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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 agricultural 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 soil productivity, and quantified (a) levels of breeding bird use of farmed land managed at three differing intensities, ranging from cultivated fields to semi-natural land and (b) changes in patterns of use throughout the breeding season, for an assemblage of species. Breeding birds use all three land management types in large numbers but, overall, bird abundance is lower in more intensively managed farmland. 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 (Foley *et al.*, 2005; Green *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, Danielson & Pulliam, 1992), but this is highly dependent on the extent and intensity of agricultural management (Gill *et al.*, 2007; Wright, Lake & Dolman, 2012). 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, Bittman & Lank, 2008), including highly threatened species (Wright *et al.*, 2012). Agricultural management often results 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, when at suitable spatial scales, and cultivated fields can provide abundant and accessible invertebrate prey resources. However, such positive effects of low-intensity 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, Vickery & Wilson, 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), ~90% of which is hayfields and ~10% arable fields (The Farmland Database, 2013). This is similar to areas such as Norway, the Faroe Islands, northern Canada and northern and western areas of the British Isles (World Bank, 2017), but contrasts sharply with the US in which ~20% of land is cultivated (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 natural or semi-natural (refers to areas that have been affected by some sort of management, often grazed or have been drained to some extent) habitats are still present and surround the hay- and arable fields that occur on farms. This arrangement creates gradients of agricultural intensity from the farm into the surrounding natural land, ranging from intensive management to moderate and light management (Fig. 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.

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), and is especially important for breeding waders (Charadrii) (Gunnarsson *et al.*, 2006). Iceland 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),with an estimated 4-5 million waders leaving Iceland each autumn, representing a very significant part of the total numbers of wintering waders in Europe and W-Africa (Guðmundsson, 1998). These high densities are likely a product of large areas of open, vegetated landscapes and high nutrient levels (Fig. 1) (Gunnarsson *et al.*, 2006, 2015; Pickett & Siriwardena, 2011).

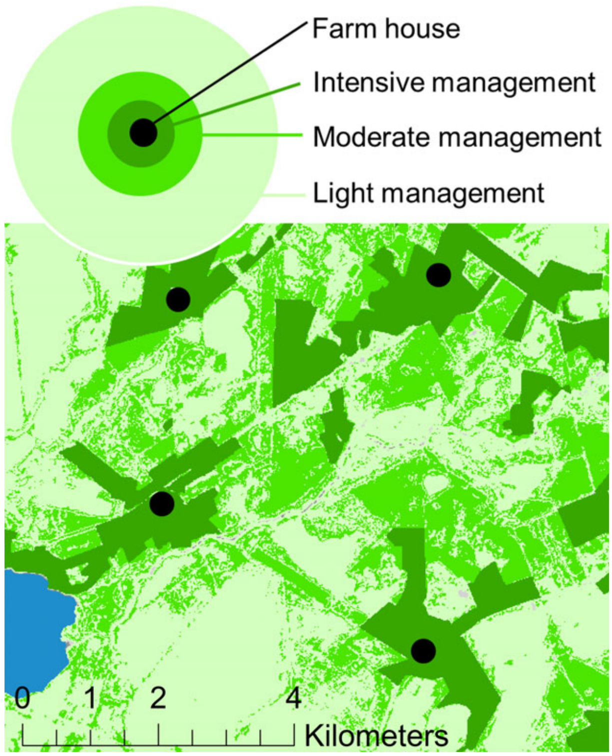

Figure 1 An example of the South Iceland landscape, showing the typical spatial structure of Icelandic agricultural areas. The most intensively managed areas (arable and hayfields; dark green) are typically close to farm houses (black circles); areas with moderate management (e.g. fertilized grazing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

The use of farmed land by wildlife might vary in relation to underlying productivity and, in Iceland, productivity varies significantly at regional scales due to the volcanic nature of the island and the resulting intense but geographically variable aeolian deposition (Arnalds, 2015). This influences fertility and pH levels of the soils and is related to bird density (likely through impacts on vegetation growth and food resources), which declines with distance from the volcanically active Mid-Atlantic ridge that runs from south-west to north-east Iceland (Gunnarsson *et al.*, 2015). However, the extent to which this regional variation in wader abundance interacts with agricultural land management within these regions is unknown.

