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Large-scale habitat associations of birds in lowland Iceland: Implications for conservation

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A B S T R A C T

Iceland is responsible for many internationally important populations of breeding bird species, yet very little is currently known about how these species use the habitats available to them. Lowland areas of Iceland, in particular, have undergone significant landscape changes over the last century, such as widespread drainage of wetlands and conversion to agriculture, changes in grazing pressure and recently, extensive afforestation. The impact of these changes on breeding bird species will depend on the relative importance of different habitats for each species, and the threats facing those habitats. Here we report the results of a large-scale survey of the factors influencing patterns of habitat selection of eight populations of Charadriiform bird species throughout lowland Iceland; 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 arctic skua *Stercorarius parasiticus*. Ordination analyses and multiple logistic regression models are constructed to explore the components of habitats that influence the distribution of these species. Five of the eight species analysed showed significant preferences for lowland wetland habitats and four significantly selected areas containing wet features such as pools and high water tables. These results allow us to identify future conflicts in land use that are likely to result from government-supported large-scale afforestation of lowland areas and hydro-electric developments.

1. Introduction

Many species of waders (Charadrii) are currently declining worldwide. Of populations with known trends, 48% are declining at present whereas only 16% are increasing, with habitat loss and degradation thought to be the main cause of decline in most species (International Wader Study Group, 2003). In western Europe, increases in intensive agricultural practices, particularly in relation to factors such as changes in grassland management, structural changes to habitats and gradual losses of wetlands, are thought to be responsible for population declines in many species such as golden plover *Pluvialis*

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apricaria, snipe *Gallinago gallinago*, dunlin *Calidris alpina*, black-tailed godwit *Limosa limosa* and lapwing *Vanellus vanellus* (Hötker, 1991; Parr, 1992; Whitfield, 1997; Beintema and Saari, 1997; Thorup, 1998; Schekkerman and Müskens, 2000; Stroud et al., 2004). Preventing and reversing these declines requires information on the relative importance of different habitat types for each species, together with assessments of the threats facing those habitats, in order to inform species conservation and management (Caughley and Sinclair, 1994).

Iceland supports internationally important populations of 10 species of breeding waders and, in some species, is responsible for a large proportion of the world population (Delany and Scott, 2002) (Table 1). It has been estimated that 4–5 million breeding adult and juvenile waders leave Iceland in autumn each year (Gudmundsson, 1998). Despite this, studies of breeding waders in Iceland are rare and have been restricted to small, localised areas (Gillandt, 1974; Gunnarsson, 2000; Summers and Nicoll, 2004; but see Gunnarsson et al., 2004, 2005). As a consequence, remarkably little is known about the key habitat requirements of these species.

Landscapes in lowland areas of Iceland have undergone significant changes over the last century, with widespread drainage of wetlands and conversion to agriculture (Oskarsson, 1998; Thorhallsdottir et al., 1998). The native birch forests and wetlands have largely been replaced by heathlands, through deforestation, and by agricultural habitats, grasslands and unvegetated areas through drainage and grazing (Johannesson, 1960). More recently, extensive afforestation has occurred, with plans to plant forest in at least 5% of lowland areas in the next 40 years (Act of Parliament no. 56/1999. http://althingi.is). During the last few decades, livestock numbers in lowland areas have also changed dramatically. Between 1974 and 2001, the numbers of horses in lowland Iceland increased from 44,000 to 74,000 while sheep declined from 860,000 to 470,000 over the same period (The Farmers Association of Iceland. http://bondi.is). These changes are likely to impact on the internationally important populations of breeding waders that Iceland supports, but little is currently known about the patterns of habitat selection of these species, either locally or nationally.

The aim of this study, for eight common Charadriiform species in lowland areas of Iceland, is to assess (1) relative habitat availability, (2) patterns of habitat association and key features of habitat selection, and (3) the potential impact of habitat modification through agriculture, grazing and tree planting.

2. Methods

2.1. Study areas

Lowlands in Iceland are distributed as basins of varying sizes along the coast, often separated by high ground (Fig. 1). We surveyed basins in the six main areas of lowland Iceland, defined according to geographical features: geographically these are located in the north, north-east, east, south, south-west and west.

2.2. Survey structure

The survey was vehicle-based and took place along roads and tracks in the six basins in areas below 200 m a.s. Within these basins, survey points were located every 2 km, or occasionally every 4 km in some larger areas. Locations where it was dangerous to stop (e.g. blind summits or narrow bridges) were not surveyed; in these cases the survey point was moved forward by 1 km. At each survey point, the habitat patch adjacent to the right side of the road was surveyed. Patches were defined as homogenous areas of habitat that were clearly visible from the road; mean estimated patch size was 1.89 ha (±1.4 SD) and was determined by multiplying the estimated length and breadth of patch.

At each stop, the type of habitat was classified into one of nine categories (Table 2) and a suite of habitat and geographical variables were recorded (Table 3). In addition, the presence and identity of all birds either seen or heard within, or displaying over, the patch were recorded from the stationary vehicle. Habitat variables and bird presence were recorded by separate observers, with habitat variables always being recorded first to ensure that they were independent of the

Table 1 – Estimated importance of Iceland for breeding wader populations

Species	Scientific name	World population[a] '000	Iceland population[b] '000	% Of world population in Iceland	% Of Icelandic population below 200 m a.s.[b]
Oystercatcher	*Haematopus ostralegus*	1180	45	4	100
Golden Plover	*Pluvialis apricaria*	1799	930	52	32
Ringed Plover	*Charadrius hiaticula*	476	150	32	33
Whimbrel	*Numenius phaeopus*	1880	750	40	75
Dunlin	*Calidris alpina*	5144	810	16	49
Purple Sandpiper	*Calidris maritima*	195	90	46	19
Snipe	*Gallinago gallinago*	10673	600	6	62
Redshank	*Tringa totanus*	2261	420	19	97
Black-tailed Godwit	*Limosa limosa*	710	71	10	97
Red-necked Phalarope	*Phalaropus lobatus*	2500	150	6	55

For the 10 species that regularly breed in Iceland, the estimated numbers of post-breeding individuals are shown along with the estimated world populations of the species, and the percent in Iceland and in lowland Iceland.
a Delany and Scott (2002).
b Gudmundsson (2002).

