UNIVERSITY OF ICELAND

PhD thesis
in Biology

Effects of land conversion in sub-arctic landscapes on densities of ground-nesting birds

Aldís Erna Pálsdóttir

Supervisors: Dr. Tómas G. Gunnarsson, Professor Jennifer A. Gill, Dr. José A. Alves & Professor Snæbjörn Pálsson

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FACULTY OF LIFE AND ENVIRONMENTAL SCIENCES

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This thesis satisfies 180 credits towards a PhD
in biology in the Faculty of Life and Environmental Sciences,
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Abstract

Biodiversity is declining globally, primarily driven by anthropogenic changes and alterations of natural habitats. In lowland Iceland, human impact has increased considerably in the past decades, often involving an increase in numbers of anthropogenic structures. The consequences of these land use changes for the important wildlife that these areas support is poorly known. The aim of this thesis was to study if and how four types of newly introduced structures/habitats (roads, summer houses, power lines and plantation forests) in the Icelandic lowlands affect the density and species composition of ground-nesting birds in the surrounding area. Surveys of bird abundance and distribution were undertaken throughout lowland areas of Iceland that varied in the number and extent of anthropogenic structures. Two species (Redwing and Snipe) were found in higher densities or showed no change with distance from the structures, while seven species (Meadow pipit, Black-tailed Godwit, Golden Plover, Dunlin, Oystercatcher, Whimbrel and Redshank) occurred in significantly lower densities close to at least one of these anthropogenic structures and, for roads and forests, these reduced densities occurred over distances up to 200 m. Reduced abundance close to structures was strongest for Golden Plover and Whimbrel, for which between 40-52% of the global populations currently breed in Iceland. The effects of land conversion of large areas of open habitats with roads, forest plantations, houses and power lines could potentially affect populations of these species. Point counts which have been carried out in the southern lowlands since 2011, in an area where anthropogenic influences are constantly expanding, have shown that while the local population of Redwing is increasing and Snipe numbers are stable, the remaining study species are decreasing. Planning of future infrastructure locations and configurations should be designed to reduce impacts on the ground-nesting bird populations for which Iceland has international obligations, and protecting the remaining large tracts of open habitat is likely to be a priority.

Útdráttur

Líffræðilegum fjölbreytileika fer hnignandi á heimsvísu, og megin ástæður þessa eru aukin umsvif manna og breytingar á landnotkun. Á láglendi Íslands hafa umsvif manna aukist töluvert undanfarna áratugi, en því fylgir aukinn fjöldi nývirkja. Lítið er vitað um áhrif þessara breytinga á þá mikilvægu líffræðilegu fjölbreytni sem þessi landsvæði búa yfir. Markmið þessarar rannsóknar var að kanna hvort og hvernig fjórar gerðir nývirkja (vegir, sumarhús, raflínur og ræktaðir skógar) hefðu áhrif á þéttleika og tegundasamsetningu mófugla í nánasta umhverfi. Svæði voru valin á láglendi Íslands þar sem þessar gerðir nývirkja voru til staðar í mismunandi fjölda og stærð, og fuglar taldir. Tvær tegundir (skógarþröstur og hrossagaukur) fundust ávallt í hærri þéttleika nálægt nývirkjum eða sýndu engan mun með fjarlægð frá nývirki, en sex tegundir (þúfutittlingur, jaðrakan, heiðlóa, lóuþræll, tjaldur, spói og stelkur) fundust í lægri þéttleika nálægt a.m.k. einni gerð nývirkja. Í kringum vegi og skóga náðu þessi áhrif 200 m út fyrir jaðar nývirkisins. Heiðlóa og spói sýndu sterkustu áhrifin, en milli 40-52% af heimsstofnum þessara tegunda verpa á Íslandi. Áhrif breytinga á landnotkun á láglendi Íslands sem hljótast af því að nytjaskógar, raflínur, vegir og hús eru sett í opin búsvæði geta haft afgerandi áhrif á stofna þessara tegunda. Fuglar hafa verið taldir á sömu punktum á hverju ári síðan 2011 á Suðurlandi, þar sem miklar breytingar hafa orðið á landnoktun, og niðurstöðurnar benda til þess að meðan skógarþresti fjölgar og hrossagaukur sýnir engar breytingar, fari öllum hinum tegundunum sem voru hér til rannsóknar fækkandi. Staðsetning og umfang nývirkja á láglendi Íslands þarf að skipuleggja með það í huga að lágmarka þessi áhrif á mófugla, en Ísland ber alþjóðlega ábyrgð á mörgum þessara tegunda og ætti verndun þeirra stóru opnu búsvæða sem eru enn til staðar að vera í forgangi.

Dedication

This thesis is dedicated to my children, Sigrún Elfa and Páll Fannar, but without them I probably would have finished this a lot sooner.

List of publications

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

Paper I: Pálsdóttir, A. E., Gill, J. A., Alves, J. A., Pálsson, S., Méndez, V., Ewing, H., & Gunnarsson, T. G. Subarctic afforestation: effects of forest plantations on ground-nesting birds in lowland Iceland. J Appl Ecol. Accepted Author Manuscript. https://doi.org/10.1111/1365-2664.14238

Paper II: Pálsdóttir, A. E., Gill, J. A., Pálsson, S., Alves, J. A., Méndez, V., Þórisson, B. & Gunnarsson, T. G. Effects of overhead power-lines on the density of ground-nesting birds in open sub-arctic habitats. Ibis. https://doi.org/10.1111/ibi.13089

Paper III: Pálsdóttir, A. E., Alves, J. A., Gill, J. A., Pálsson, S., Méndez, V. & Gunnarsson, T. G. Fragmentation of semi-natural habitats with summer houses: effects on ground-nesting birds. *Manuscript.*

Paper IV: Pálsdóttir, A. E., Gill, J. A., Alves, J. A., Pálsson, S., Méndez, V., Þórisson, B. & Gunnarsson, T. G. Effects of moderate to low-traffic roads on density of ground-nesting birds in subarctic habitats. *Manuscript.*

Author’s contribution

Paper I: Aldís Erna Pálsdóttir collected and analysed the majority of the data, lead the writing of the paper in collaboration with co-authors and is the corresponding author.