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.

The aim of this study was to quantify (a) levels of breeding bird (mostly wader species) 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, 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.

Materials and 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° West longitude. Average temperatures ranges from *c.* −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). Icelandic agriculture is mostly livestock-based and pastoral, with arable crop production in Iceland being limited due to the cold climate and short growing season. Cultivated land consists mainly of hayfields (90%) which are established by cultivation and periodically cultivated again and re-seeded for fodder for livestock, but barley and rapeseed are grown on limited areas (Jóhannesson, 2010). These most intensively used patches of Icelandic farmland (intensive category, see below) are cultivated with maximum fertilizer inputs (on average ~100 kg/ha of N FAI, 2005, which is similar to the UK Defra, 2015), but low levels of use of other chemicals like pesticides. Most hayfields were created between 1950 and 1980 and have therefore been in use for ~40–70 years (Snorrason *et al.*, 2015). Length of the growing season is limited at these latitudes but sowing, fertilizing and harvesting is undertaken as early as possible. In this sense, Icelandic farmland is managed as intensively as possible at this latitude, as is the practice in most other agricultural systems that are important for waders. The most distinguishing feature of Icelandic agricultural landscapes is that cultivated land in the main agricultural areas comprises only a minor part (~2%) of the landscape.

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; Fig. 2) which encompass the majority of agricultural production in Iceland (Statistics Iceland, 2015). These farms were all similar in farming practices, landscapes and biodiversity, and were all livestock-based farms, grazing a mixture of sheep, cattle, and/or horses. 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).

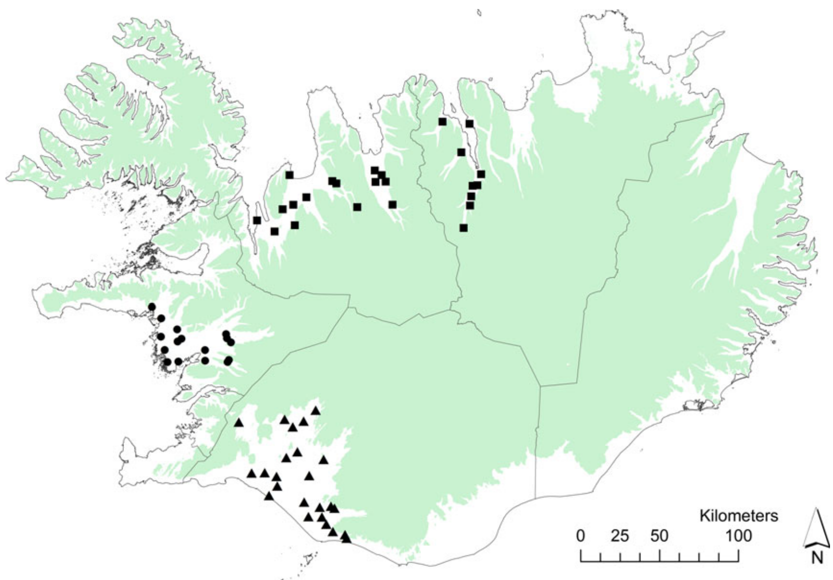

Figure 2 Locations of the 64 farms surveyed in lowland Iceland across three different regions: south (triangles), west (circles) and north (squares). Area above 200 m a.s.l. is shaded (area which is mostly unsuitable for agriculture). Large unsurveyed lowland areas towards the SE are barren glacial outwash plains not suitable for agriculture.

Bird surveys

At each farm, three survey fields 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 (each transect was located within a single field) but the single observer (LJ) aimed to keep the surveyed area similar to ensure constant survey effort (average transect length (± SD) = 253 ± 75 m; width = 92 ± 24 m, corresponding to an average survey area (± SD) of 2.3 ± 0.8 ha). Given the transect width (~100 m) and consistency of vegetation height within the transects, we assumed constant detectability. 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.

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 waders 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. These interactions were included to test for regional and seasonal variation in the effects of management (two-way interactions) and for seasonal variation in region-specific management effects (three-way interaction). Farm identity was included as a random factor to control for the non-independence of the multiple surveys on each farm and the model including all wader species also had species as an additional random factor to account for differences in species composition among sites. 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.