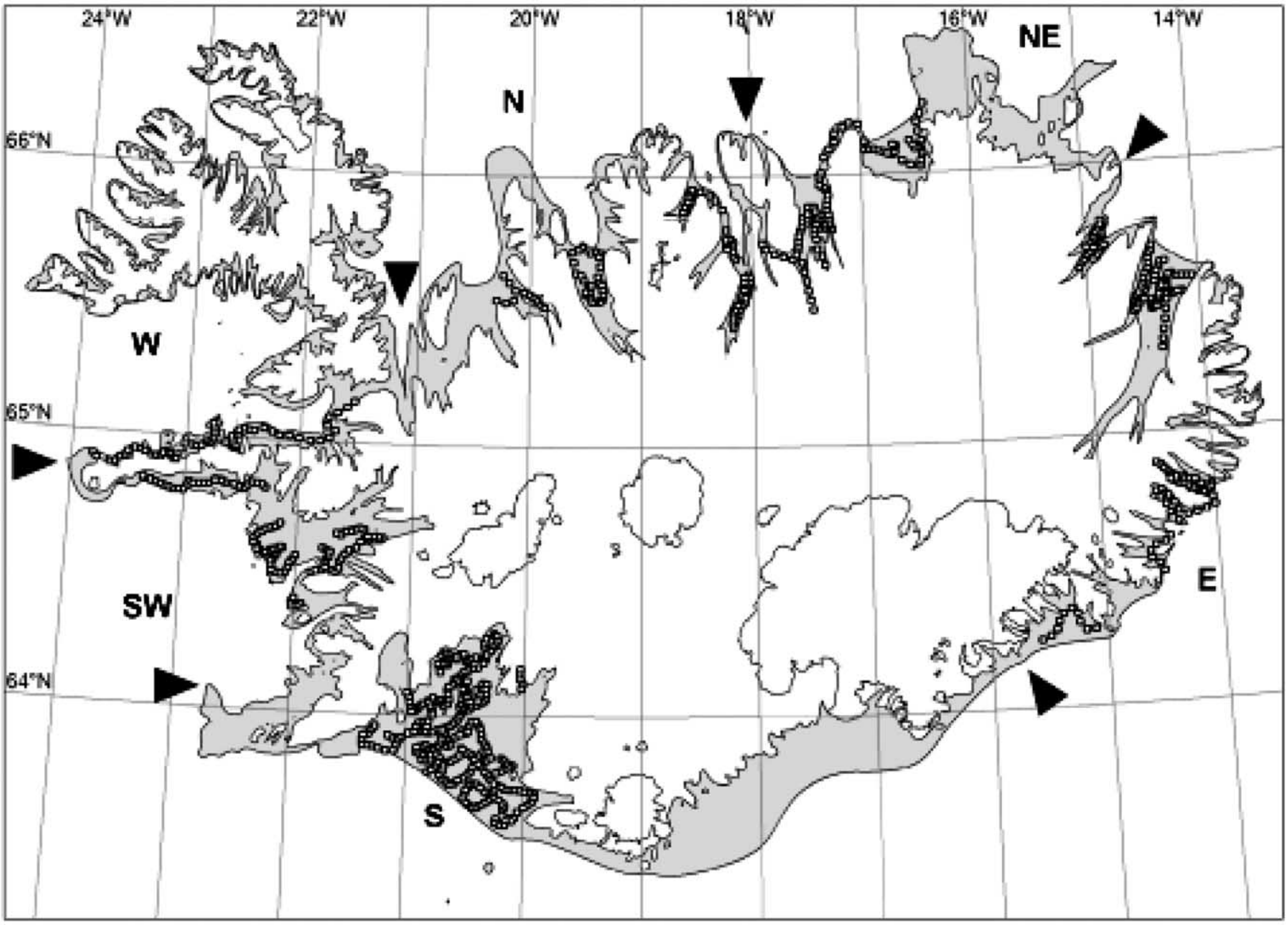

Fig. 1 – Map of Iceland showing the position of the survey points (open circles) and the boundaries of the six geographical areas used in the study (arrows). The 200 m a.s. contour and glaciers are also shown. The large, unsampled area in the south of Iceland is dominated by unvegetated glacial sandplains.

Table 2 – Descriptions and frequency (number of survey points at which they were recorded) of the nine categories of habitat type recorded during the survey of lowland Iceland

Name	Description	Number of points
Agriculture	Mostly (95%) hayfields with 5% crops, potatoes and kale	195
Grassland	Aggregation of habitat types dominated by grasses (often *Deschampsia caespitosa* and/or *Agrostis* spp.), indicating a waterlevel too low for sedges. Varied profile	185
Heath	Heathland, most often rather dry and hummocky elevated land, dominated by small shrubs such as *Calluna vulgaris*, *Empetrum nigrum*, *Vaccinum* spp.; sparse grasses and moss (frequently *Racomitrium* spp.)	152
Marsh	Aggregation of habitat types dominated by sedges (*Carex* spp.) indicating a high waterlevel on an annual basis. Usually rather flat. Saltmarsh (2 points) and floodplains (8 points) included	78
Riverplain	Low lying land adjacent to larger rivers, most often of glacial origin and consisting of patchy sand or gravel. Characterised by the presence of *Juncus arcticus* and *Salix* spp.	58
Dwarf-birch bog	Homogenous marshes dominated and characterised by *Betula nana* often with *Carex rostrata* or *Eriophorum* spp.	37
Unvegetated	Areas with less than 1% vegetation cover. Most commonly sandflats (12 points) and gravel (15). Rare types include scree slopes (1), bare earth (2), lakes (3) and sandy coast (1)	34
Woodland	Natural *Betula pubescens* scrubland (7 points) and patches of planted treas. Often also coniferous trees or *Populus trichocarpa* (7 points)	14
Town	Town or village. Not included in any analyses	5
Total points		758