Paper II: Aldís Erna Pálsdóttir collected and analysed the data, lead the writing of the paper in collaboration with co-authors and is the corresponding author.

Paper III: Aldís Erna Pálsdóttir collected and analysed the data, designed the methods in collaboration, and is the corresponding author.

Paper IV: Aldís Erna Pálsdóttir collected the bird data in collaboration with Böðvar Þórisson and Tómas Grétar Gunnarsson. Aldís analysed the data and was lead in writing the manuscript.

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I would also like to thank my amazing supervisor and role model Jennifer Gill. She is the John Lennon to my Ringo Starr. For the past years I have collected data, made some basic model analyses, and written some non-exceptional words about it before sending it to Jenny. With the simple addition of a few words here and there, she somehow manages to apply an element of magic to scientific text, producing unique never before heard phrases, making statistics sound like poetry, data collection as a journey through Middle earth and mind blowing results chapters. To continue the Beatles analogy, when I send her my draft to Octopus's garden, she will in less than a day turn it in to the Abbey Road album. I am ever grateful to be able to work with her and can only hope that one day I will have half of the talent that she has.

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A PhD is a strenuous task to take on, and involves many working weekends and nights, along with general absentmindedness for a few years of your life. There is no way I would have had the time, will or strength to finish this task if it had not been for my family and friends. To my husband Hilmar, I would like to thank for putting up with me in this time, and with his calmness and rational thinking helping me stay relatively mentally stable and focused on the task at hand. I would also like to thank my parents Páll Ólafsson and Elínborg Guðmundsdóttir for all the philosophical and mathematical discussions, and helping me see things in a wider context, and always being ready to listen and give (sometimes unwanted but always great) advice.

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1 Introduction

1.1 Human expansion

Human populations are rapidly increasing across the world and according to UN projections, the global human population is expected to peak at around 10.9 billion at the end of the century (Roser, 2013). This increase has been accompanied by the expansion of anthropogenic structures and other human altered landscapes in previously natural habitats. This has resulted in loss and degradation of natural habitats which is considered to be one of the major causes of global biodiversity decline (Koellner & Scholz, 2008; Sala *et al.*, 2000), and currently the earth's biota is entering its sixth mass-extinction (Ceballos *et al.*, 2015). When anthropogenic structures are introduced into natural or semi-natural areas, the amount of previous habitat declines and multiple secondary factors may accompany this process which can further alter the structure and quality of the remaining habitat. In order to manage and mitigate the effects that an ever increasing number of anthropogenic structures have on biodiversity, the primary objective should be to identify if and how these structures affect abundances and species composition when placed in natural or semi-natural areas, and the processes through which they occur. Identifying these factors will allow for effective planning, both on a local and global scale, and the protection of important areas.

1.2 Effects of novel structures on wildlife

When novel structures are introduced into natural or semi-natural habitats, the abundance and species composition of wildlife can be impacted in the area where the structure is placed and in the surrounding landscapes (Jameson & Willis, 2014). The drivers behind these effects can range from small alterations in conditions, such as changes to microclimate, vegetation and pathogen-host interactions, to large-scale changes, such as changes in predation pressure, resource abundance, collision risk and human disturbance (Chace & Walsh, 2006; Ewers & Didham, 2006; McKinney, 2008; Murcia, 1995; Prugh *et al.*, 2009). Proximity to structures could affect key demographic rates such as survival, productivity and recruitment (e.g. through increased collision and predation risk) of local populations (Howe *et al.*, 2014;

What are structures?

Here the effects of novel structures in open habitats on densities of ground-nesting birds are studied. Examples of such structures are houses, trees, power lines, roads and wind farms. When novel structures are introduced into open natural or semi-natural habitats, they can change the density and/or species composition where the structure is placed, and also affect wildlife in the surrounding habitats. Structures can change the vegetation, resource abundance and/or species composition (and thereby predation and infection rates) in the surrounding habitats. The distribution of animals may then shift as a result of changes in demographic factors, or due to individuals perceiving an altered habitat and shifting distribution by avoiding or being attracted to the structures.

Lepczyk *et al.*, 2004; Loss *et al.*, 2015; Prugh *et al.*, 2009). Ultimately, these effects could induce changes in population density surrounding the edges of the structures, particularly if natal philopatry and breeding site-fidelity are strong (Balkiz *et al.*, 2010; Thompson & Hale, 1989; Waser & Jones, 1983). Even though the habitat or species composition does not change in the surrounding habitat, animals may perceive that it has changed and thereby alter their behaviour by avoiding or being attracted to the structures (Jameson & Willis, 2014; Larsen & Madsen, 2000; Łopucki *et al.*, 2017). Additionally, anthropogenic structures are often accompanied by an increase in human presence, which may further affect the spatial and temporal distribution of animals (Barrueto *et al.*, 2014; Ditchkoff *et al.*, 2006).

The introduction of anthropogenic structures and/or habitats could have species-specific effects, possibly benefitting some species while being detrimental to others (Chace & Walsh, 2006; Croci *et al.*, 2008; Ludlow *et al.*, 2015; Morelli *et al.*, 2014). How structures affect individuals within populations could depend on factors such as the previous and altered habitat type and composition (Jóhannesdóttir *et al.*, 2019), the life history traits of the affected species (Croci *et al.*, 2008), and the size and characteristics of the structure. With increased urbanisation and changes in land-use to facilitate resource production (e.g. agricultural fields and plantation forests), natural habitat heterogeneity will be reduced, and specialist species may be impacted more than generalist species (Clavel *et al.*, 2011; Devictor *et al.*, 2007).

