijn et al. 2010, Schroeder et al. 2012, Schekkerman and Beintema 2007)
Leaving pools intact	Pools are an important source of invertebrate prey, and of water for drinking and plumage maintenance	(Eglington et al. 2008, Smart et al. 2006, Gunnarsson et al. 2005)
Sparing important areas	Maintaining large areas that can provide the range of nesting locations, prey resources and places for chicks to hide from predators, at appropriate scales	(Whittingham 2007, Schekkerman et al. 2008)

We also wanted to know whether Icelandic farmers might be more willing to consider participating in conservation management if financial compensation were available, much like the agri environment schemes that currently operate in many European countries (Kleijn and Sutherland 2003). Iceland is not a member of the EU but has considered joining in recent years. There are currently no conservation efforts aimed at breeding waders in Iceland, despite the international importance of the large wader populations in Iceland; but Iceland's involvement in relevant international conservation agreements, such as the Ramsar Convention, the Bern Convention, and the African-Eurasian Waterbird Agreement (van Schmalensee et al. 2013), provides a potential platform for the development of appropriate conservation strategies. The concept of protecting wildlife is well established in Iceland, through protected areas and species protection legislation, but the there is no history of providing financial compensation to landowners for conservation actions.

Methods

Study location

This study was undertaken in Iceland, an island in the North-Atlantic Ocean located between 63° and 66° North on the mid Atlantic ridge. Agriculture in Iceland is still of relatively low intensity, and large patches of semi-natural habitats, e.g., marshes, bogs, heaths, and river plains, are present in most agricultural areas. There has never been any biodiversity conservation action developed on agricultural land in Iceland.

Icelandic agriculture is primarily pastoral, and livestock number and composition vary regionally (Figure 1a, b). Livestock in the South and North mostly comprise cattle and horses; the West has similar numbers of the three livestock species, while farms in East and in the West fjords have fewer horses and proportionally more sheep. Consequently, farms in three regions (South, West, and North; Figure 1) were visited to explore any regional variation in views and attitudes.
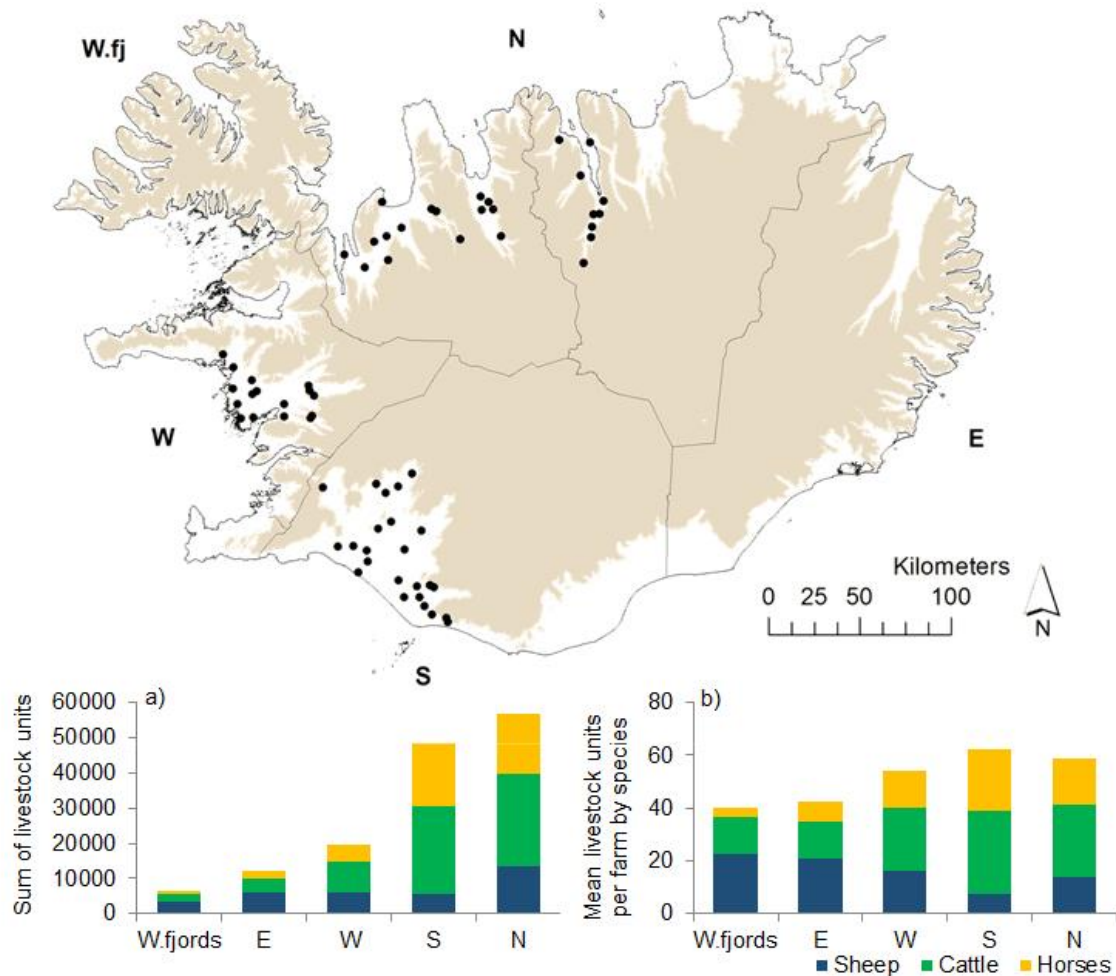
Figure 1 - Map of Iceland (top) showing areas below 400 m a.s.l. in white and the surveyed farms (filled circles) in each of the regions (indicated by lines), and the regional variation in (a) total livestock units (LU: cattle=0.9; horses=0.8; sheep=0.1) and (b) composition of livestock units per farm (Statistics Iceland 2015a).

Questionnaire survey

In the summers of 2013 and 2014, 62 farms (2.4% of the total number of farms in Iceland; Statistics Iceland 2012) were visited (Figure 1) and the farmers were questioned about their intentions regarding future farming practices and their views on bird conservation, the importance of birdlife, and their willingness to participate in different actions aimed at bird conservation. The farmers' age and gender and their farm characteristics (livestock number and composition) were recorded. For comparison livestock numbers were converted to livestock units (LUs) based upon the feed requirement of each livestock type: cattle = 0.9 LU (with dairy cow = 1 LU and cattle for meat production = 0.8), horses = 0.8 LU, and sheep = 0.1 LU (Eurostat 2013). To measure farmers' views or plans, a 5-point Likert scale was used in which respondents were asked to assign a score that reflects the extent to which they agree or disagree with a series of statements (1 = very likely, 2 = likely, 3 = uncertain, 4 = unlikely, 5 = very unlikely and 1 = strongly agree, 2 = agree, 3 = no opinion, 4 = disagree, 5 = strongly disagree; Likert 1932). The Likert scale assumes the strength of

experience is linear; on a continuum from strongly agree to strongly disagree, and that attitudes can be measured. This is vital to be able to quantify farmer's responses and views.

Farms were visited in three main agricultural regions (24 in the North and in the South and 16 in the West), which encompass the majority of agricultural production in Iceland (Figure 1). Similar proportions of farms were surveyed in each region (39% in the South, 26% in the West, and 35% in the North). Farms were selected visually from maps, ensuring similar numbers across the three regions, capturing geographical variation in farming practices, landscapes, and biodiversity, as well as the range of farm types regarding production capacity and livestock composition. To avoid spatial clustering, surveyed farms were selected to be >5 km apart. However, in some areas recruiting farmers to participate in the study was difficult; often they were busy at the time of visiting and others did not want to participate. Consequently, on eight occasions farms were closer than the desired level (minimum distance = 2 km).