Table 3 – Definitions of the 16 habitat and geographical variables recorded at survey points around lowland Iceland

Variable	Metric	Definition
Patch size	ha	Calculated from visual estimate of length and breadth
Elevation	m	Metres above sea-level recorded by GPS (Garmin e-trex)
Habitat type		Type of habitat in patch (see Table 2)
Sward height	cm	Visual estimate of sward height in categories: 0–5, 5–10, 10–20, 20–40 and >40 cm
Salix	%	Visual estimate of cover of willows, but excluding *S. herbacea*
Betula	%	Visual estimate of cover of birch. Usually *B. nana* but, in the case of woodland, *B. pubescens*
Juncus	%	Visual estimate of cover of rushes
Bare ground	%	Visual estimate of cover, includes sand, earth, gravel or rocks
Hummock size	cm	Visual estimate of modal size of hummocks in patch in four categories: small (<20), medium (20-40), large (40-60) and very large (>60) (cm)
Hummocks	%	Visual estimate of cover
Ditches	no.	Number of drainage ditches surrounding or intercepting the patch
Water table	cm	Depth of water table below ground level, estimated from water level in ditches
Number of pools	no.	Number of pools in patch
Number of sedgepools	no.	Number of pools in patch surrounded predominantly by sedges (*Carex* spp.) indicating a high waterlevel for prolonged time, in contrast to temporary vernal pools
Pools	%	Visual estimate of cover of pools in patch
Distance to hayfield	m	Visual estimate

species recorded. Surveys took place for 8 days during the last 2 weeks of May in each of 2001–2003. At this time, breeding birds will most often have established territories but no chicks will yet have hatched. Thus the presence of birds is likely to indicate the presence of a breeding territory or a feeding location. GPS readings were taken of all survey points.

2.3. *Habitat classification*

The habitat classification carried out in the field (Table 2) was based on the dominant vegetation type, land use (e.g. agriculture), water-levels and adjacent geographical features (e.g. the presence of a large river for riverplain habitat). This was done *a priori* to avoid grouping of habitats that are obviously biologically distinct, e.g. natural grasslands and hayfields. In order to explore how our habitat classification related to the individual habitat variables recorded in the survey, we ran a principal components analysis of the habitat variables to explore the combination of variables that can be used to define each habitat.

2.4. *Analysis of potential survey bias*

The road-based survey allowed large numbers of points to be surveyed in a short time period. However, the frequency of the nine habitat types is likely be influenced by their proximity to roads (e.g. towns and agriculture are likely to be more common closer to roads). In order to assess how representative this road-based survey was of habitat types in lowland Iceland generally, we used a GIS approach to relate the location of the 758 survey points as recorded by GPS, a digital vegetation map and a digital road map from the Public Roads Administration. The digital road map includes all roads maintained by the Public Roads Administration, but does not include all minor roads and tracks. Only 23 survey points fell outside the roads covered by the digital road map.

The digital vegetation map of Iceland (Gudjonsson and Gislason, 1998) allows seven habitat types to be identified: (a) an aggregation of heath, grassland and cultivated land, (b) wetlands, (c) birch woodland, (d) moss heath, (e) unvegetated land, (f) rivers and (g) lakes. The frequency of these seven habitat types on our 758 survey points was assessed by overlaying these points on the vegetation map (see Burrough and McDonnel, 2000 for overlaying techniques). The frequency of the habitats adjacent to all roads in lowland Iceland was calculated from the proportions of the area of each habitat type within 100 m of either side of every road. Finally, the proportion of each habitat type throughout all areas in Iceland below the 200 m contour was calculated.

2.5. *Habitat selection of individual species*

The analyses of habitat associations are restricted to the eight species of Charadriiform birds that occurred on more than 20 survey points. The habitat selection patterns of each species were explored using the Jacobs (1974) preference index, which relates the proportionate use of each habitat to its proportionate availability, and ranges from maximum preference (+1) to maximum avoidance (−1). Differences in these proportions were examined with G-tests. We use frequency of survey points on which each species was recorded as the measure of species distribution, as the correlation between total estimated area and number of survey points for each habitat type in our survey was extremely high ($r = 0.97$, $P < 0.001$, $n = 8$ habitat types).

In order to explore the patterns of presence and absence of the bird species in relation to the environmental parameters, we used ordination techniques (ter Braak, 1986) within the software programme CANOCO. A canonical correspondence analysis incorporating all eight bird species and 12 of the environmental variables was carried out. Habitat type was excluded from this analysis because the aim was to explore the direct components of the habitats that influenced bird distribution. For clarity in presentation, water-table depth, number of pools and hummock cover were also excluded because of high positive correlations with number of ditches, pool cover and hummock size, respectively.

To explore the components of habitat structure that influenced species distributions, we constructed multiple logistic regression models for the more common species (those that occurred on more than 5% of sampling plots). These models included the habitat variables listed in Table 3, as well as geographic region (Fig. 1), habitat type (Table 2), and a region-habitat type interaction term. As our survey was not designed to produce accurate predictive models of species presence, these models were primarily built to inform which habitat variables might be related to species distributions. However, the probabilities of correct classification of presence or absence are shown. The probability cut-off point used to predict presence or absence was 0.5.

3. Results

We recorded 16 species of Charadriiform birds at 758 sample points. The eight most commonly recorded species were oystercatcher, golden plover, dunlin, snipe, whimbrel, black-tailed godwit, redshank and arctic skua, all of which were recorded on at least 3% of sites. The remaining Charadriiform species recorded were either occasional passage migrants or colonial gull and tern species for which this survey method was not appropriate.