1.3 Effect of structures on breeding birds

Overall, species richness and biodiversity tend to be reduced in more urbanized areas (Koellner & Scholz, 2008; McKinney, 2008). Open-habitat bird species have been considered one of the groups most vulnerable to increased anthropogenic influence and studies have shown that when natural or semi-natural areas are transformed into urban habitats, the abundance and species composition of these birds can change drastically (Koellner & Scholz, 2008; McKinney, 2008; Torres *et al.*, 2016). However, urban areas may benefit species that are able to use anthropogenic resources such as cavity breeders which can nest in building and trees, and have been shown to increase in numbers with increased urbanization (Wang *et al.*, 2015). Other anthropogenic structures may also be beneficial to breeding birds, e.g. studies have shown that up to 25% of the Portuguese White stork (*Ciconia ciconia*) population currently nest on electricity pylons (Moreira *et al.*, 2017). Man-made structures can thus sometimes provide suitable nesting sites for birds, which could potentially enhance the nest success and reproduction rate of these populations, but they could also act as ecological traps by providing nesting opportunities in otherwise sub-optimal areas (Mainwaring, 2015). Apart from nesting, tall structures can also be utilized for roosting by passerines or for perching by predator species (D'Amico *et al.*, 2018; DeGregorio *et al.*, 2014). The influence of novel structures may also vary depending on species' life history traits, for example the introduction of pylons may provide perches for predators, which could alter predation risk for their prey species.

Many studies have been performed on the effects of anthropogenic structures on ground-nesting birds in the surrounding areas (e.g. Pearce-Higgins *et al.* (2009), van der Vliet *et al.* (2010), Silva *et al.* (2010)). Initially when novel structures are introduced into natural or semi-natural habitats, some part of the habitat which could have potentially been used for nesting is lost. Although this effect may be negligible when the area of the structure is small, the effect may become considerable on local populations as the number and size of structures increases. In addition to habitat loss, placing anthropogenic structures in natural habitats may increase direct mortality risk, as collision with structures and electrocutions at power lines are considered important causes of bird mortality (Loss *et al.*, 2015). Structures may also alter predator communities in the surrounding area (Suvorov *et al.*, 2014; Svobodová *et al.*, 2010; Tryjanowski, 2001; van der Vliet & Wassen, 2008), and affect the surrounding habitats through changes in the vegetation composition, whether intentional or not (Londe *et al.*, 2019; Ludlow *et al.*, 2015), which may affect abundances of ground-nesting birds (Buchanan *et al.*, 2017). Impacts of structures may also depend on their characteristics (e.g. height of perches, amount of occupied habitat, associated traffic of vehicles) (Andersson *et al.*, 2009; Benítez-López *et al.*, 2010; Kociolek *et al.*, 2011; Seiler, 2001). The presence of anthropogenic structures is often accompanied by an increase in human presence, either through use of the structure (e.g. summer houses) or by ease of access (e.g. roads and tracks). The presence of humans can also affect breeding birds through disturbance by traffic (pedestrian and/or vehicles), or by introducing pets, such as cats which can be important nest predators (Lepczyk *et al.*, 2004; Loss *et al.*, 2015). All of these processes could alter densities of ground-nesting birds in areas in which anthropogenic structures occur. Additionally, novel structures may also affect the distribution of individuals which may change their temporal or spatial activity patterns by avoiding or being drawn to these structures (Dinkins *et al.*, 2014; Ditchkoff *et al.*, 2006; Jameson & Willis, 2014; Łopucki *et al.*, 2017), even if the habitat surrounding these structures remains the same.

Few ground-nesting species are found in urban areas (Chace & Walsh, 2006; Croci *et al.*, 2008; Jokimäki *et al.*, 2016); and as these species tend to be associated with open habitats, infrastructure development and the introduction of novel structures into open landscapes is of particular concern. Reduced densities of ground-nesting birds in the vicinity of novel structures have been identified for structures ranging from tall structures that might be view-obstructing, such as plantation forests, wind farms and houses (Pearce-Higgins *et al.*, 2012; Reino *et al.*, 2009; van der Vliet *et al.*, 2010; Żmihorski *et al.*, 2018), to flat structures such as roads, railways and canals (Forman *et al.*, 2002; Morán-López *et al.*, 2017; Thompson *et al.*, 2015). In arctic and subarctic areas, where open habitats are vast, avian diversity is low compared to temperate and tropical regions but the abundance in many areas is high (Gunnarsson, 2020; Jóhannesdóttir *et al.*, 2014; Katrínardóttir, 2012; Smith *et al.*, 2020; Thorup, 2004). The majority of bird species breeding in the arctic and subarctic are migratory and winter further south, and if infrastructure development impacts the distribution and abundance of these species, the consequences may be apparent throughout their non-breeding ranges. For Icelandic breeding waders, this would refer to Europe and Africa (Carneiro *et al.*, 2021; Gunnarsson *et al.*, 2006b; Méndez *et al.*, 2020).