Data analysis

Because views about biodiversity conservation may vary with age, respondents were classified as either younger (born after the median birth year of 1966, range: 1943-1990) or older (born before 1966; for interviewed couples the average age was used), and responses of these two groups to each question were compared with Fisher's exact tests. Similarly, response may vary regionally as a consequence of differences in land type, habitat, and landscape structure, and availability of land or livestock requirements; thus, regional differences were also compared with Fisher's exact tests.

Responses to questions regarding willingness to participate in conservation actions were classified as willing (very likely or likely) or unwilling (unlikely or very unlikely). The characteristics of respondents who were either willing or unwilling to both spare important land for birdlife and manage grazing for birdlife (the two relevant questions with sufficient variation in responses) were then compared with Mann-Whitney U tests, G-tests, or Fisher's exact tests, as appropriate. Statistical analyses were performed in the program IBM SPSS Statistics 22.0.

RESULTS

Demographic characteristics of respondents

The 62 farmers included in the surveys were all owners of the land they farm (all farms were family run), and the questionnaires were primarily completed by one member of the family, but in some cases (10 farms) by both members of a couple. Respondents varied in demographic characteristics; the oldest was born in 1943 and the youngest in 1990. Average year of birth was 1964 in the South (±13 years), 1960 in the West (±14 years), and 1971 in the North (±12 years). The majority were male (69%), whereas 15% were female and 16% were couples (Figure 2).
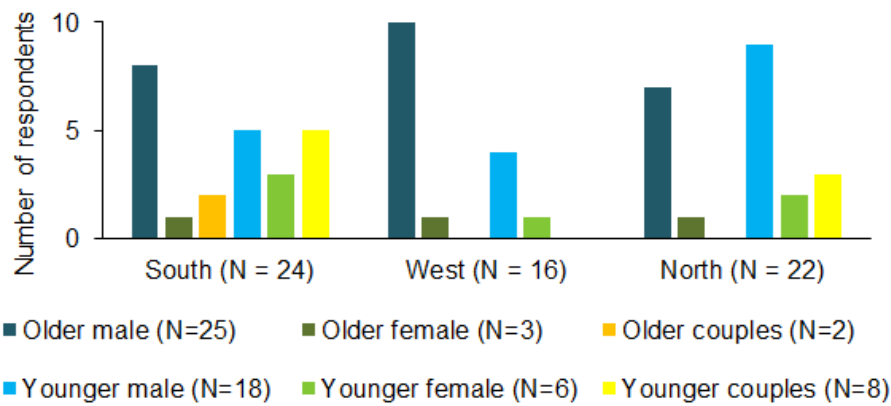
Figure 2 – Numbers of older and younger (than median birth year of 1966) farmers in each regions who answered questions as individuals (men or women) or as couples.

Farm type

Farms varied in numbers, type, and combination of livestock (Figure 3a). Most farms in Iceland have a mixture of the three most common livestock: sheep, cattle, and horses. The vast majority of the farms in this study (93%) had a mixture of two or three of these livestock types, and farms varied considerably in livestock numbers, ranging from 11 to 402 LUs (Figure 3b).

Figure 3 - Variation in (a) numbers and (b) livestock units of sheep, cattle and horses on study farms in the three regions

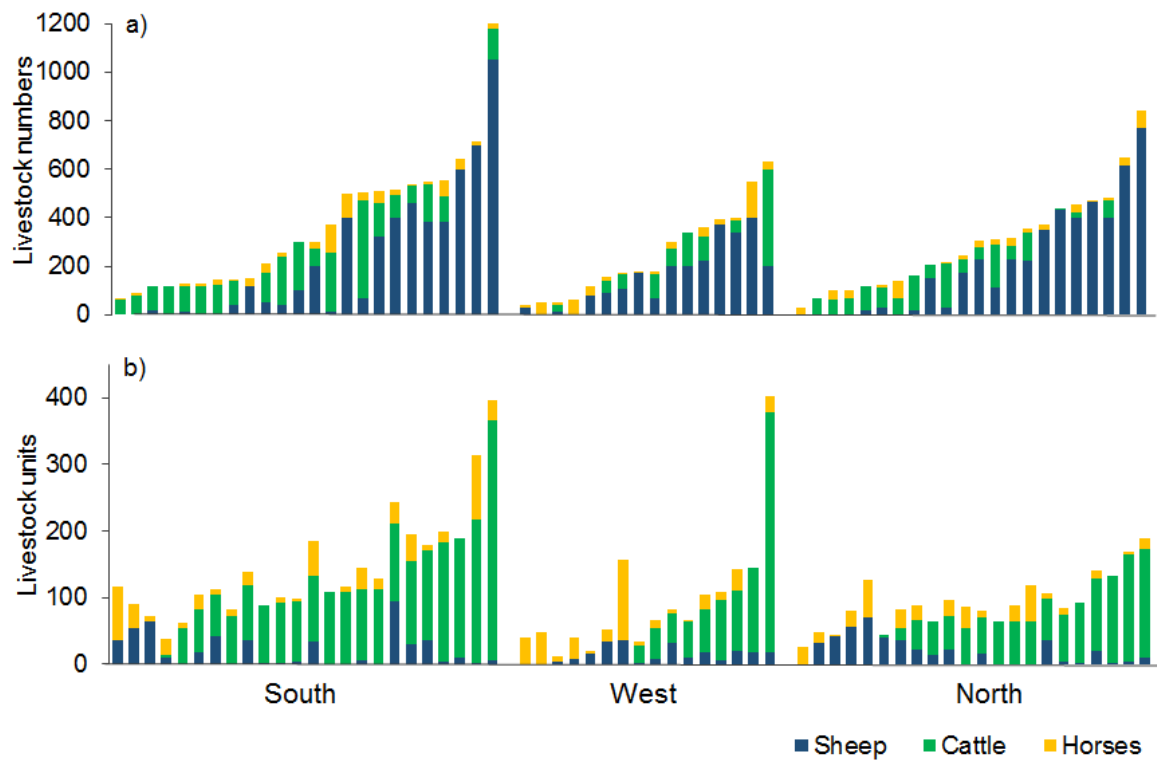| Nr	Question	N	Mode	Region (P-value)	Age	Very likely / Likely / Uncertain / Unlikely / Very unlikely
1	How likely is it that you will increase area of cultivated area on your property in the next five years?	57	1	0.081	0.283	
	General attitude towards birdlife on the estate					Strongly agree / Agree / No opinion / Disagree / Strongly disagree
2	I think it is important to have rich birdlife on my estate.	62	1	0.919	**0.015**	
3	I take birdlife into consideration in land use management.	62	4	0.525	**0.034**	
4	I would be willing to take birdlife into consideration in management if payment were available.	62	4	0.896	0.210	
	Attitudes towards land management for birdlife					
5	If information on favourable levels of grazing for birds were available I would be willing to manage grazing according to that information.	60	2	0.457	0.206	
6	If information on favourable levels of grazing for birds were available I would be willing to manage grazing according to that information if payment were available.	60	2	0.637	0.074	
7	I think delaying the timing of harvesting could be possible.	62	5	**0.006**	0.553	
8	I would be willing to shift the timing of harvesting to benefit birds, even though it might reduce the harvest.	11	5	0.561	0.424	
9	I would be willing to shift the timing of harvesting to benefit birds, if payment for loss of harvest was available.	12	5	0.372	0.606	
10	I allow pools to stay intact on my estate.	43	1	0.096	0.660	
11	I am willing to keep pools on my estate intact because of their importance for birds.	22	1	0.452	1.000	
12	I would be willing to keep pools on my estate intact, because of their importance for birds, if payment were available.	29	1	0.965	0.939	
13	If information on important sites for birds on my estate were available I would be willing to direct land-use elsewhere on my estate to benefit birds.	51	2	0.479	0.079	
14	If information on important sites for birds on my estate were available I would be willing to direct land-use elsewhere on my estate to benefit birds if payment were available.	51	2	0.283	0.692	

Figure 4 - The number of farmers responding to each question, their modal (most frequent) response (the mode number refers to the answers going from left to right: 1 = very likely/strongly agree to 5 = very unlikely/strongly disagree, and the percentage of respondents selecting each of the five possible responses), and the results of Fisher's exact tests of independence of differences in responses to each question between age groups (older or younger than median age) and regions (South, West, and North).