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, ranging from sparsely vegetated habitats to habitats with abundant vegetation (where grasses and bushes dominate the vegetation) and with a broad wetness gradient

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).

Large numbers of waders were recorded on all transects in all regions. The mean observed density of all wader species in the three main management types varied significantly from 147 (± 31 SE) waders/km^2 in intensive management to 176 (± 23 SE) in moderate management and 204 (± 27 SE) in light management in the early round, in all regions combined, with similar differences between management types in the later round (Table 2, Fig. 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 (mean densities of ~100–150 waders/km^2 in both rounds), whereas the highest densities (~300 waders/km^2) were recorded in the intensive management category in the west (Table 2, Fig. 3). Wader density did not differ significantly between rounds or in its interaction with management type (Table 2, Fig. 3). However, the seasonal differences in density on the three management types 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 (Fig. 3).

Factors influencing density of individual species

Dunlin, Black-tailed Godwit, Whimbrel and Meadow Pipit all showed similar variation in density across management types, with densities in intensive management sites generally being less than half of that in light management sites (Fig. 4, Table 3). In contrast, observed densities of Snipe and Redshank were ~1.2 to 3 times higher in intensive than moderate or light management, but only in the west (Fig. 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 (mean density = ~14/km^2) in the south, and densities in this region were greatest in moderate management (mean density = ~30–40/km^2). 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 (Fig. 4).

Table 2 Results of a generalized linear mixed model (GLMM) of density predictions (plus SE) and 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)

	Mean (SE)	F	d.f.	*P*
Corrected model intercept		4.98	17	**<0.001**
Management		5.04	2	**0.007**
Intensive	16 (4)			
Moderate	20 (4)			**0.017**
Light	20 (4)			**0.020**
Region		0.27	2	0.766
South	17 (4)			
West	20 (5)			0.507
North	19 (5)			0.601
Round		2.62	1	0.106
1	17 (4)			
2	19 (4)			0.128
Management × Region		10.57	4	**<0.001**
Management × Round		1.90	2	0.150
Management × Region × Round		2.90	6	**0.008**

Transect area was included as an offset and farm identity and species as random factors. Mean values and significance from post hoc tests are given for each category and significant values are highlighted in bold.

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; Wright *et al.*, 2012). 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 waders but this varies across species, with some, such as Oystercatcher and Redshank, extensively using

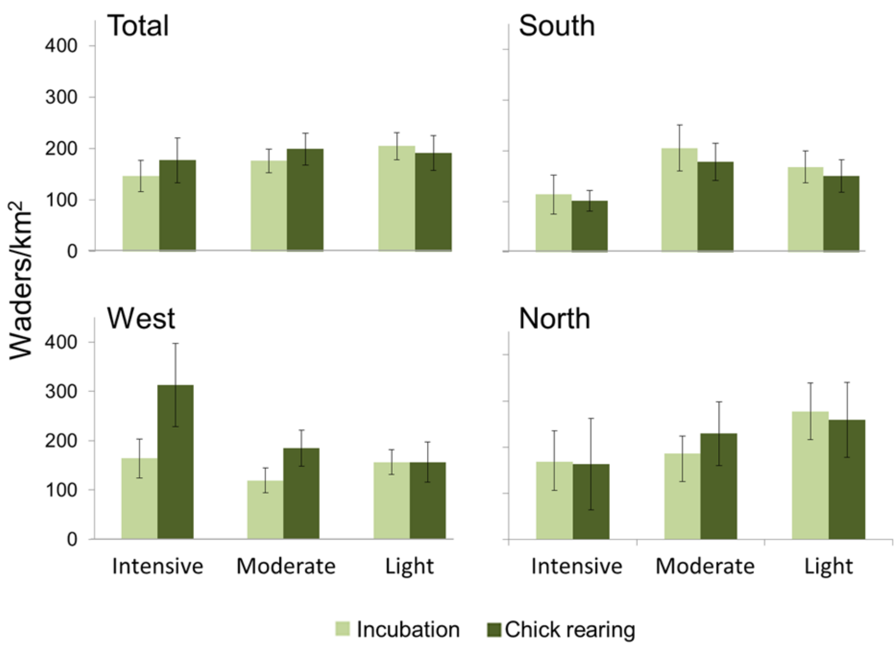

Figure 3 Mean (±SE) densities of the seven most common wader species on the three different management types in the early (light green) and late (dark green) season surveys across all survey sites (total) and in each of the three regions (see Fig. 1 for regions).