1.4 Study area

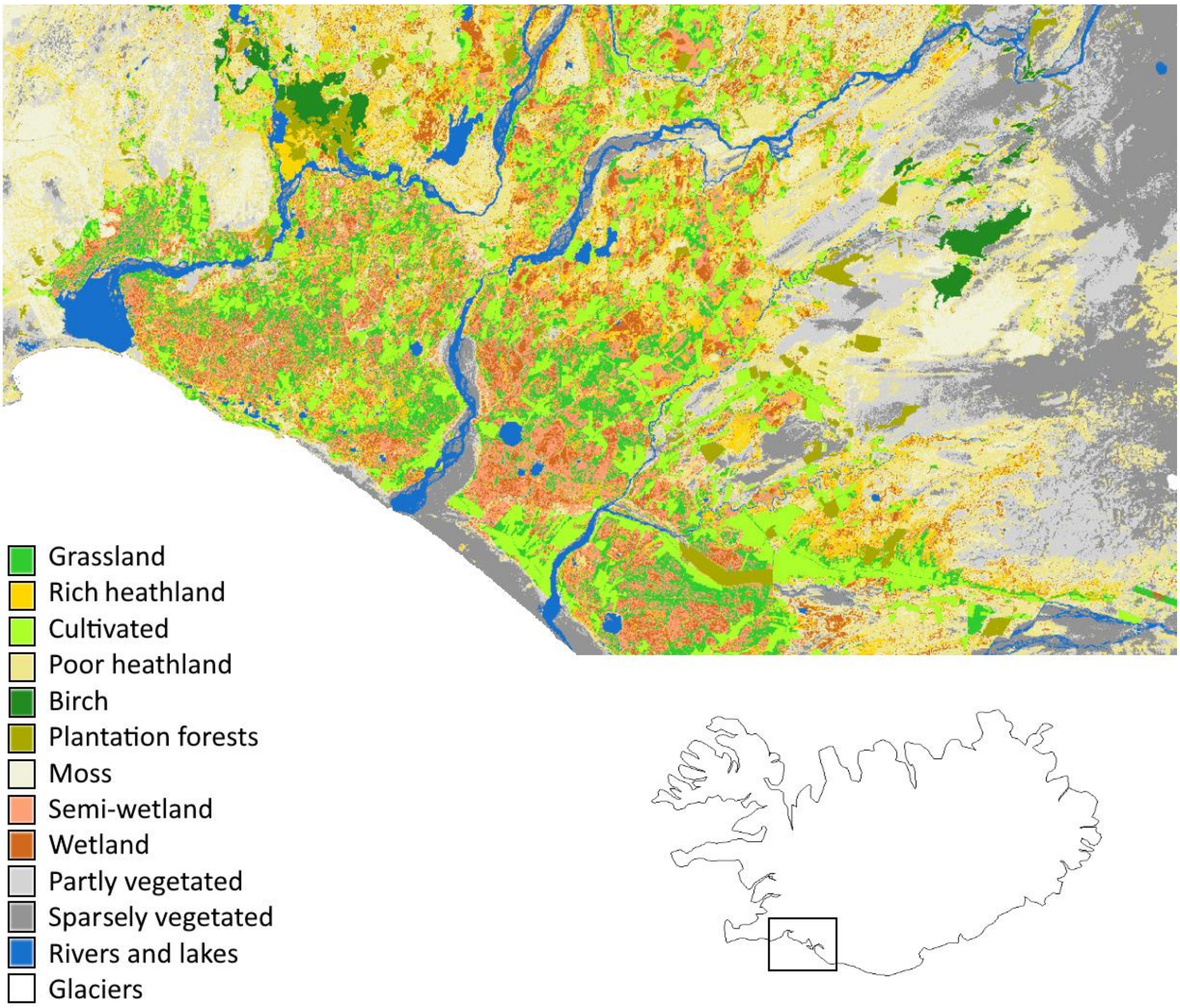

Figure 1: Example of habitat type classes and their distribution in the southern lowlands. Data from the Icelandic farmland database (Nytjaland) (Gísladóttir et al., 2014)

The study was carried out in Iceland, a country with among the lowest human population density in the world, at around 4 people/km^2 (The World Bank, 2018). The majority of the Icelandic human population is concentrated in coastal areas, while most of the country is at higher altitudes, where species richness and biodiversity are low (Magnússon *et al.*, 2009). Stretching between the coastal areas around the country and the high altitude heartland (> 300 m a.s.l.) are the Icelandic lowlands which cover ca. 33,000 km^2 and still contain large areas of semi-natural habitats where the main human influence is due to grazing of livestock (Gunnarsson, 2020; Jóhannesdóttir *et al.*, 2014). The majority of lowland areas are covered with low growing vegetation such as grasses, mosses and shrubs (Ottósson *et al.*, 2016), and the most important habitat type classes for ground-nesting birds are wetlands, river plains, grasslands, heathlands and moss lands (Figure 1, Table 1) (Jóhannesdóttir *et al.*, 2014; Katrínardóttir, 2012). These habitat type classes can be arranged from sparsely vegetated and dry (poor heathland and river plains), to the soil being completely covered in vegetation (grassland and rich heathland) and finally wetlands which are highly vegetated and wet. These classes vary in vegetation composition; river plains and heathlands are dominated by mosses and lichens and occasional small shrubs such as Black crowberries (*Empetrum nigrum*), while grassland mainly contains grasses accompanied by flowering plants or mosses and wetland is dominated by sedges (*Carex spp.*), horsetail (*Equisetum spp*.) and grasses (Ottósson *et al.*, 2016).

Table 1: Overview of habitat type classes relevant to the project and the estimated area of these classes in Iceland. Data obtained from (Ottósson et al., 2016)

Habitat type classes	**Area**
River plains	~2,800 km^2
Moss lands	~9,200 km^2
Coastal lands	~600 km^2
Wetlands	~7,800 km^2
Grasslands	~4,400 km^2
Heathlands	~18,500 km^2
Woodland	~1,500 km^2
Constructed, industrial and other artificial habitats	~360 km^2
Cultivated agricultural, horticultural and domestic habitats	~1,800 km^2
Mixed forestry plantations	~400 km^2
Total area of Iceland	~103,001 km^2

1.4.1 Statutory commitments

Iceland is a signatory to numerous agreements relating to the protection and conservation of wild birds and their habitats. In 1956, Iceland signed the *International Convention for the Protection of Birds*, which states that all birds should be protected in the breeding season and during migration, and endangered birds should always be protected. In 1977, Iceland became a party to the *Convention on Wetlands of International Importance Especially as Waterfowl Habitat*, often referred to as the RAMSAR convention (Schmalensee *et al.*, 2013). This states that all forms of wetland should be protected, however this agreement is currently limited to only six wetland areas in Iceland that are classified as RAMSAR sites (Icelandic Institute of Natural History, 2013). The Icelandic wetlands are key habitats for breeding waders and currently hold the highest wader densities of all habitats types considered (Jóhannesdóttir *et al.*, 2014). In 1994, Iceland became a signatory to the *Convention on Biological Diversity*, which focuses on protecting biodiversity and using natural resources sustainably. Iceland is also a signatory to the *Convention on the Conservation of European Wildlife and Natural Habitats*, sometimes referred to as the Bern convention, since 1993. This convention has a main goal of protecting all animals and plants native to Europe and countries that share populations/species with Europe (Schmalensee *et al.*, 2013). Lastly, but perhaps the most important agreement for ground-nesting birds, Iceland became a signatory to the AEWA (*Agreement on the Conservation of African-Eurasian Migratory Waterbirds*) in 2013, thereby committing to the protection of waterbirds, and almost all breeding birds in Iceland fall under this agreement (Icelandic Institute of Natural History, 2022). In addition to these international agreements, the protection of animals and their habitats are stated in current legislations in Iceland, under the acts on animal welfare (No. 55/2013), nature conservation (No. 60/2013) and the protection of wild birds and mammals (No. 64/1994). As a member of aforementioned conventions, Iceland has committed to protecting birds and their habitats. To ensure their protection, it is important to identify and quantify how and if anthropogenic land-use changes affect these species, and to consider those effects when planning new infrastructure, ideally to identify locations, designs and/or configurations that reduce negative effects on important ground-nesting bird populations.