Prospects for future expansion of agriculture area

More than half of the farmers (63%) were likely or very likely to expand their agricultural area in the next five years, and this did not vary significantly across regions or between older and younger respondents (Figure 4, question 1). Of the 20% of farmers that did not intend to increase their area of agricultural land, 8% have used all the suitable land they own for agriculture so they do not have the option to expand.
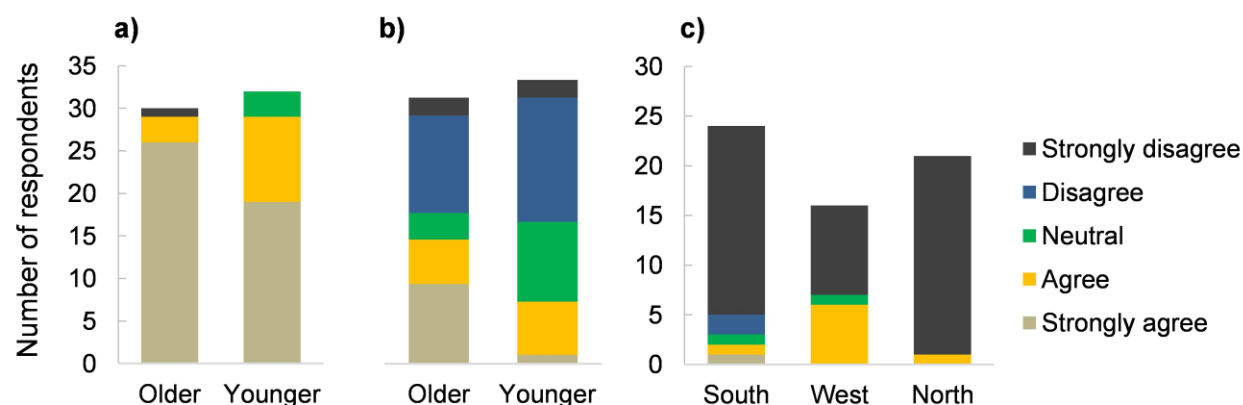
Figure 5 - Differences in responses between older and younger farmers to the statements (a) I think it is important to have rich birdlife on my estate and (b) I take birdlife into consideration in land use management, and between farmers in different regions to the statement (c) I think delaying the timing of harvesting could be possible (see Figure 4 for statistical analyses).

Respondent views on birdlife and attitudes to managing for birdlife

Nearly all farmers (97%) agreed or strongly agreed that it is important to have rich birdlife on their estate, and older farmers were significantly more positive about this than younger farmers (Figure 4, question 2; Figure 5a). However, only ~30% currently take birdlife into consideration when managing their land and this was not influenced by the concept of receiving financial incentives for these actions (Figure 4, questions 3, 4). Again, significantly more older than younger farmers strongly agreed that they currently took birdlife into consideration (Figure 4, Figure 5b). The definition of "taking birdlife into consideration" was left open in order not to constrain farmers' ideas of what they thought would be beneficial to waders, but discussions with farmers about this issue focused around actions such as taking special care during mowing to protect nests and chicks and leaving wet features available.

Responses regarding willingness to take part in different land management for birdlife varied depending on the proposed actions. More than 50% indicated that they would be willing to manage grazing at a favourable level for birds (Figure 4, question 5), around 90% either did not or would be willing not to drain pools on their estate (Figure 4, questions 10, 11), and approximately 60% are willing to spare important patches for birds on their land (Figure 4, question 13). However, delaying harvest of hayfields or arable land was an action most farmers did not undertake and would not consider undertaking, even if financial incentives were available (Figure 4, questions 7-9). Only 9 farmers thought that such action would be possible and, of those, only 3 were willing to do so (Figure 4, question 7). Farmers in the West were significantly more positive about delaying harvest (Figure 4, Figure 5c), although most still strongly disagreed that this was possible.

Identifying farmers most likely or unlikely to participate in bird conservation

The questions on whether farmers would be willing to manage their grazing and spare important sites for birdlife (Figure 4, questions 5, 13) had a range of responses and provided the opportunity to explore whether farmers with similar attitudes toward participating in bird conservation shared demographic characteristics. Farmers that responded as being likely or very likely to consider both actions were categorized as being willing (21 farmers) and farmers that were unlikely or very unlikely were categorized as unwilling (6 farmers, Figure 6). Comparison of the two groups showed that they did not differ significantly in proportion of livestock and age, but they did differ between regions (Table 2), with a greater percentage of willing farmers both in the West (45%) and the South (36%) than in the North (18%).
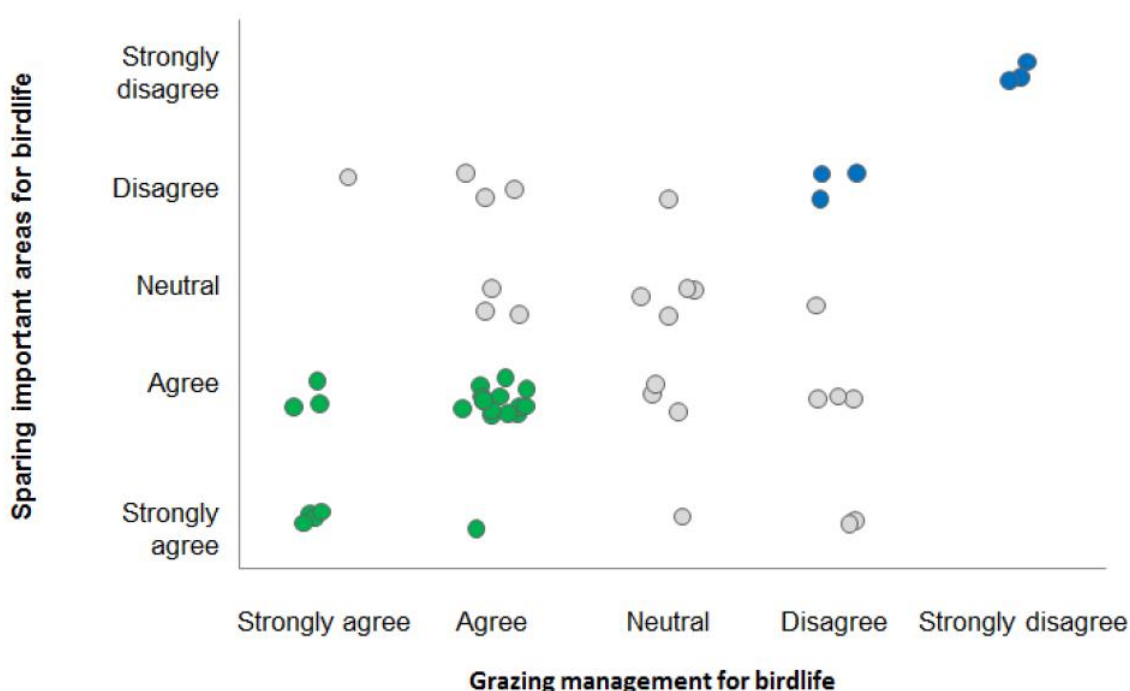

Figure 6 - Identification of farmers who were willing (green circles) or unwilling (blue circles) to both manage grazing levels and spare important land to benefit birdlife. Grey circles indicate farmers who were either neutral or gave contrasting responses to these two questions. Points have been jittered to prevent overplotting.

Table 2 – Result of tests of the numbers of farmers that were either willing or unwilling to both manage grazing and spare important land to benefit birdlife in relation to their farm characteristics (Mann-Whitney tests), region (G-test) and age (older or younger than the median birth year of 1966, Fisher´s exact test).