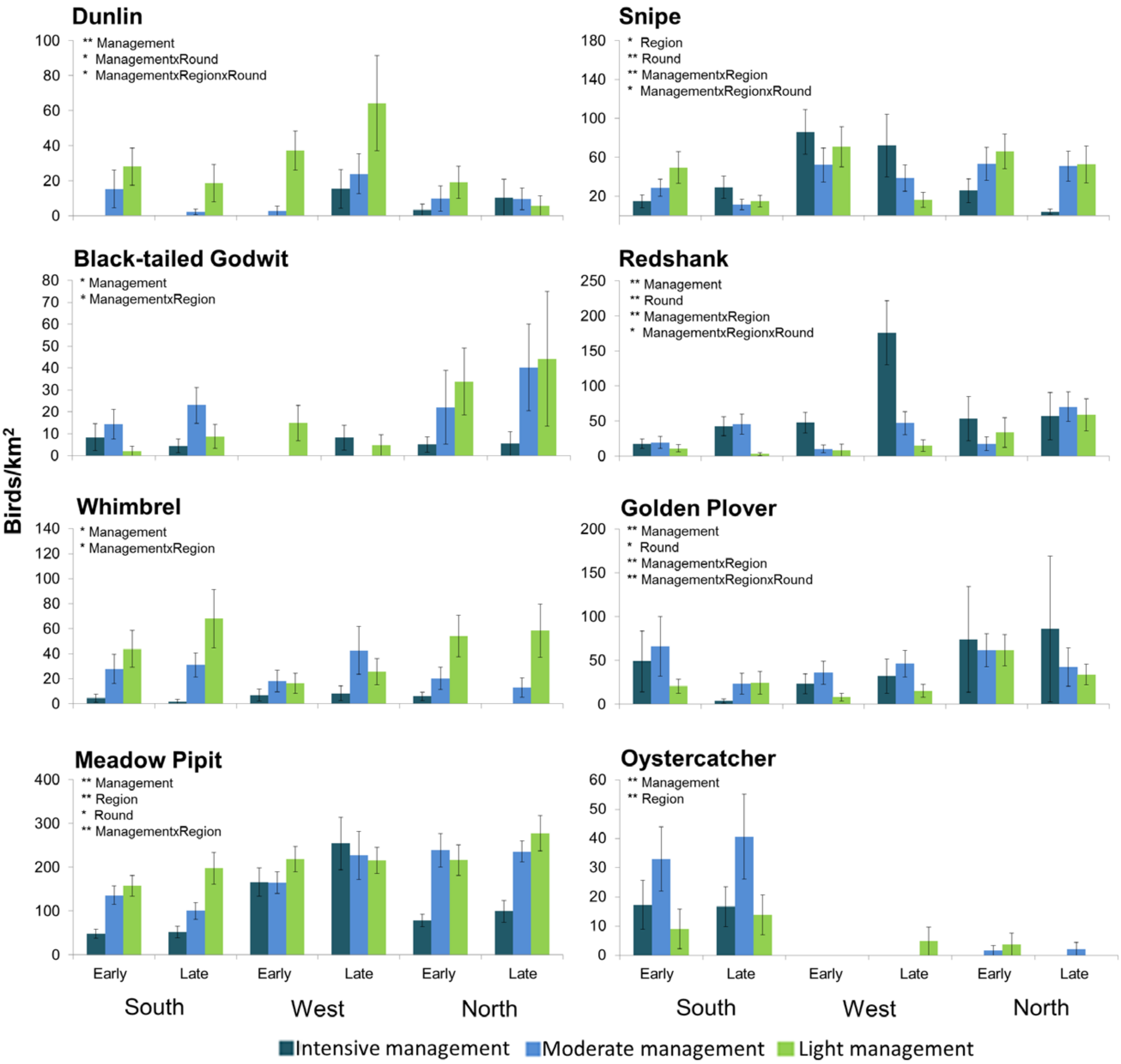

Figure 4 Mean (± SE) densities of the seven most common wader species and one passerine (Meadow Pipit) in habitats with differing management (Table 1), in early and late breeding season and in different regions of Iceland. Asterisks and terms indicate significant differences from generalized linear mixed models (see Table 3) with *$P < 0.05$, **$P < 0.005$. Note different scales on each plot.