1.5 Drivers of habitat loss and fragmentation and their effect on breeding birds in Iceland

Anthropogenic structures, agricultural fields and human-made surfaces are increasing rapidly in Iceland (EEA, 2018; Wald, 2012). This expansion mainly takes place in the lowlands which are also the most important areas for breeding birds (Jóhannesdóttir *et al.*, 2014; Skarphéðinsson *et al.*, 2016). This continuing increase in anthropogenic impacts is reducing the amount of semi-natural habitats, and fragmenting landscapes, which reduces the availability of large areas of open habitat, with possible effects on populations of ground-nesting birds. Four of the most common structures introduced in the Icelandic lowlands are forest plantations, power lines, houses and roads, and here the effect of these structures on densities of ground-nesting birds in the surrounding areas was explored.

1.5.1 **Forest plantations**

In recent decades, climatic amelioration at higher latitudes has facilitated rapid forestry development in areas where tree growth was previously limited by harsher environmental conditions (Halldórsson *et al.*, 2008). The only tree species in Iceland to naturally form forests is Downy birch (*Betula pubescens*) (Eysteinsson, 2017). In recent years, the Icelandic government has provided additional funding to the Icelandic forest service to enhance carbon sequestration capacity (Ministry for the Environment and Natural Resources, 2018) and forests are therefore expected to increase even further. Forestry in Iceland primarily operates through government grants to landowners to plant trees on their land (Halldórsson *et al.*, 2008), which has resulted in large numbers of small forest patches spread throughout lowland Iceland. Plantation forests in Iceland typically consist of non-native species such as Sitka spruce (*Picea sitchensis*), Larch (*Larix spp.*), Lodgepole pine (*Pinus contorta*) and Black cottonwood (*Populus trichocarpa*), along with Downy birch (Brynleifsdóttir, 2018).

An increase in forested areas could increase breeding opportunities for species that use forest resources, but is also likely to result in habitat loss for ground-nesting species in open habitats (Halldórsson *et al.*, 2008; Reino *et al.*, 2009). Additionally, studies have shown depressed densities of ground-nesting birds close to forest edges (Hancock *et al.*, 2009; Stroud *et al.*, 2009;

Wilson *et al.*, 2014). These effects could arise because of the visual obstruction of trees altering the attractiveness of breeding sites, or increases in perceived or actual risks of predation (Angelstam, 1986; Laurance, 2000). However, little is known about the fitness consequences for these species of breeding close to forests (Bertholdt *et al.*, 2017; Holmes *et al.*, 2020).

1.5.2 **Power lines**

In Iceland, further expansion of power lines is expected in the coming years due to a growing human population, increasing electrification of systems and the infrastructure needed for planned linking of Iceland's electric grids with those in other countries (Landsvirkjun, 2014). Power lines differ from the other structures in the studies presented here as they are less likely to obstruct visibility and/or movement of birds compared to trees, roads and houses. Power lines can benefit certain species by providing them with places to roost, nest or perch (Howe *et al.*, 2014; Moreira *et al.*, 2017), but they are also considered an important source of mortality through collision risk and electrocution (Bevanger & Brøseth, 2001; Loss *et al.*, 2014). Certain species are more susceptible to the negative effects of power lines, for example larger species may be more at risk of electrocution as the birds have to touch two wires simultaneously (Loss *et al.*, 2015), and nocturnal species have greater risks of collision because of reduced visibility during darkness (D'Amico *et al.*, 2018). In addition to these direct effects, power lines could influence predator distribution in the surrounding areas (DeGregorio *et al.*, 2014), thereby affecting predation rates. Power lines also generate an electromagnetic field which has been shown to affect avian behaviour, physiology and development (D'Amico *et al.*, 2018; Fernie & Reynolds, 2005) along with emitting ultraviolet light which may result in avoidance behaviour of species that perceive this light (Tyler *et al.*, 2014).

1.5.3 **Houses**

The construction of houses and the accompanying infrastructure in natural areas in Iceland is increasingly rapidly, particularly through increased numbers of summer/recreational houses, most of which are located in the Icelandic lowlands (Registers Iceland, 2022a; Statistics Iceland, 2021) and placed both birch woodlands as well as open habitats. The placement of houses in previously open habitats will not only reduce the amount of breeding habitat for these species, but can also induce changes in the surrounding habitat through processes such as vegetation changes, increased human presence and car traffic, along with the introduction of household pets and potentially other predators (Chace & Walsh, 2006). These processes can then influence survival and/or reproductive success of ground-nesting birds in the surrounding habitats (Chace & Walsh, 2006; Lepczyk *et al.*, 2004; Loss *et al.*, 2015) and/or affect the spatial and temporal distribution of individuals, both of which can have an effect on density of birds in the surrounding landscapes. Many summer houses in Iceland also have trees planted around them as protection from adverse weather, which may further exacerbate such effects.