Farm characteristics	$U_{22,6}$	p
Livestock units (LU)	65	0.955
Sheep proportion	45	0.237
Cattle proportion	62	0.821
Horse proportion	47	0.287

Farmer characteristics	G	df	p
Region	6.182	2	**0.045**
Age		1	0.676

DISCUSSION

The majority of the Icelandic farmers who took part in the survey plan to expand their agricultural land in the next five years, and this is likely to be driven further by increasing demands for farming products (Barkarson et al. 2014). This implies that conversion of semi-natural land into farmland is likely to greatly increase in the near future, with potentially severe and widespread impacts on the internationally important bird populations that currently breed in these areas. Such expansion could put Iceland on a similar trajectory to many other countries that have experienced substantial biodiversity declines due to agricultural intensification and expansion (Millennium Ecosystem Assessment 2005). To maintain these globally important populations during agricultural expansion, it is important to know what conservation actions farmers may be willing and able to undertake (Young et al. 2005). Determining farmer attitudes toward having a rich birdlife on their land is an important first step in this process, because farmers that value birdlife may be more willing collaborators in the development of conservation management actions on their land. This is especially important because governance of land management is currently weak in Iceland and the socioeconomic system is unbalanced, with farmers having full control in the use of the remaining seminatural land resource (Ostrom 2009). This information could either be used to improve the governance or encourage farmers to take on self-governance to protect the resource.

Farming for birds in Iceland

The abundance of bird populations on agricultural land is typically a function of the intensity of agricultural operations (Schifferli 1999, Chamberlain et al. 2000, Donald et al. 2001, Murphy 2003). Agricultural processes such as the use of fertilizer, changes in landscape structure, and water level management can sometimes be beneficial at low

intensities. Fertilizer-fueled increases in vegetation growth may provide more opportunities for chicks and adults to shelter from predators, and tall vegetation can support abundant invertebrate prey resources (Gunnarsson 2010, Jóhannesdóttir et al. 2014). Breeding waders often have a preference for mosaic landscapes (Milsom et al. 2002, Schekkerman et al. 2008, Oosterveld et al. 2011), which can be enhanced through agricultural processes, especially during the earlier stages of agricultural expansion, e.g., through drainage of wetlands creating drier areas that might be suitable for nesting, ditches providing open water resources, and hayfields providing abundant and accessible prey resources. However, increases in agricultural intensity typically result in rapid landscape homogenization, with the result that the resources required by breeding birds are no longer available at the appropriate scales. The negative impacts of agricultural intensification on birdlife are well described (Chamberlain et al. 2000, Donald et al. 2001, Donald and Evans 2006, Perlut et al. 2006), but the point at which landscapes begin to become unsuitable will likely depend on the system and species involved. The high densities of breeding waders in the lowland regions of Iceland (Jóhannesdóttir et al. 2014) in which agriculture is common may suggest that landscape structural complexity is still sufficient to provide the necessary resources. For that reason, it is understandable that Icelandic farmers might not perceive their farming practices as a particular threat to local biodiversity. However, given that farmers manage a large proportion of lowland areas in Iceland, where the vast majority of waders breed and where there are virtually no regulations on land use, their future actions have the potential to greatly impact wader populations.

Farmers' views toward birds and their conservation

The vast majority of the questioned farmers considered it important to have rich birdlife on their estate. This may be beneficial in developing and targeting successful conservation measures, because farmer attitudes are likely to reinforce their actions (Lynne et al. 1988, Vogel 1996). In Iceland, most farms are family owned, as was the case for all farms surveyed in this study, and many farmers had lived their entire life on the same farm. Such strong connections to the land can be beneficial for conservation, and can have a positive effect on the persons' concern for nature (Mayer and Frantz 2004). Although only onethird of the farmers reported that they currently take waders into consideration in their land management, they were generally measures proposed. About 60% were likely or very likely to be willing to manage their grazing at levels favorable to waders if they were provided with appropriate instruction. The timing of farming operations, such as harvesting/mowing, can be crucial for breeding waders because they can result in the destruction of nests, chicks, and adults during the breeding season. For example, advances in timing of mowing of hayfields in the Netherlands has meant that this now coincides more frequently with wader nesting and chick rearing, causing unsuccessful breeding attempts and leading to lower recruitment (Kleijn et al. 2010). Because of the short growing season and changeable weather conditions in Iceland, particularly the relative lack of periods of dry weather that are required for hay processing, farmers have a short time window in which to mow their fields. Hence, few farmers (<20%) think they have flexibility to change their timing of mowing, and the few who thought it would be possible reported they would be very unlikely to do it. A few farmers mentioned they might be willing to do this if they could be compensated with hay, but as the limitations on hay production (particularly the short growing season) are similar across Iceland, it is unlikely that the necessary excess hay

production would be available. Delaying mowing is therefore a management action that is very unlikely to be achievable in Iceland at present.

High water levels and pools are very important for breeding waders as sources of invertebrate prey (Gunnarsson et al. 2005, Smart et al. 2006). It is therefore encouraging that about 90% of the farmer's reported that they already allow pools to stay intact on their property and that the great majority would be willing to spare them for birds. Maintaining pools is probably one of the most important management actions that farmers can undertake to support farmland biodiversity (Smart et al. 2006, Eglington et al. 2008). This is also linked to whether farmers would be willing to spare certain areas if they were known to be important to waders. Around 65% of farmers agreed or strongly agreed that their farming actions, e.g., natural land conversion, could be adapted to spare areas for birdlife, if they had appropriate support information to identify such areas. A focus on sparing wet areas would be an obvious first step, given the importance of water and wetlands for these species (Eglington et al. 2008, Jóhannesdóttir et al. 2014).

Financial compensation

In contrast to what was anticipated, the prospect of financial compensation did not increase the proportion of farmers who were willing to participate in the different conservation actions. Interestingly, some farmers reported that they were less likely to participate if they were to receive financial compensation, which probably reflects how unfamiliar this concept is to Icelandic farmers. Studies in the EU have shown that financial compensation is the most common reason for joining agrienvironment schemes (Wilson and Hart 2000), and Icelandic farmers did and do receive state subsidies for actions on their land, e.g., ditch construction for drainage and afforestation. However, there is no history of conservation measures in Icelandic farming, so both the concept of agri-environment schemes and compensation for participating in conservation efforts are novel to Icelandic farmers, many of whom had never previously considered the possibility of financial incentives for conservation management.

Conservation implications

Conservation action at these northern latitudes is likely to become necessary very soon, given the impending increase in the extent and intensity of agricultural activities. It is important to use experience from other countries to effectively integrate conservation actions with land use and management in farmed areas, and also to successfully cooperate with farmers and identify those most likely to be sufficiently engaged to allow long-term sustainable actions to be delivered. Although our questionnaire allowed identification of farmers who were consistently willing or unwilling to engage in conservation management actions, there was no clear link to any demographic group or farm type, other than farmers in the North were less willing to spare land or manage their grazing at favorable levels. However, this difference is probably caused by the fact that in the river valleys in the central North region, nearly all areas suitable for farming have been used, so farmers in the North have less flexibility in their management. This lack of demographic difference between the two groups of willing and unwilling farmers suggests that willingness to participate is an individual attribute, and studies such as ours are needed to identify willing

participants. Older farmers did report more often that they found it important to have rich birdlife on their estate, but there was no evidence that they were more likely than younger farmers to participate in conservation management. Key steps in developing conservation management on Icelandic farmland will likely be raising awareness of the issues and providing farmers with sufficient time to process the available information, and thus to decide whether or not they wish to participate. This study will hopefully provide a platform for developing conservation actions for the globally important breeding wader populations in Iceland and potentially other sub-arctic environments. Planning and regulations for land management in these regions are rare, but rapid changes in land use are likely, given the changing climatic conditions and potential for global trade in agricultural products. However, as a signatory to international agreements on conservation of birds and wetlands (Ramsar Convention, Bern Convention and African- Eurasian Waterbird Agreement), the Icelandic government is required to take action to protect the internationally important bird populations breeding in the country. Understanding what farmers believe is possible and would be willing to do, given their production aims, could help facilitate a more coordinated and collaborative approach to achieving these aims.