3.1. *Habitat classification*

The principal components (varimax rotation with Kaiser normalisation, SPSS 11.0 for Windows) analysis of habitat structure across all the survey points throughout lowland Iceland identified four factors, which together explained 58% of the variance in the data (Table 4). The mean factor scores for each of the eight habitat types (excluding towns) are shown in Fig. 2. Factor 1 was characterised by high sward heights, high birch cover and a large hummocks. This was most strongly positively associated with dwarf-birch bog (Fig. 2). Factor 2 was characterised by high numbers of pools and sedge pools and showed the greatest correlation with the marsh habitat. Factor 3 described bare ground, with an absence of ditches, away from hayfields and was most strongly correlated with unvegetated land. Factor 4 was characterised by a high cover of *Juncus* and was most correlated with the riverplain habitat. All four factor scores contributed highly significantly to distinguishing between the habitat types (ANOVA; Factor 1: $F_{7,724} = 86.8$, $P < 0.001$, Factor 2: $F_{7,724} = 16.2$, $P < 0.001$, Factor 3: $F_{7,724} = 94.1$, $P < 0.001$, Factor 4: $F_{7,724} = 22.3$, $P < 0.001$). The geographic distribution of the habitat types is shown in Table 5.

Table 4 – Component matrix from a principal components analysis of the variables used to describe habitat structure at survey points around lowland Iceland

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Elevation	0.18	−0.07	−0.10	**−0.61**
Sward height	**0.68**	0.26	−0.19	0.22
% Cover of *Salix*	0.50	−0.01	0.04	0.35
% Cover of *Betula*	**0.78**	−0.02	0.14	−0.13
% Cover of *Juncus*	0.11	0.00	0.01	**0.76**
% Cover bare ground	−0.32	−0.11	**0.76**	−0.06
Hummock size	**0.66**	−0.01	0.00	−0.28
Number of ditches	−0.12	−0.10	**−0.65**	−0.15
Distance to hayfield	0.47	0.11	**0.59**	0.03
Number of pools	0.05	**0.87**	0.03	0.05
Number of sedgepools	−0.02	**0.82**	−0.03	−0.06
% Cover of pools	0.10	**0.69**	0.08	0.13
% Variance explained	**21**	**15**	**12**	**10**

The loading of each habitat variable on each factor is shown and all loadings >0.5 and <0.5 are shown in bold.

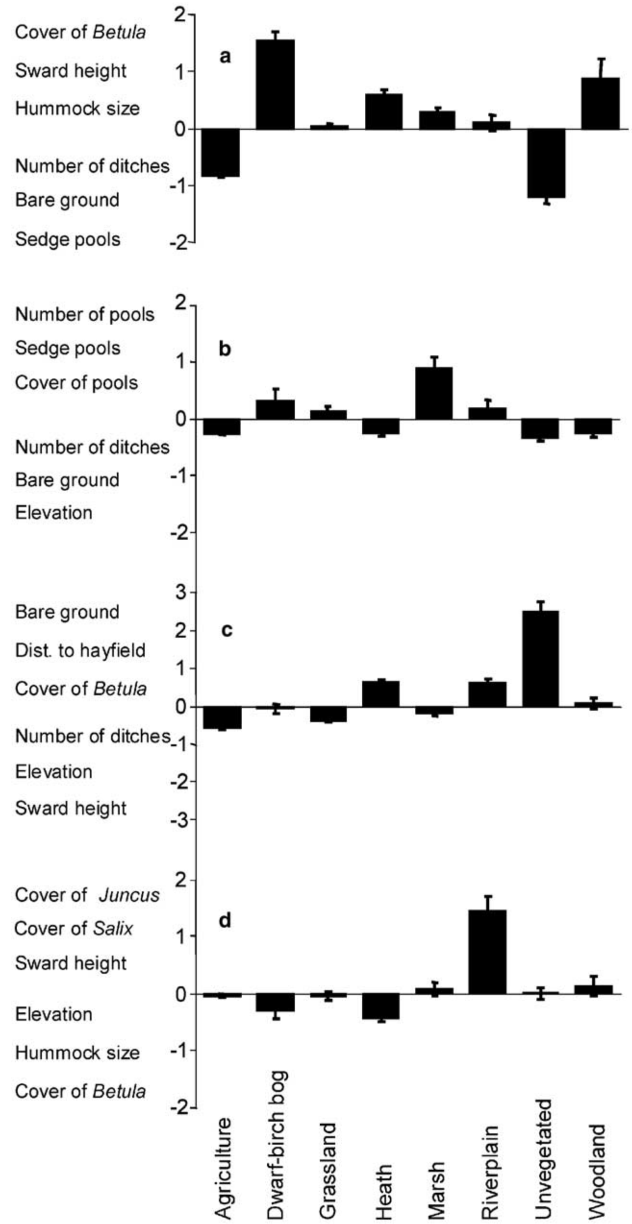

Fig. 2 – Mean (± SE) factor scores of the four factors (a–d) from a principal components analysis of the habitat variables recorded across all survey points (Table 4), for each of the eight habitat types recorded during the survey (Table 2). The three habitat variables that gave the most positive and most negative loadings are shown for each factor.

Table 5 – Percentage occurrence of eight habitat types recorded at 758 survey points in different regions of lowland Iceland

	Agriculture	Dwarf-birch bog	Grassland	Heath	Marsh	Riverplain	Unvegetated land	Woodland
East Iceland	17.2	**11.0**	16.6	33.1	4.1	**13.1**	3.4	1.4
West Iceland	10.0	0.0	**22.0**	**34.0**	**22.0**	2.0	**8.0**	2.0
Southwest Iceland	24.0	1.0	16.7	8.3	**38.5**	0.0	**10.4**	1.0
Northeast Iceland	13.6	**9.9**	12.3	**49.4**	1.2	9.9	3.7	0.0
North Iceland	**48.9**	1.1	14.9	11.7	12.8	2.1	4.3	**4.3**
South Iceland	**29.6**	3.8	**38.3**	9.8	3.8	**9.8**	2.8	**2.1**
Total occurrence	25.9	4.9	24.6	20.2	10.4	7.7	4.5	1.9

The location of the regions is indicated on Fig. 1. The two areas in which a given habitat type was most common are shown in bold.