1.5.4 **Roads**

The majority, if not all, anthropogenic structures in Iceland are accompanied by roads or tracks, which are therefore expected to increase in frequency alongside increases in other structures. Multiple studies have documented lower breeding densities of grassland breeding birds closer to roads (Thompson *et al.*, 2015). Roads may have an effect on birds by increased mortality rates due to collision and pollution, increased predation rates, disturbance through noise pollution and/or by presenting a barrier in the landscape, which may induce avoidance behaviour (Kociolek *et al.*, 2011; Seiler, 2001). However, some studies have found evidence showing positive effects of roads on birds, through processes such as reduced predation pressure, or increased availability of foraging habitats or perching opportunities on associated infrastructure (Morelli *et al.*, 2014). The presence of roads and car traffic may play a large role in the aforementioned negative effects of anthropogenic structures such as houses on bird densities, but a study from Nevada identified major roads as the most important urban structure influencing avian richness and abundance, which were always lowered in areas with high road density (Trammell & Bassett, 2012).

1.6 The study species

The Icelandic bird community is characterized by relatively few breeding species compared to other European countries. Nests of only 110 species have ever been identified, with only 75 being frequent breeders (Guðmundsson & Skarphéðinsson, 2012). Even though bird diversity is low, abundance of some species is high, with density of ground-nesting birds in the lowlands among the highest found in Europe, ranging from 275 birds/km^2 in heathland habitats to 640 birds/km^2 in wetlands (Jóhannesdóttir *et al.*, 2014). High breeding density, along with extensive open landscapes, has resulted in Iceland holding internationally important numbers of several wader populations, for example it has been estimated that 40-52% of the global population of Whimbrel (*Numenius phaeopus*) and Golden plover (*Pluvialis apricaria*) breed in Iceland (Gunnarsson *et al.*, 2006a). Many wader populations are currently declining globally and a major driver behind this is considered to be habitat destruction (Burns *et al.*, 2021; International Wader Study Group, 2003; Rosenberg *et al.*, 2019). Waders are long-lived and site-faithful (Méndez *et al.*, 2018; Pellissier *et al.*, 2013), and they nest primarily on the ground in open habitats. In Iceland, these species breed between May-June, with occasional nests being found in April/July (Figure A1). Long-term monitoring of bird populations in Iceland is lacking, and therefore long-term population trends are rarely known. Yearly counts of open-habitat birds have only been systematically conducted since the year 2006, and only in a handful of sites (Skarphéðinsson *et al.*, 2016). The bird community in the Icelandic lowlands is mainly comprised of seven wader species (Snipe (*Gallinago gallinago*), Whimbrel, Black-tailed Godwit (*Limosa limosa*), Dunlin (*Calidris alpina*), Redshank (*Tringa totanus*), Golden plover and Oystercatcher (*Haematopus ostralegus*)), and two passerines (Meadow pipit (*Anthus pratensis*) and Redwing (*Turdus iliacus*)) (Table 2) (Gunnarsson & Þórisson, 2019; Jóhannesdóttir *et al.*, 2014).

1.6.1 **Redwing**

Redwing is one of two passerine species in this study. It is classified globally as near threatened (NT) as it is assumed to be declining (IUCN, 2022). Redwings in Iceland are found in the highest density within forested areas (46,4 pairs/km^2), fields of Nootka lupine (*Lupinus nootkatensis*) (21 pairs/km^2) and agriculture (9,1 pairs/km^2) (Skarphéðinsson *et al.*, 2016). Even though Redwings generally nest in trees and forests, the nest itself is often on the ground (Figure 2) (Meilvang *et al.*, 1997; Svensson *et al.*, 2009).

Figure 2: A Redwing nest on the ground. Photo: Jennifer A. Gill.

1.6.2 **Meadow pipit**

Meadow pipit, the second passerine in this study, is predominantly found breeding in open habitats. The global population is considered decreasing, but this decrease has slowed down in recent years, resulting in Meadow pipits being considered least concern (LC) (BirdLife International, 2021). Icelandic Meadow pipits are one of the most numerous bird species found in Iceland. The nest is well hidden on the ground, and they can be found in most vegetated areas, but they are found in the highest density in grassland (78,4 pairs/km^2), wetland (69,2 pairs/km^2) and lupine (67,4 pairs/km^2) (Skarphéðinsson *et al.*, 2016).

1.6.3 **Black-tailed Godwit**

Icelandic Black-tailed Godwits (hereafter Godwit) breed at varying densities in grassland (12.9 pairs/km^2), wetland (7 pairs/km^2) and agricultural habitats (7.8 pairs/km^2) (Gunnarsson *et al.*, 2006a; Skarphéðinsson *et al.*, 2016). The Godwit population in Iceland has been expanding from the southern lowlands to more northern areas (Alves *et al.*, 2019; Gunnarsson *et al.*, 2005). Although globally Godwits are decreasing and defined as near threatened (NT) (BirdLife International, 2017), the Icelandic population has been increasing, which is why Godwits in Iceland remain of least concern (LC) (Icelandic Institute of Natural History, 2018). Godwit nests are typically concealed in tall vegetation (Laidlaw *et al.*, 2020).

1.6.4 **Dunlin**

The Icelandic breeding Dunlin population consists of individuals from the population *Calidris alpina schinzii*, but Greenland-breeding individuals (*Calidris alpina arctica*) use Iceland as a stopover site. Dunlin is one of few species in our study that breeds in the highlands, with about 15% of the population breeding at altitudes >300 m a.s.l (Magnússon *et al.*, 2009). Dunlin mainly breed in wetland habitats (lowlands: 19.9 pairs/km^2; highlands: 5.7 pairs/km^2), along with heathland (Gunnarsson *et al.*, 2006a; Skarphéðinsson *et al.*, 2016). Both globally and in Iceland, Dunlins are categorized as least concern (LC), although a certain part of the population which winters in the Baltic sea seems to be decreasing (van Roomen *et al.*, 2015). Dunlin nests are typically found in tall vegetation, such as tussocks, in wetlands.