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Identifying important bird habitats in a sub-arctic area undergoing rapid land-use change

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BTO
Looking out for birds

Identifying important bird habitats in a sub-arctic area undergoing rapid land-use change

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Capsule Habitats in lowland South Iceland sustain bird populations of international importance, with highest densities in wet habitats.

Aims In areas important for biodiversity there is an urgent need to assess large-scale variation in the biodiversity value of habitats to inform management. We carried out a large-scale survey to assess the conservation value of sub-arctic, Icelandic bird habitats.

Methods Bird counts were carried out on 200 transects in the five most common vegetated habitat types in South Iceland. Based on these counts, breeding bird density and diversity were compared between habitats and total population sizes of common species in these habitats were calculated.

Results Overall, eight species (seven waders and Meadow Pipit) composed over 95% of all birds counted. The combined density of those species exceeded 275 birds/km^2 in all habitats. The two wettest habitat types had the highest density of birds.

Conclusion Wet habitats in lowland South Iceland held particularly high densities of breeding birds, notably waders, which constitute populations of international importance. Wet habitat types are generally of higher value for more species, than dryer ones.

Habitats are being altered extensively at an accelerating rate to fulfil the ever-growing human need for resources. These changes are often the cause of a degradation of environmental conditions, and are one of the major drivers of biodiversity loss (Vitousek *et al.* 1997, Sala *et al.* 2000). Reducing the impact of land-use intensification on biodiversity is one of the most urgent challenges in conservation. Identifying areas which are important for biodiversity is key to developing land-use planning approaches that are able to consider impacts on biodiversity (Myers *et al.* 2000, Eken *et al.* 2004), but often there is a lack of information on which to build this identification. Rapid environmental changes are occurring in many poorly studied areas in the arctic and sub-arctic, as a result of agricultural intensification, fossil fuel mining and climate change (ACIA 2005). These changes are likely to have a major impact on many migratory populations throughout their range and, as migratory populations can be regulated by interactions between factors that operate in both winter and summer (Gill

et al. 2001, Gunnarsson *et al.* 2005), the effects of habitat change in one season can have consequences for populations throughout their migratory ranges (Newton 2004).

Icelandic ecosystems support internationally important populations of 21 breeding bird species (Einarsson *et al.* 2002) and, for some species, are responsible for a large part of the world population (Wetlands International 2006). Iceland is of particular importance for breeding waders (Charadrii) in the northern hemisphere (Gunnarsson *et al.* 2006); and is thought to be the second most important breeding area for waders in Europe, after the vastly larger Russia (Thorup 2004). Nearly half of the species which occur in internationally important numbers in Iceland are waders, but wader populations have been declining worldwide in recent years; mostly because of habitat degradation and destruction (International Wader Study Group 2003). Reversing such declines requires information on the relative importance of different habitat types for individual species, and on the threats facing these habitats, to implement successful conservation. The global importance of Iceland for

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migratory wader populations is likely because of expanses of suitable open habitats, a sparse human population and fairly low-intensity agriculture (Gunnarsson *et al.* 2006). Despite the country being still quite sparsely populated, land-use intensity increased very rapidly during the last decades of the 20th century. About 55–75% of Icelandic wetlands have been drained to some extent (Óskarsson 1998) and nearly 97% of the wetlands in South Iceland, the largest lowland basin, have been partially or entirely drained (Thorhallsdottir *et al.* 1998). In the first decade of the 21st century, land-use changes accelerated greatly; conversion of natural landscapes into man-made surfaces in Iceland increased by about 20% between the years 2000 and 2006, and by over 30% in South Iceland, while in most European countries the increase was less than 5% during the same period (EEA 2010, Wald 2012). Man-made surfaces refer to roads, urban, industrial and recreation areas (EEA 2010). These rapid land-use changes make the assessment of landscape-scale biodiversity patterns matter of urgency.

The aim of this study was to assess the relative importance of key habitats in the lowlands of South Iceland for breeding birds, both in a national and an international perspective. South Iceland is the largest lowland basin and has 21% of the total lowland area in Iceland below 200 m a.s.l. (National Land Survey of Iceland 2013). Land-use changes have been most rapid in South Iceland due to the proximity to the capital (Wald 2012) and the density of breeding waders is also greatest there (Gunnarsson *et al.* 2006). We used data from ground surveys of birds and a digital land cover database to assess density, population sizes and distribution of common birds in the mosaic of lowland habitats in South Iceland.

METHODS

Study area

Bird counts were carried out in the lowlands of South Iceland. The boundaries of the study area were defined as within the two administrative regions (counties), Árnessýsla and Rangárvallasýsla, and below 200 m a.s.l. (Fig. 1). The landscapes in the lowlands of South Iceland are generally flat, only 2.5% of the area below 400 m a.s.l. has a gradient of more than 20° (Wald 2012). The area is one of the most important agricultural regions in Iceland, providing 36% of annual agricultural GDP in the year 2010 (FAI 2010) and
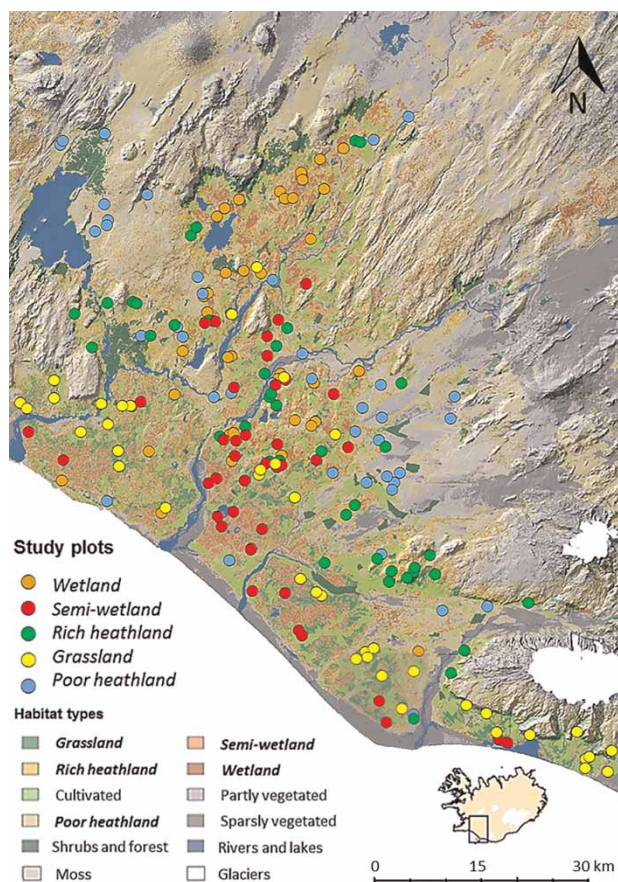

Figure 1. Map of South Iceland, including the study area, showing the position of study plots where bird abundance was surveyed. Sampling was restricted to areas below 200 m a.s.l.

about 10% of land below 400 m a.s.l. comprises cultivated hayfields (Wald 2012).