3.2. *Habitat composition in the survey and in lowland Iceland*

The frequency of habitats recorded in the sample of roads covered in this survey was generally very similar to those adjacent to all roads in Iceland and in all areas under 200 m a.s. in Iceland (Pearson correlations; this survey vs. all roads: $r = 0.99$, $n = 7$, $P < 0.001$, this survey vs. all habitat below 200 m a.s.: $r = 0.97$, $n = 7$, $P < 0.001$, Fig. 3). The main differences were that wetlands (which comprise mainly the marsh and dwarf-birch bog habitats) were less common in general than this survey suggested. Of the rarer habitat types, our survey recorded moss heath and unvegetated land less frequently than is generally present in lowland Iceland.

3.3. *Overall distribution of species and environmental parameters*

The canonical correspondence analysis highlighted the importance of several key habitat components for different species (Fig. 4, Table 6). The ordination plot (Fig. 4) illustrates the importance of features such as high densities of sedge pools, tall swards and high cover of willow, dwarf-birch and hummocks for species such as black-tailed godwit, snipe and dunlin. Similarly, oystercatchers are strongly associated with areas with a high cover of bare ground while arctic skuas and whimbrels are associated with areas at low elevations and a high cover of *Juncus arcticus*, which is a species highly indicative of riverplains. The habitat associations of golden plover and redshank were far less clear, reflecting the more generalist nature of these two species.

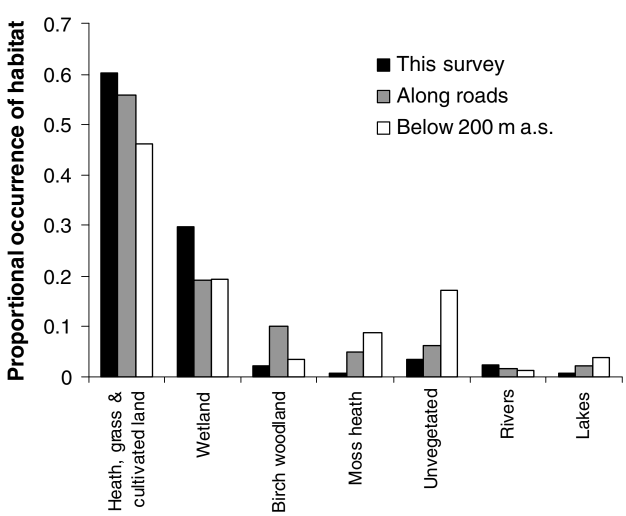

Fig. 3 – A comparison of proportional frequency of habitat types recorded during this survey, along roads in lowland areas of Iceland, and throughout lowland Iceland (all areas under 200 m.a.s.). The habitat types shown are extracted from a digital vegetation map; details of how these relate to the habitat types recorded during the survey are described in the text.

3.4. *Predictors of species distribution*

3.4.1. *Oystercatcher Haematopus ostralegus*

Oystercatchers were found on 4.7% of the sampling points. They occurred most often in S Iceland and were not recorded in N and NE Iceland (Table 7). They significantly avoided heath but showed no significant preference for any habitats (Fig. 5). The ordination, however, suggested a strong positive relationship with amount of bare ground.

3.4.2. *Golden Plover Pluvialis apricaria*

Golden Plovers were found on 20% of the sampling plots. They were very common in all parts of the country but most common in NE Iceland (Table 7). They significantly avoided riverplains and woodland but showed no significant habitat preferences (Fig. 5). Habitat type and patch size significantly influenced the presence of golden plovers (Table 8).

3.4.3. *Dunlin Calidris alpina*

Dunlin were found on 4.7% of the sampling plots. They were most common in S and W Iceland but were not located at all in the NW (Table 7). They showed a highly significant preference for marshes (Fig. 5).

3.4.4. *Snipe Gallinago gallinago*

Snipe were found on 28% of the sampling plots. They were common in all parts of the country but most common in NE Iceland and least common in E Iceland (Table 7). They significantly preferred marsh and woodland and avoided unvegetated land (Fig. 5). Their presence was influenced by region, and was more likely in larger patches, with high birch cover, medium and large sizes of hummocks, high number of ditches and high cover of pools (Table 8).