1.6.5 **Eurasian Oystercatcher**

The global population of Eurasian Oystercatcher (hereafter Oystercatcher) is considered decreasing and categorized as near threatened (NT) (BirdLife International, 2019b). Additionally, counts from the wintering locations of the Icelandic populations in W-Europe indicate a consistent decrease for the past 30 years and Icelandic Oystercatchers are now classified as vulnerable (VU) (van Roomen *et al.*, 2015). Oystercatcher nests are often found in poorly vegetated areas, such as on gravel and rocky coasts and their nests are generally not well-concealed and often consist of a simple scrape in open habitats (Laidlaw *et al.*, 2020). In inland areas, Oystercatchers are mainly found in grassland (3.1 pairs/km^2) and agriculture habitats (2.0 pairs/km^2) (Skarphéðinsson *et al.*, 2016). Oystercatchers in Iceland have also been found nesting in human-made habitats, such as golf courses and rooftops.

1.6.6 **European Golden plover**

The European Golden plover (hereafter Golden Plover) can be seen in Iceland for over half the year, from April to November (Gunnarsson *et al.,* 2006a), and it is estimated that over half of the global population breeds in Iceland (Gunnarsson *et al.*, 2006a). Golden plovers are known to nest in the highlands, although the majority breeds in the lowlands (Table 2). They are found in the highest densities in heathland habitats (lowland: 13 pairs/km^2; highlands: 4.7 pairs/km^2) (Skarphéðinsson *et al.*, 2016). Their nests are generally not well concealed, with adults relying on camouflage and nest defense to protect against predators (Laidlaw *et al.*, 2020). There are no indicators of population change, either globally or in Iceland, and Golden plover is therefore categorized as of least concern (LC) at both levels (Icelandic Institute of Natural History, 2018; IUCN, 2022).

1.6.7 **Eurasian Whimbrel**

It is estimated that around 40% of the global population of Whimbrels nests in Iceland (Gunnarsson *et al.*, 2006a). Icelandic Whimbrels breed throughout the country but are most common in the south (Gunnarsson *et al.*, 2006a), with around 95% of the population nesting in the lowlands (Skarphéðinsson *et al.*, 2016). Whimbrels are typically found in the highest densities in grassland (13.5 pairs/km^2) and rarely on agricultural land (Gunnarsson *et al.*, 2006a). Whimbrels are also common in less vegetated areas such as heathlands (Skarphéðinsson *et al.,* 2016) and densities on some riverplain sites have exceeded 30 pairs/km^2 (Katrínardóttir, 2012). Whimbrel nests are usually a small depression which is not covered by vegetation (Laidlaw *et al.*, 2020). Whimbrel is currently estimated as a least concern (LC) in Iceland and globally, but the global population is decreasing, which is a cause for concern (BirdLife International, 2016a; Icelandic Institute of Natural History, 2018).

1.6.8 **Common Redshank**

Around 19% of all Redshanks in the world breed in Iceland (Gunnarsson *et al.*, 2006a). Redshank breed almost exclusively in the lowlands and are found in the highest density in agricultural lands (10.8 pairs/km^2) and grassland (8.6 pairs/km^2) (Skarphéðinsson *et al.*, 2016). Redshank nests are generally concealed in tall vegetation (Laidlaw *et al.*, 2020). Although the global populations of Redshank is considered of least concern (LC), the population trend is unknown (BirdLife International, 2016b). Counts from wintering countries of the Icelandic population (surrounding the North Sea) suggest that the population is slowly decreasing by about1% a year and therefore Redshanks in Iceland are considered to be near threatened (NT) (Icelandic Institute of Natural History, 2018; Skarphéðinsson *et al.*, 2016; van Roomen *et al.*, 2015).

1.6.9 **Common Snipe**

The Common Snipe (hereafter Snipe) breeds throughout Iceland but is most common in the west. Snipes are rarely found in un-vegetated areas and are most common in wetlands (21.3 pairs/km^2), grassland (19.7 pairs/km^2) and areas with lupins (19.5 pairs/km^2) (Skarphéðinsson *et al.*, 2016). Snipe presence in study plots in Iceland was higher in areas with birch cover, hummocks, ditches and pools (Gunnarsson *et al.*, 2006a). Snipe is the only wader in our study that is known to nest in and around forests. The nest itself is generally well concealed (Laidlaw *et al.*, 2020), and the incubating adult will not leave the nest easily, relying on crypsis rather than active nest defence. Snipe is considered of least concern (LC) both globally and in Iceland (BirdLife International, 2019a; Icelandic Institute of Natural History, 2018).

Table 2: Latin names, population estimates (Skarphéðinsson et al., 2016), conservation status (according to the International Union for Conservation of Nature (IUCN, 2022) and the Icelandic Red List (Icelandic Institute of Natural History, 2018), estimated percentage of the Icelandic population breeding in the lowlands, migration status and wintering locations (Skarphéðinsson et al., 2016) of the Icelandic populations of the nine study species.

Species	Latin name	Icelandic subspecies	Icelandic population (estimated number of pairs)	IUCN red list	Icelandic red list	% breeding under 300 m a.s.l.	Migration status	Wintering locations
Redwing	*Turdus iliacus*	*T.i. coburni*	165,000	NT	LC		Migrant/resident	W-Europe
Meadow pipit	*Anthus pratensis*	-	1,500,000	LC	LC		Migrant	S-Europe N-Africa
Black-tailed Godwit	*Limosa limosa*	*L.l. islandica*	68,000	NT	LC	>99	Migrant	W-Europe (N-Africa)
Dunlin	*Calidris alpina*	*C.a. schinzii*	165,000	LC	LC	85	Migrant/resident	W-Africa
Oystercatcher	*Haematopus ostralegus*	*H.o. ostralegus*	10-20,000	NT	VU	>99	Migrant/ resident	W-Europe
Golden plover	*Pluvialis apricaria*		400,000	LC	LC	66	Migrant	W-Europe
Whimbrel	*Numenius phaeopus*	*N.p. islandicus*	165,000	LC	LC	95	Migrant	W-Africa
Redshank	*Tringa totanus*	*T.t. robusta*	75,000	LC	NT	>99	Mostly migrant	W-Europe
Snipe	*Gallinago gallinago*	*G.g. faeroensis*	300,000	LC	LC	>99	Mostly migrant	W-Europe

1.7 Aims of the thesis

Currently, Iceland has large areas of semi-natural lands which experience little or no anthropogenic influence. It is estimated that ~1.5 million pairs of waders breed in Iceland, of which 85% are located in the lowlands. These populations are currently considered stable in numbers (Gunnarsson, 2020), although evidence of population decreases have started to emerge in some cases (Icelandic Institute of Natural History, 2018). These features make Iceland an ideal location in which to quantify the effects of introduction of anthropogenic structures on ground-nesting birds in the surrounding habitats, and to identify strategies that might reduce these effects.