The land cover information used in the study was extracted from the Icelandic Farmland Database. This database uses satellite images with extensive ground truth verification to classify the surface of Iceland into 12 different classes (Arnalds & Barkarson 2003). The classification represents variables that reflect productivity, mostly vegetation cover, soil and drainage, and these variables are often strongly related to biodiversity (Noss 1990). The Icelandic Farmland Database classifies land down to the scale of 196 m^2 (pixel size 14×14 m). Survey sites within the five most common vegetated habitat classes, which land-use intensification is likely to mostly affect, were selected by a stratified random method, employing *ArcGis 10.1 GIS software*. Sites were selected so they covered at least 20 ha of a single habitat type to reduce effects of adjacent habitats. For practical reasons, sites

were selected so they were no more than 2 km from roads but not closer than 0.5 km to each other, which should be enough for independence of survey points. Previous studies have shown that the distribution of habitat types in lowland Iceland is comparable in respect to distance from roads (Gunnarsson *et al.* 2006). In total, 200 sites were surveyed, 40 of each habitat (Fig. 1). These five classes were wetland (total cover in the study area: 301 km^2), semi-wetland (426 km^2), rich heathland (420 km^2), grassland (384 km^2) and poor heathland (862 km^2) (Table 1) (habitat types in italics from now). These habitat types together comprised 2393 km^2, or 58%, of the study area. Other habitat types in the area, not surveyed for practical reasons, were mainly agriculture (95% of which are hayfields), forests and sparsely vegetated (sandy areas) habitat types.

Censuses

The surveys were conducted from the middle of May until the end of June, which is the peak breeding season for most species, in 2011 and 2012. Counts were performed during periods of greatest bird activity, in the morning from 06:00 to 13:00 and in the afternoon from 17:00 to 22:00 (Davíðsdóttir 2010). Surveys were only conducted when wind speed was lower than 6 m/s and in dry weather to avoid

Table 1. Description of the five habitats from the Icelandic Farmland Database where counts of birds were conducted in this study (Arnalds *et al.* 2003).

Habitat type	Characteristics
Wetland	Dominated by sedges (*Carex* spp.) (indicating a high water level), horsetail (*Equisetum* spp.), cotton-grass (*Eriophorum* spp.) and heathland vegetation. Highly vegetated habitat and with a dense sward
Semi-wetland	Dominated by plants found both in wet and dry land such as sedges, horsetail, wood-rush (*Luzula* spp.), grasses, willow species (*Salix* spp.) and sometimes birch (*Betula pubescence*). Semi-wetlands are wetland areas with partial drainage, often at the margin of the wetlands
Rich heathland	Dominated by small shrubs such as common heather (*Calluna vulgaris*) and black crowberry (*Empetrum nigrum*); sparse grasses and moss. Often rather dry and hummocky land
Grassland	Dominated by grasses and sometimes flowers (indicating a groundwater level too low for sedges). Grasslands are often common on alluvial substrate near streams. Grasslands include some former wetland areas that have been drained
Poor heathland	Dominated by mosses, small shrubs and sometimes lichen. Dry land, often partly vegetated

conditions of low bird detectability (Bibby *et al.* 2000). At each site, birds were counted along one line transect (Bibby *et al.* 2000). Transects were on average 511 m long (sd = 69.4 m). The total length of transects covered was 101 km. The perpendicular distances of birds from the transect line was recorded in four distance bands, 0–25, 25–50, 50–75, 75–100. The observer used binoculars with a built-in laser range-finder to determine distances to birds.

In 2012, invertebrate surveys were carried out simultaneously with the bird surveys on all the last 58 survey points (average 11.6 survey points per habitat, sd = 2.4) to relate bird abundance to variation in food abundance between habitats (Gunnarsson *et al.* 2005). The surveys were designed to sample the part of the invertebrate community that is the main food source for breeding birds, especially foraging chicks, by focusing sampling on foliar invertebrate communities. A sweep net (diameter 39 cm, mesh size 0.3 mm) was used to sample invertebrates with ten equal strokes through vegetation at three points on the line transect (at 25, 250 and 450 m). Invertebrates were sorted into broad groups and all individuals ≥3 mm were counted from the sweep net in the field and then released. The groups used were spiders (*Araneae*), beetles (*Coleoptera*), true bugs (*Hemiptera*), butterflies (*Lepidoptera*), flies (*Diptera, Hymenoptera and Trichoptera*) and larvae.

Data analysis

Bird densities were calculated using the length of transects and number of observations for each species and their observation distances (Bibby *et al.* 2000). Birds detected outside the 100 m belt were excluded from the analysis. Birds passing by were not recorded, only those using the habitat, on the ground or displaying over it. The density unit calculated was individuals/km^2, a conservative measure which avoids biases associated with estimation of status (e.g. breeding or foraging). The programme *Distance* (version 6.0) was used to estimate bird density on the line transects. The programme models the decline in detectability of birds with increasing distance from the transect line and uses this information and transect length to calculate density. Density estimates were only calculated for the eight most common species, which were Oystercatcher *Haematopus ostralegus*, Golden Plover *Pluvialis apricaria*, Dunlin *Calidris alpina*, Snipe *Gallinago gallinago*, Whimbrel *Numenius phaeopus*, Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus* and Meadow Pipit *Anthus pratensis*. This

is because a minimum number of observations is required to derive sensible detection curves for individual species (Buckland 2001). These eight species comprised 95% of the total number of birds recorded on transects. For density analyses of the eight most common species, three key functions were calculated; uniform, half-normal and hazard-rate, with either cosine, simple or hermite polynomials adjustment terms. The key function with the lowest Akaike's Information Criterion (AIC) score was used. When producing a single density estimate of all species combined, for the comparison of habitats, the same detection curve for each bird species (calculated from its abundance across different distance bands) was used for all habitats. When producing density estimates for individual sites (used to model individual species density in different habitats), every species was assigned a specific detection curve for each habitat, based on lowest AIC scores.

Differences in bird densities between habitat types were modelled with generalized linear models with a negative binomial error distribution and a log link function to account for overdispersion (Zuur 2009). The explanatory variable was a 5-level factor of habitat type.

To assess variation in bird diversity between habitats, the total number of species, mean number of species and the Shannon–Wiener index were computed (Shannon 1948).

To estimate the relative importance of South Iceland for birds, regional population sizes of common species were estimated, for the surveyed habitat types. These population sizes are a minimum estimate for the study area because several habitat types were excluded from the surveys, which included only the five most common vegetated habitat types. Population estimates were derived by multiplying the density estimates and 95% confidence intervals obtained from the Distance programme by the total area of each habitat type in South Iceland, and then summing these across habitats to produce regional population estimates for the surveyed habitat types.

Statistical analyses, other than estimates of species density, were performed in the programmes SPSS (IBM Corp 2012) and R (R Development Core Team 2008).

RESULTS

A total of 5128 birds of 22 species were recorded on the 200 sites surveyed. Most of the species were uncommon
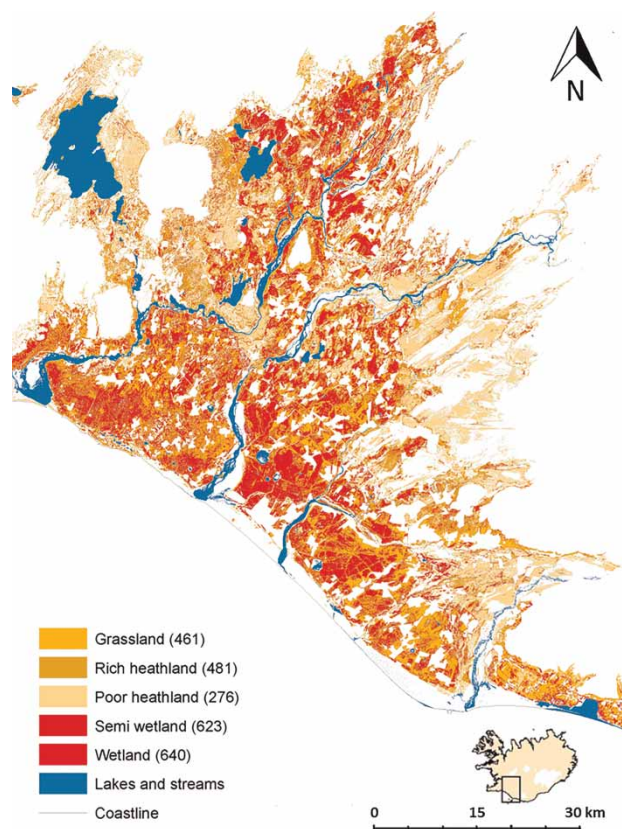

Figure 2. Distribution of the combined density of the eight most common bird species in the five habitats from the Icelandic Farmland Database below 200 m a.s.l. Total density (individuals/km^2) of the eight species per habitat is shown in parenthesis in the legend of the map.

and eight species dominated: Oystercatcher, Golden Plover, Dunlin, Snipe, Whimbrel, Black-tailed Godwit, Redshank and Meadow Pipit made up 95% of the total number of individuals recorded. The average combined density of the eight most common species was highest in *wetland* and *semi-wetland* with around 630 individual birds per km^2 (Fig. 2, Table 2). *Rich heathland* and *grassland* were similar with bird density around 470 individuals per km^2 but *poor heathland* had the lowest density with 275 individuals per km^2 (Table 2).