more intensively managed agricultural land, whereas others (e.g. Dunlin and Whimbrel) only occur at very low densities. It should be noted that the accuracy of the survey methods might vary between species (due to differences in behaviour) and thus the capacity to detect effects of management may vary among species.

The current landscape structure in lowland Iceland, with agricultural land embedded within semi-natural land, may therefore be benefitting the breeding bird community, whereas 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, Sanderson & Heath, 2001; Newton, 2004; Roodbergen, Van Der Werf & Hötker, 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

Table 3 Results of generalized linear mixed models (GLMMs) of the predicted density (SE) and 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

	Dunlin *n* = 117				Snipe *n* = 289			
	Mean (SE)	*F*	d.f.	*P*	Mean (SE)	*F*	d.f.	*P*
Corrected model intercept		3.37	17	**<0.001**		4.01	17	**<0.001**
Management		9.22	2	**<0.001**		2.35	2	0.097
Intensive	17 (3)				22 (3)			
Moderate	16 (3)			0.800	30 (4)			0.079
Light	33 (3)			**0.001**	32 (5)			0.032
Region		0.28	2	0.756		5.25	2	**0.006**
South	19 (4)				18 (3)			
West	20 (5)			0.752	43 (8)			**0.006**
North	22 (5)			0.461	27 (5)			0.148
Round		3.66	1	0.057		16.93	1	**<0.001**
1	17 (4)				37 (4)			
2	24 (5)			0.065	20 (3)			**<0.001**
Management × Region		2.34	4	0.057		7.27	4	**<0.001**
Management × Round		5.4	2	**0.005**		1.19	2	0.307
Management × Region × Round		2.37	6	**0.029**		2.91	6	**0.009**

	Black-tailed Godwit *n* = 111				Redshank *n* = 300			
	Mean (SE)	*F*	d.f.	*P*	Mean (SE)	*F*	d.f.	*P*
Corrected model intercept		3.94	9	**<0.001**		7.64	17	**<0.001**
Management		4.16	2	**0.016**		19.9	2	**<0.001**
Intensive	2 (1)				38 (6)			
Moderate	1 (13)			0.858	22 (4)			**0.002**
Light	7 (2)			**0.011**	12 (3)			**<0.001**
Region		0.21	2	0.814		0.99	2	0.374
South	5 (2)				17 (4)			
West	1 (6)			0.430	25 (7)			0.322
North	7 (3)			0.534	26 (6)			0.210
Round		2.58	1	0.109		23.66	1	**<0.001**
1	1 (47)				15 (3)			
2	1 (64)			0.983	32 (5)			**<0.001**
Management × Region		2.73	4	**0.029**		5.88	4	**<0.001**
Management × Round								
Management × Region × Round						2.06	8	**0.039**

	Whimbrel *n* = 226				Golden Plover *n* = 326			
	Mean (SE)	*F*	d.f.	*P*	Mean (SE)	*F*	d.f.	*P*
Corrected model intercept		5.00	17	<0.001		3.67	17	<0.001
Management		3.93	2	**0.021**		9.40	2	**<0.001**
Intensive	1 (17)				19 (4)			
Moderate	16 (3)			0.394	31 (5)			**0.009**
Light	25 (5)			0.167	15 (3)			0.274
Region		0.01	2	0.991		2.32	2	0.100
South	12 (4)				15 (4)			
West	11 (4)			0.902	19 (6)			0.536
North	2 (50)			0.836	31 (7)			**0.050**
Round		0.01	1	0.956		5.70	1	**0.018**
1	11 (2)				25 (4)			
2	4 (71)			0.916	17 (3)			**0.023**
Management × Region		3.42	4	**0.009**		4.74	4	**0.001**
Management × Round		0.063	2	0.939		1.84	2	0.160
Management × Region × Round		0.579	6	0.747		4.20	6	**<0.001**

Table 3 Continued.