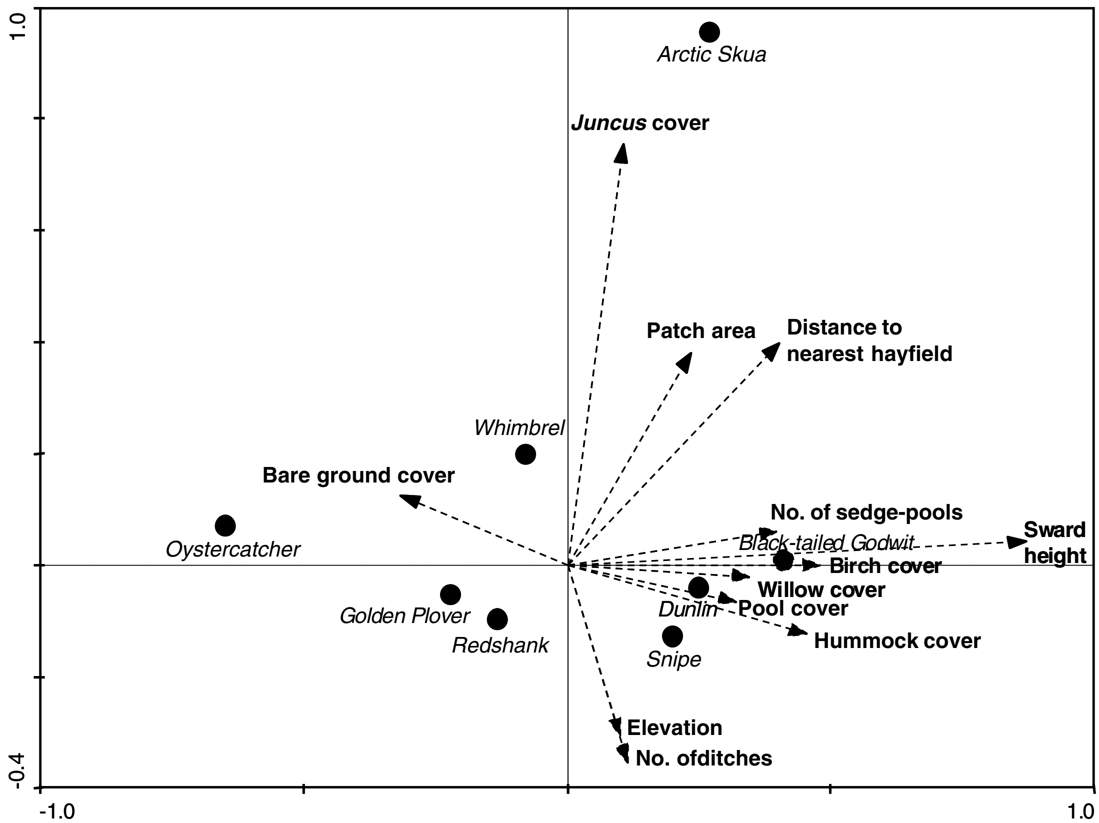

Fig. 4 – Ordination plot from a canonical correspondence analysis of the distribution of eight bird species in relation to 12 environmental variables (see Table 3 for details). The biplot of axes 1 and 2 is presented; the orientation of each environmental variable in relation to each of these axes is represented by an arrow, the length of which indicates the degree of correlation with those axes.

3.4.5. *Whimbrel Numenius phaeopus*

Whimbrels were found on 17% of the sampling plots. They were common in most parts of the country but by far the most common in S Iceland, where 27% of the sightings occurred (Table 7). They showed a highly significant preference for riverplain and avoidance of agriculture (Fig. 5). Whimbrel presence was more likely in larger patches, with high cover of *Juncus* and sedge pools, and varied between regions (Table 8).

3.4.6. *Black-tailed godwit Limosa limosa*

Black-tailed godwits were found on 9% of the sampling plots. They were most common in S Iceland, N Iceland and NE Iceland but were relatively scarce in other parts (Table 7). They significantly preferred both marsh and dwarf-birch bog and avoided heath and unvegetated land (Fig. 5). Godwit presence was more likely in larger patches, at higher elevations and in areas with high cover of sedge pools (Table 8).

3.4.7. *Redshank Tringa totanus*

Redshanks were found on 14% of the sampling plots. They were most common in S Iceland and least common in W and E Iceland (Table 7). They significantly avoided heath and agriculture (Fig. 5), and their presence was more likely in patches with 10–20 cm sward height, small and medium hummocks, large numbers of sedge-pools, low watertables and low cover of hummocks (Table 8).

3.4.8. *Arctic Skua Stercorarius parasiticus*

Arctic Skuas were found on 3% of the sampling plots. They were most common in W and E Iceland but were not located in the NW (Table 7). They significantly preferred riverplains and avoided agricultural habitats (Fig. 5).

4. Discussion

In this study we have, for the first time, described important aspects of the large-scale habitat selection and distribution patterns of Charadriiform birds in lowland Iceland. Five of the eight species analysed showed significant preferences for lowland wetland habitats (marshes, dwarf-birch bogs and riverplains), and four of the five species included in logisitic regression analyses were significantly more likely to occur in areas containing wet features such as pools and high water tables. There is therefore strong evidence that wetland habitats are of major importance for breeding birds in Iceland. Areas classified as wetland habitats account for 23% of the area surveyed and 20% of all lowland areas in Iceland, but most have undergone significant drainage and degradation in recent decades.

The most common habitats in lowland Iceland are heaths and the grassland and agriculture habitats, which together comprised about 70% of all survey points. None of these habitats were significantly preferred by any species, although

Table 6 – Results of a canonical correspondence analysis of the presence of eight breeding bird species in relation to 12 environmental variables at 758 sites around lowland Iceland (see Table 3 for details of environmental variables)

Axes	1	2	3	4
Eigenvalue	0.11	0.07	0.06	0.02
Species-environment correlations	0.45	0.34	0.35	0.23
Cumulative % variance of species data	3.2	5.1	6.7	7.2
Cumulative % variance of species-environment data	39.9	64	84.8	91.7
Correlation coefficients				
Elevation	0.10**	−0.31***		
Patch size	0.24***	0.38***		
Sward height	0.87***			
% *Salix* cover	0.35***			
% *Betula* cover	0.48***			
% *Juncus* cover	0.11**	0.75***		
% Bare ground cover	−0.32**	0.12**		
Hummock size	0.46***	0.13**		
Number of ditches	0.12**	−0.36***		
Distance to hayfields	0.40***	0.40***		
Number of pools	0.40***			
Number of sedgepools	0.32***			

The correlation coefficients for those variables significantly correlated with axes 1 and 2 are shown.
** $P < 0.01$.
*** $P < 0.001$.

birds were recorded on 65% of agricultural survey points, 61% of heath points and 77% of grassland points. Thus, despite the lack of statistically significant preference for these habitats, their widespread availability and use suggests that they could be important for several species. For example, in this survey, 16% of all points with golden plover and 17% of all points with snipe were on heathland. Heathland habitats are extremely abundant in both lowland areas and at higher latitudes in Iceland (Gudjonsson and Gislason, 1998) and are thus likely to support very high proportions of several populations. Similarly, 28% of all points with golden plover were on agricultural land, although golden plover was by far the most common species on agricultural habitats. Thus, although this survey identifies wetlands as key habitats for many species, several other habitats also support substantial numbers of birds