The abundance of most individual species was similar to the combined pattern (Table 2) but with some exceptions. Abundance was generally highest in *wetland* and *semi-wetland* for most species: Dunlin, Snipe, Whimbrel, Black-tailed Godwit and Meadow Pipit occurred in their highest densities in these two habitats (Table 2), but Whimbrel also occurred at similarly high densities in both *heathland* types.

Table 2. Comparison of measures of bird and invertebrate density (±se) and bird diversity in the five habitats surveyed in lowland South Iceland in 2011–2012.

Density	Wetland	Semi-wetland	Rich heathland	Grassland	Poor heathland
Sum of the estimated mean density (±se) of the eight most common bird species	640 (±79)	623 (±81)	481 (±78)	461 (±81)	275 (±54)
Estimated mean density (±se) of:					
Oystercatcher	1 (±1)	7 (±5)	5 (±3)	17 (±5)	2 (±1)
Golden Plover	27 (±5)	25 (±6)	43 (±10)	27 (±12)	48 (±8)
Dunlin	81 (±13)	60 (±11)	34 (±9)	17 (±7)	17 (±10)
Snipe	72 (±9)	57 (±9)	44 (±7)	38 (±8)	15 (±4)
Whimbrel	67 (±12)	48 (±5)	58 (±15)	27 (±5)	40 (±9)
Black-tailed Godwit	20 (±4)	16 (±5)	12 (±3)	8 (±2)	1 (±1)
Redshank	8 (±3)	11 (±4)	5 (±2)	15 (±4)	0.3 (±0.3)
Meadow Pipit	364 (±32)	399 (±32)	280 (±29)	312 (±38)	152 (±21)
Sum of average invertebrate abundance (±se) (sum of three random samples per transect)	77 (±14)	60 (±11)	69 (±14)	73 (±8)	26 (±6)
Bird diversity:					
Total number of bird species recorded	14	18	15	20	15
Mean number of bird species per site (±se)	5.65 (±0.25)	5.45 (±0.28)	4.925 (±0.28)	4.85 (±0.31)	3.65 (±0.23)
Shannon–Wiener index (±se)	1.35 (±0.05)	1.23 (±0.06)	1.19 (±0.07)	1.16 (±0.08)	1.01 (±0.06)

Oystercatcher and Redshank occurred in highest densities in *grassland* and the latter also in *wetland* and *semi-wetland*. Golden Plover occurred in highest densities in *poor* and *rich heathland*. All models predicting the abundance of individual species in different habitat types were highly significant with all species showing a significant difference in density between one or more habitats (Tables 2–4).

Total number of species ranged from 14 in *wetland* to 20 in *grassland*. This was in contrast with the mean number of species which was highest in *wetland*, followed by *semi-wetland*, *rich heathland* and *grassland* which had a similar mean number of species, but *poor heathland* had the fewest (ANOVA on average number of species; $F_{4,195} = 8.3$ $P < 0.0001$). The Shannon–Wiener index ranged from 1.01 to 1.35; *wetland* had the highest score and *poor heathland* the lowest (ANOVA on Shannon–Wiener index; $F_{4,195} = 3.66$, $P = 0.007$) (Table 2). The abundance of large (>3 mm) invertebrates captured by sweep-netting varied significantly among the five habitats. Comparison of invertebrate density between habitats showed an overall significant difference (Kruskal–Wallis: $H_4 = 15.0$, $P = 0.005$). Overall variation between habitats was similar ranging from 83 to 96 invertebrates on average per transect. Only *poor heathland* showed a significant difference in invertebrate abundance with, on average, 35 invertebrates per transect (Table 2). There was not a significant correlation between the abundance of birds and invertebrates on individual transects across all habitats (Pearson $r = 0.09$, $P = 0.49$, df = 56).

Population size estimation showed that 25% or more of the Icelandic populations of Oystercatcher, Snipe, Whimbrel, Black-tailed Godwit and Meadow Pipit breed in the five surveyed habitat types in the lowlands of South Iceland, including over 50% of the Black-tailed Godwit population and at least 30% of Oystercatcher and Meadow Pipit populations (Table 5). Furthermore, the lowlands of South Iceland accommodate 10–20% of the estimated European populations of Dunlin, Whimbrel and Black-tailed Godwit.

DISCUSSION

Iceland supports internationally important breeding bird populations of a range of ground-nesting species. The measures of avifauna in the five different habitats from the Icelandic Farmland Database showed that the wetter habitats are more important for bird biodiversity; *wetland* and *semi-wetland* have higher density of birds, higher mean number of species per transect and higher diversity index scores than other habitats in the study. Massive decline in area of wetlands in Iceland (Óskarsson 1998, Thorhallsdottir *et al.* 1998), and worldwide (OECD & IUCN 1996), further enhances the importance of these habitats for biodiversity on an international scale.

This study has shown that densities of the eight most common species are extremely high across the major vegetated, semi-natural habitats of lowland Iceland. All the five habitat types have very high densities of these species, in comparison to estimates from similar

Table 3. Results of generalized linear models (negative binomial with log link) predicting species abundance in different habitats (see Table 2). Number of individual birds per transect was modelled with transect length in km as an offset variable. Reference habitat was wetland.

	Oystercatcher				Golden Plover			
	B	Wald LR	df	P	B	Wald LR	df	P
Grassland	2.9 (±0.6)	20.2	1	<0.001	−0.042 (±0.3)	0.02	1	0.88
Poor heathland	0.85 (±0.7)	1.4	1	0.24	0.59 (±0.3)	4.8	1	0.029
Rich heathland	1.6 (±0.7)	5.8	1	0.016	0.46 (±0.3)	2.8	1	0.092
Semi-wetland	1.9 (±0.7)	8.8	1	0.003	−0.11(±0.3)	0.1	1	0.71
Overall model fit		47.1	4	<0.001		11.4	4	0.022
Deviance/df	1.0				1.3			

	Dunlin				Snipe			
	B	Wald LR	df	P	B	Wald LR	df	P
Grassland	−1.6 (±0.3)	29.7	1	<0.001	−0.6 (±0.3)	6.2	1	0.013
Poor heathland	−1.5 (±0.3)	28.1	1	<0.001	−1.6 (±0.3)	29	1	<0.001
Rich heathland	−0.99 (±0.3)	10.8	1	0.001	−0.49 (±0.3)	3.7	1	0.056
Semi-wetland	−0.3 (±0.3)	1.4	1	0.23	−0.26 (±0.3)	1.04	1	0.31
Overall model fit		51.1	4	<0.001		32.1	4	<0.001
Deviance/df	1.4				1.0			

	Whimbrel				Black-tailed Godwit			
	B	Wald LR	df	P	B	Wald LR	df	P
Grassland	−0.92 (±0.3)	12	1	0.001	−0.94 (±0.3)	9.6	1	0.002
Poor heathland	−0.50 (±0.3)	3.8	1	0.051	−2.64 (±0.5)	30.6	1	<0.001
Rich heathland	−0.14 (±0.3)	0.3	1	0.57	−0.56 (±0.3)	3.8	1	0.051
Semi-wetland	−0.33 (±0.3)	1.7	1	0.19	−0.26 (±0.3)	0.9	1	0.35
Overall model fit		13.9	4	0.007		48.7	4	<0.001
Deviance/df	1.1				1.2			