	Meadow Pipit n = 1287				Oystercatcher n = 89			
	Mean (SE)	F	d.f.	P	Mean (SE)	F	d.f.	P
Corrected model intercept		10.33	17	<0.001		8.00	5	<0.001
Management		51.93	2	**<0.001**		7.25	2	**0.001**
Intensive	89 (8)				2 (1)			
Moderate	160 (12)			**<0.001**	4 (1)			**0.035**
Light	193 (14)			**<0.001**	2 (1)			0.530
Region		12.43	2	**<0.001**		12.89	2	**<0.001**
South	88 (10)				14 (4)			
West	188 (24)			**<0.001**	1 (1)			**<0.001**
North	165 (18)			**<0.001**	1 (1)			**<0.001**
Round		5.84	1	**0.016**		0.10	1	0.751
1	130 (10)				2 (1)			
2	150 (11)			**0.017**	2 (1)			0.752
Management × Region		12.86	4	**<0.001**				
Management × Round		0.52	2	0.596				
Management × Region × Round		0.72	6	0.635				

Grey box indicates when a species had too few observations to test for the interactions. Mean values and significance from post hoc tests are given for each category and significant values are highlighted in bold.

and incubation) season. This suggests that further expansion of frequently cut hayfields and arable fields would be likely to result in reduced overall densities through mechanisms such as depressed reproductive success caused by mowing (Schekkerman, Teunissen & Oosterveld, 2008) and loss of important wet features (Eglington *et al.*, 2008). 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, where the highest density occurred in different management type based on regions and round. 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

Regional-scale variation in bird density is often large but the drivers of this variation remain unexplained (Buchanan *et al.*, 2017). Often this variation is driven by mechanisms that are hard to measure or detect but occasionally such patterns are revealed. In a recent study from Iceland, regional variation in wader density was linked to the distribution of volcanic dust (Gunnarsson *et al.*, 2015). Frequent volcanic eruptions in Iceland have resulted in the dispersal of large amounts of volcanic dust over many thousands of years, originating from the tectonic plate boundary that crosses Iceland along the North-Atlantic ridge (Arnalds, 2015). The volcanic dust has an important fertilizing effect that causes a regional difference in underlying productivity, where there is greater deposition closer to the plate boundary, thus accounting for some of the variance in wader density (Gunnarsson *et al.*, 2015). This fertilizing effect is likely to have parallels to other anthropogenic and natural processes, such as artificial fertilization and flooding/irrigation.

Although there is no strong regional difference in wader density in this study, the regional variation in relative use of different management intensities indicates an important influence of underlying productivity, caused by distribution of volcanic dust, 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. Interestingly this regional difference in bird density was not apparent on the agricultural land that was the focus of this 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 liming and fertilization of the soil, improving the productivity of these sites relative to the surrounding land. Liming has been shown to affect distribution of Northern Lapwing *Vanellus vanellus* chicks through the impact on earthworms (McCallum *et al.*, 2015, 2016), 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). Previous studies also 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 earthworm species (Sigurðardóttir & Þorvaldsson, 1994). The seasonal increase in bird density on intensively managed sites in the west (Fig. 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 (Fig. 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 (Fig. 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).

Implications for breeding wader conservation

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 (~100–200 waders/km^2) are typically much higher than those recorded in other countries in which these species breed, with the exception of some very small areas which retain high densities (Fuller *et al.*, 2010; Calladine *et al.*, 2014). 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). 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. Throughout much of temperate western Europe, rapid declines in breeding wader populations have been linked to wetland drainage and agricultural developments, reducing the availability of key resources for nesting and chick-rearing (Eglington *et al.*, 2008, 2010; Schekkerman *et al.*, 2008; Laidlaw *et al.*, 2015). The findings of this study suggest that commercial production and breeding wader conservation can co-exist in areas in which agriculture does not dominate, and targeting of actions to reverse population declines in breeding waders in such areas might be a particularly effective means of maintaining sustainable breeding wader populations.

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