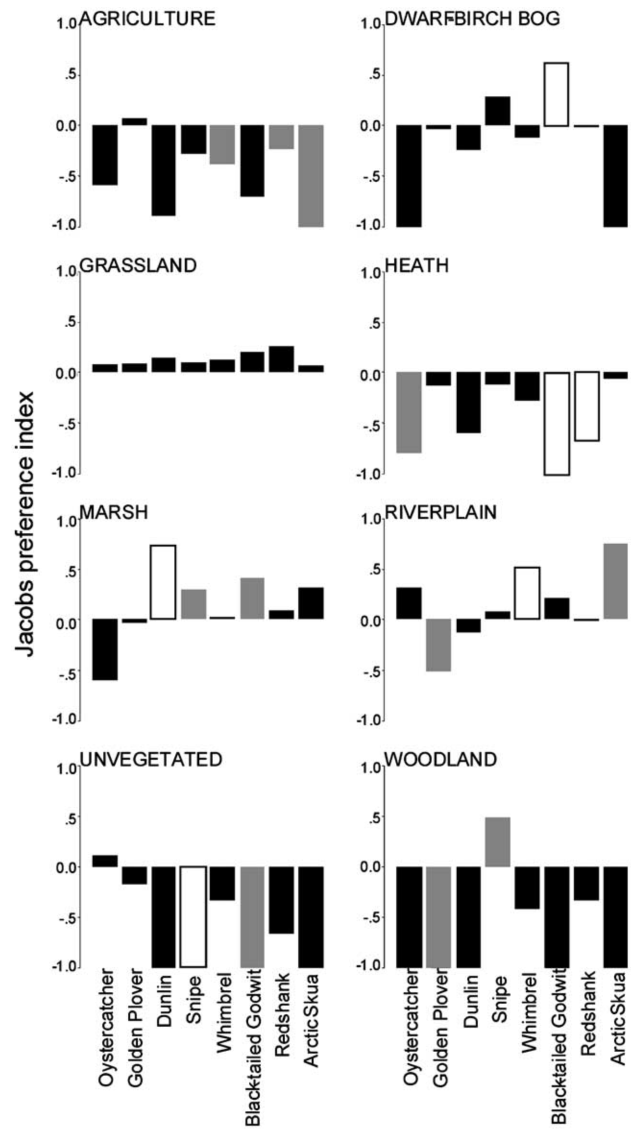

Fig. 5 – Indices of habitat preference (Jacobs (1974) preference index) for the eight species of breeding birds recorded during the survey. Significance values are obtained by G-tests. Closed bars indicate non-significant values, grey bars indicate significance at $P < 0.05$ and open bars at the Bonferroni-adjusted $P < 0.0006$.

Table 7 – Percentage occurrence of species at survey points in different regions (see Fig. 1) of Iceland

Area	Total points	Oystercatcher	Golden Plover	Dunlin	Snipe	Whimbrel	Black-tailed Godwit	Redshank	Arctic Skua
South Iceland	290	**10.3**	18.6	**6.2**	**31.4**	**27.2**	**12.4**	**19.0**	2.4
Southwest Iceland	51	**3.1**	16.5	**9.3**	28.9	9.3	2.1	11.3	**5.2**
West Iceland	97	1.9	**21.6**	0.0	21.6	1.9	0.0	7.8	0.0
North Iceland	81	0.0	21.3	3.2	24.5	6.4	**14.9**	**14.9**	1.1
Northeast Iceland	94	0.0	**27.2**	1.2	**39.5**	11.1	12.3	13.6	2.5
East Iceland	145	1.4	21.4	1.4	18.6	**17.2**	5.5	7.6	**4.8**
Total	758	4.7	20.3	4.4	28.0	17.0	9.2	14.0	2.9

The two areas where a species was most common are shown in bold.

Table 8 – Results of a multiple logistic regression analysis of the environmental variables influencing presence of those species that occurred on more than 5% of survey points

Environmental variable	Species				
	Golden plover	Snipe	Whimbrel	Black-tailed Godwit	Redshank
Region		**	***		
Habitat	*				
Elevation				$+1.01^{***}$	
Patch size	$+1.3^{**}$	$+1.3^{***}$	$+1.2^{**}$	$+1.44^{***}$	
Sward height					*
% Cover of *Betula*		$+1.01^{**}$			
% Cover of *Juncus*			$+1.03^{**}$		
Hummock size		**			**
% Cover of hummocks					-0.98^{*}
Number of ditches		$+ 1.23^{*}$			
Water table in ditches					-0.99^{*}
Number of pools					
% Cover of pools		$+ 1.06^{***}$			
Number of sedgepools			$+ 1.90^{**}$	$+ 11.75^{***}$	$+ 2.28^{*}$
Overall model χ^2_1	31.4_8^{***}	86.5_{12}^{**}	77.5_8^{***}	114.2_3^{***}	31.1_{10}^{***}
% Correct presence	0.6	22.2	7.8	24.3	13.1
% Correct absence	99.8	95.1	98.4	98.9	98.0
% Correct overall	79.3	74.3	82.8	91.3	81.6

Only the variables that significantly influenced a species presence are shown. Signs (indicating the direction of association between predictor variables and species presence), odds ratios and significance levels ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$) are given for continuous variables. For categorial variables, overall significance levels are given and the shape of the association is reported in the text. Regions are shown in Table 5 and habitats in Fig. 3. Note that for water tables, negative values indicate a higher water table. The percent correct classification (at the 0.5 cutoff point) for presence, absence and overall are also shown for each species.

during the breeding season, either as nesting or feeding locations. By contrast, wooded areas were generally very small and patchily distributed, and only snipe showed any preference for this habitat.

Both the canonical ordination (Fig. 4) and the comparison of proportional habitat selection and habitat availability (Fig. 5) produced quite robust predictions of the habitat types selected by most species. The logistic regression models all predicted species absences well but had a poor capacity to predict species presence. Thus, the statistical significance of the models was largely a function of the capacity to predict absences. Large-scale surveys of this type for which sampling points are not stratified (e.g. restricted to habitats in which the species has been previously recorded) are always likely to suffer from over-representation of sites where a species is absent, particularly when species are not particularly abundant or widespread. However, the models were able to predict the presence of two species (black-tailed godwit and snipe) with approximately 25% accuracy. As these are generally the two most hydrophilic species in the study (Cramp and Simmons, 1983), it is likely that our ability to predict their presence is related to their restriction to wet habitats.