	Redshank				Meadow Pipit			
	B	Wald LR	df	P	B	Wald LR	df	P
Grassland	0.58 (±0.3)	2.8	1	0.092	−0.17 (±0.06)	7.4	1	0.006
Poor heathland	−3.14 (±1.0)	9.0	1	0.003	−0.86 (±0.07)	130.9	1	<0.001
Rich heathland	−0.43 (±0.4)	1.1	1	0.29	−0.26 (±0.06)	17.8	1	<0.001
Semi-wetland	0.33 (±0.4)	0.9	1	0.34	0.068 (±0.06)	1.4	1	0.23
Overall model fit		39.7	4	<0.001		205	4	<0.001
Deviance/df	0.9				4.7			

Table 4. Significance scores from a generalized linear model pairwise comparison of density of common species between habitats (Table 3). Habitats that were significantly different are shown, habitats with significantly higher densities are shown in bold and habitats with significantly lower densities are shown normal. W = wetland, SW = semi-wetland, RH = rich heathland, G = grassland, PH = poor heathland. Direction of relationships was determined with Least Significant Difference Post-Hoc tests.

	Wetland	Semi-wetland	Rich heathland	Grassland	Poor heathland
Oystercatcher	**SW-RH-G**	W-**G**-PH	W-**G**	W-SW-RH-PH	**SW-G**
Golden Plover	**PH**	**RH-PH**	SW	**PH**	W-SW-G
Dunlin	RH-G-PH	RH-G-PH	**W-SW**-G-PH	**W-SW-RH**	**W-SW-RH**
Snipe	G-PH	PH	PH	**W**-PH	**W-SW-RH-G**
Whimbrel	G	G	G	**W-SW-H**	
Black-tailed Godwit	G-PH	G-PH	PH	**W-SW**-PH	**W-SW-RH-G**
Redshank	PH	PH	**G**-PH	RH-PH	**W-SW-RH-G**
Meadow Pipit	RH-G-PH	RH-G-PH	**W-SW**-PH	**W-SW**-PH	**W-SW-RH-G**

Table 5. Estimated population sizes (individuals/km²) of the eight common species in the five surveyed habitat types in South Iceland. Proportions of estimated Icelandic and European populations in the five habitats in the study area are shown.

	Population estimate	Confidence interval (95%)	% of Iceland population	% of Europe population
Oystercatcher	14 984	6655–37 770	37–75[a]	2–3[c]
Golden Plover	89 144	57 733–141 004	14[b]	6–9[c]
Dunlin	92 471	58 181–153 812	17[b]	8–12[c]
Snipe	104 756	75 450–145 978	29[b]	3–6[c]
Whimbrel	117 754	75 488–184 598	24[b]	16–19[c]
Black-tailed Godwit	27 010	16 111–44 870	54[b]	10–12[c]
Redshank	17 637	9594–33 057	6[b]	1–2[c]
Meadow Pipit	703 240	573 013–864 245	35–70[+]	2–5[c]

Populations estimates according to [a]Ministry for the Environment (1992), [b]Thorup (2004) and [c]Birdlife International (2004).

habitats in other countries. For example, density estimates on grasslands from the Netherlands (for Oystercatcher, Snipe, Black-tailed Godwit and Redshank), are on average 44% of density in Iceland (Teunissen & Van Paassen 2013). Density estimates from moorland, the largest extent of semi-natural habitat remaining in the UK for seven of the eight species involved (excluding the Black-tailed Godwit) are on average only 6% of the density recorded in Iceland (Grant & Pearce-Higgins 2012). So on a broad scale, density is relatively high in Iceland even though smaller areas of habitats with exceptional concentrations of waders can be found, for example, the machair habitat, on the north-west coast of the UK (Calladine *et al.* 2014). Overall, 22 species of birds were recorded in the five habitat types but only eight of them composed 95% of the recorded individuals: 7 species of wader and one passerine (Meadow Pipit). Densities of birds differed between habitat types although there was a general preference for wetter habitats. This is in agreement with other studies on habitat preferences of waders and the Meadow Pipit in Iceland (Gunnarsson *et al.* 2006, 2007) and other countries (Fuller *et al.* 2005, Smart *et al.* 2006). A few species did not fall into the general pattern. *Grassland* was significantly more favoured by two species; Oystercatcher and Redshank, and *heathland* habitats were preferred by the Golden Plover. Redshank and Oystercatcher are usually associated with agricultural grasslands and the results presented here are supported by previous studies in Iceland and elsewhere (Gunnarsson *et al.* 2006, Smart *et al.* 2006). Golden Plover occurs most frequently on heathland throughout its range (Byrkjedal & Thompson 1998) which was confirmed in this study.

Habitats did not only differ in density of species but also in diversity (Table 2). Considering species richness, there was a slight difference between the habitats which had the highest and the lowest total numbers of species recorded per habitat of 30%. Most species were found in *grassland* but fewest in *wetland*. Measures of mean number of species per transect in different habitats and the Shannon–Wiener index ranked *wetland* at the top and *poor heathland* with the lowest diversity which is more in accordance with the preference of most species for *wetlands*. A possible explanation for the highest overall number of species occurring in *grassland* could be higher heterogeneity of the *grassland* habitat, due to more intensive drainage and higher variation in grazing as habitat heterogeneity is closely linked to species richness (Benton *et al.* 2003). However, the total number of species in these habitats is relatively low, so absolute differences in species diversity between habitats are small.

The invertebrate survey yielded similar invertebrate catches between habitats but only *poor heathland* was significantly different with lower catches on average. This was in accordance with bird densities which were also lowest on *poor heathland*.

The estimated regional population sizes suggest that the lowlands of South Iceland support very large populations of most of the common species despite the fact that several other habitat types (e.g. agriculture, forests and sparsely vegetated habitat types) were not surveyed for practical reasons. Three of the common species, Golden Plover, Dunlin and Whimbrel, occur in internationally important numbers in Iceland (Einarsson *et al.* 2002) and the rest, Black-tailed Godwit, Redshank, Meadow Pipit, Snipe and Oystercatcher, are all species facing a decline in their European breeding range (Birdlife International 2004). Previous studies comparing density of waders in wet habitat types across different parts of Iceland suggest that the average density of waders in South Iceland is generally higher (up to five fold higher than in West

and East Iceland) than elsewhere (Gunnarsson 2010). A recent study suggests that this large-scale variation is largely due to the fertilizing effects of volcanic dust which shows a gradient in deposition across Iceland (Gunnarsson *et al.* submitted). So it is evident that South Iceland supports a substantial part of the total Icelandic populations of many of the focal species and a large part of the European population of some. If subspecies were considered, the international conservation status would be increased, because most of the wader species in Iceland have a subspecies status (Guðmundsson & Skarphéðinsson 2012).

All of the five habitats have high densities but different habitats are disproportionally important for bird biodiversity. *Wetland* and *semi-wetland* have higher densities than the other habitats, and host a higher mean number of species, and more declining species. There have been major declines in wetlands, both in Iceland (Óskarsson 1998, Thorhallsdottir *et al.* 1998) and worldwide (OECD & IUCN 1996) so the scarcity of wetlands makes them relatively more important. *Wetlands* in the study area account for 16% of the total area of wetlands in Iceland (The Farmland Database 2013). Judging by both their higher biodiversity value and scarcity, it is evident that *wetland* and *semi-wetland* habitats have the highest conservation value. But it is also important to consider that different habitats are important for different species and though wetter habitats are of relatively greater importance for more species, drier habitats can be important for some, notably the Golden Plover.

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