Where the logistic regression models are particularly useful is in the information that they provide about the relative importance of different habitat variables for individual species. In particular, the habitat variables that were important for most species were also those that, in many cases, best defined the eight habitat types, suggesting that despite the necessarily large-scale nature of this survey, the most biologically relevant variables for individual species were identified by the approach. More detailed studies of habitat selection of individual species within the key habitats identified by this survey would hopefully improve the capacity of the models to predict species presence (see Milsom et al., 2000). The CANOCO ordination of habitats and species generally supported both the preference index analysis and the logistic regression models in identifying the key habitat features for each species.

The large spatial scale of this study will inevitably influence the patterns that are revealed. For example, the preference of snipe, a very hydrophilic species, for areas with high numbers of ditches may seem surprising. This could either be because ditches are used as feeding areas or because, at these scales, the presence of ditches is likely to indicate areas with relatively high watertables. This survey thus provides important information about country-wide patterns of habitat selection of these species, but will be less effective at identifying the fine-scale details of habitat preferences.

4.1. *Conservation implications*

The lowland regions of Iceland have undergone significant changes in recent decades, with extensive drainage and conversion of wetlands to agricultural land. Previous studies have shown that, since the mid 20th century, over 90% of wetlands (which include marsh and dwarf-birch bog habitats) in south and west Iceland have been drained to some extent (Oskarsson, 1998; Thorhallsdottir et al., 1998). Our study demonstrates the conservation status of these wetlands as a key habitat type for breeding birds. Only recently have efforts to restore wetlands begun on a small scale in Iceland (Magnússon, 1998).

Riverplains are also an important and relatively scarce habitat type for breeding birds in Iceland, extending to 7.7%

of the lowlands. They are most extensive on the banks of large glacial rivers although they occur as narrower stretches along minor rivers throughout the country. The breeding success of whimbrels in Iceland is higher on riverplains than on heathland, possibly as a result of the significantly higher invertebrate densities and different vegetation structures on riverplains (Gunnarsson, 2000). Invertebrate densities are likely to be influenced by the seasonal flooding of these areas by adjacent rivers, which also interrupts vegetation succession, keeping the vegetation profile and composition favourable for open-habitat species. The main source of power in Iceland is hydroelectric powerplants, which require damming of large rivers and manipulation of water levels. Such regulation is likely to affect the seasonal flood regime and the morphological diversity of the catchments (Fruget, 1992; Nilsson and Dynesius, 1994). This can potentially interfere with the process of vegetation succession within riverplains and alter their attractiveness to birds (Nilsson and Dynesius, 1994; Merritt and Cooper, 2000).

Much of lowland Iceland has been converted to agriculture and remaining areas are increasingly being afforested, often with non-native species. The results of this study strongly suggest that the majority of species in this survey avoid woodland and preferentially select open areas. Afforestation has been identified as one of the main threats to populations of waders and many other bird species in the highlands of Scotland (Stroud et al., 1987; Thompson et al., 1988; Reid, 1993), principally through the loss of breeding and feeding places for open habitat species (Thompson et al., 1988). Our findings suggest that minimising afforestation on marshland, riverplains and dwarf-birch bogs is likely to help reduce the impact on breeding birds. Similarly, many bird species that nest in open habitats often avoid slopes and hillsides (Whittingham et al., 2002); planting preferentially on these sites may therefore also be beneficial.

During the last few decades, numbers of sheep and horses in Iceland have changed dramatically, with large decreases in sheep numbers and increases in horse numbers. Grazing commonly occurs on heathlands, marshes and grasslands, and occasionally on hayfields. The selectivity in grazing by these species (Ausden, 2004) results in different effects on vegetation composition and structure (Hongo and Akimoto, 2003), which are important predictors of bird distribution here and in other studies (Brown and Stillman, 1993; Stillman and Brown, 1994; Milsom et al., 2000; Perkins et al., 2000). Although the extent of the changes in grazing patterns and their effects on bird populations are poorly understood, the extensive nature of livestock grazing in lowland Iceland suggests that the influence on bird populations could be considerable.

There is currently no monitoring of breeding wader populations in Iceland so it is difficult to relate any population changes to the potentially important habitat changes discussed above. One exception to this is the Icelandic black-tailed godwit population, which is almost entirely restricted to Iceland in the breeding season and to western Europe in the winter. Approximately half of this population winters in Britain and Ireland and counts of this species undertaken as part of the Wetland Bird Survey have shown that it has rapidly increased in recent decades (Musgrove et al., 2001; Gill et al., 2001; Gunnarsson et al., 2005b). Anectodal evidence suggests that Icelandic breeding populations of oystercatcher and redshank have been also been increasing, while the dunlin population is decreasing (Petersen, 1999). Whether any of these population changes reflect changes in habitat quality or composition is currently unknown but given the tremendous importance of Iceland for breeding birds, there is an urgent need to assess how current and future habitat changes are likely to influence these species. In addition, arctic and sub-arctic habitats are currently the subject of great concern over the likely impact of climate change on these fragile habitats (Norris et al., 2004; Watkinson et al., 2004). Understanding how these habitats are used by breeding birds is a key first step in predicting species' responses to climate-induced habitat changes.

In this study, we have identified large-scale patterns in distribution and habitat selection of several bird populations in lowland Iceland that will hopefully serve as a basis for assessing the potential impacts of future habitat changes. We have also identified and discussed potential threats to habitats and bird populations, and identified the great need for improved monitoring of the wader populations in Iceland. Such a scheme would ideally include measures of breeding distributions and population levels but also of annual variation in breeding output, as waders are generally long lived and changes in adult populations are thus likely to be slow. Iceland, with its low human population density and extensive open habitats, is of unique importance for breeding waders in the northern hemisphere and an area of global importance for several populations. The information presented here can potentially allow efforts to be focused on habitats that are both threatened and highly important for key species.

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