The main objective of this thesis is to explore the evidence for changes in density and species composition of ground-nesting birds in the landscapes surrounding anthropogenic structures, when those structures (forest plantations, power lines, houses and roads) are present at low densities and surrounded by semi-natural, open habitats. It is hoped that the findings from the thesis will help to guide the development of strategies for future planning of anthropogenic structures to limit their effects on this key component of Icelandic birdlife.

2 Material and methods

2.1 Data collection

Data on density and species composition of ground-nesting birds in Iceland was collected through bird counts. These counts were performed in the years 2017-2019, between May and June, which spans the breeding period of the target species (Figure A1). Counts were not conducted in strong winds (above 7 m/s) or in heavy rainfall, as this may affect the activity and detectability of the target species (Hoodless *et al.*, 2006). All counts took place in the Icelandic

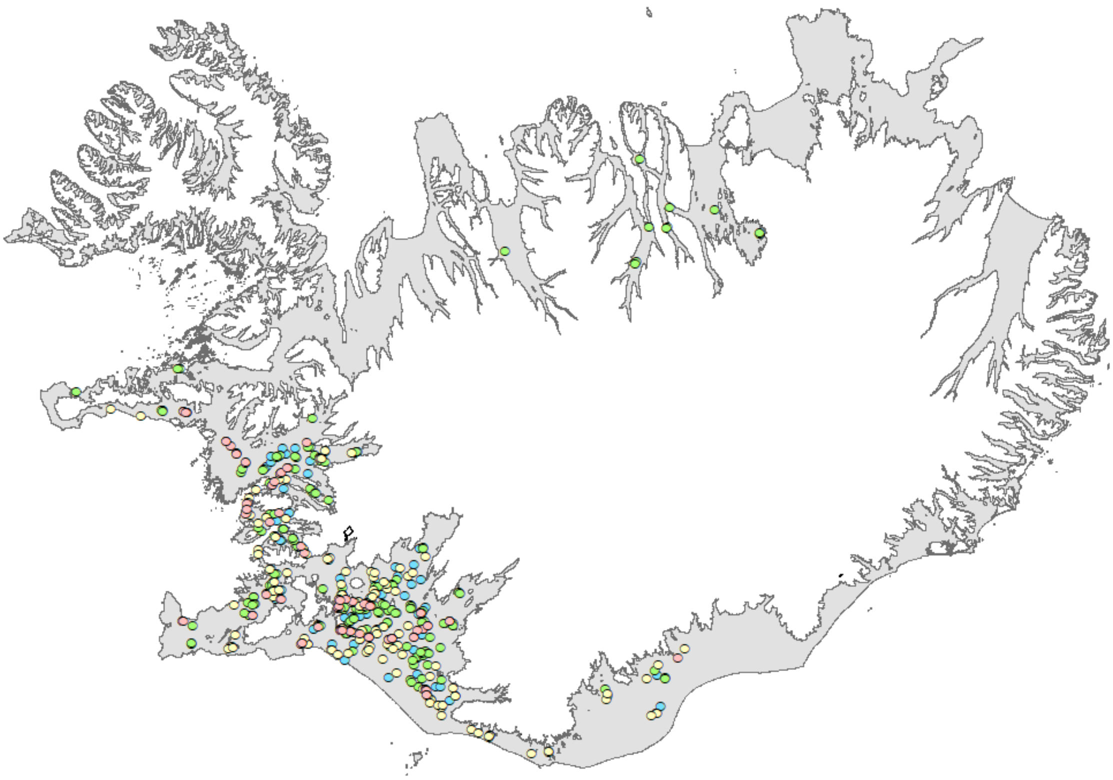

Figure 3: Location of all bird counts in our study, identified by which structure was present as; plantation forests (green), power lines (pink), houses (blue) and roads (yellow). Areas below 300 m a.s.l. are shown in grey.

lowlands (<300 m a.s.l.) which are the most important areas for ground-nesting birds (Gunnarsson *et al.*, 2006a; Jóhannesdóttir *et al.*, 2014; Skarphéðinsson *et al.*, 2016). The majority of counts were performed in SW-Iceland (Figure 3) which holds the largest amount of vegetated lowlands and is comprised of a mosaic of various natural and semi-natural habitats such as wetlands and heathlands, intertwined with agricultural land, forest plantations and anthropogenic structures and urban areas. When studying the effects of forests, counts were also conducted in N-Iceland, as this area contains many forest plantations. However, N-Iceland is more sparsely populated and contains few high density summer house sites, no high voltage power lines and the roads have less traffic than SW-Iceland, and therefore counts surrounding these structures were not performed in N-Iceland to avoid confounding effects (Figure 3).

Bird surveys were conducted as either transect counts or point counts. All birds seen or heard within a previously defined area surrounding the observer were documented. Each summer, data collection surrounding one of the aforementioned structures was conducted: forest plantations, summer houses and power lines were counted in 2017, 2018 and 2019, respectively, along with road counts which were counted alongside other data in the summers of 2018 and 2019 (Table 3).

Table 3: Time, census methods and total number of counts performed for each part of the project.

Dataset	**Year collected**	**Census method**	**Number of points/transects**
Plantations	2017	Transect	161
Summer houses	2018	Point	292
Power lines	2019	Transect	85
Roads	2018 & 2019	Transect	122 (60 & 62 respectively)

When birds were counted surrounding power lines and plantation forests, transects were walked either to or from the structures, as the movement of the observer could have an effect on the behaviour of birds, by corralling them in front of the surveyor. The road transects were all walked in the same direction (away from the road) as walking them in the opposite direction would require the observer to walk away from the road before conducting the transect, thereby possibly influencing bird distribution. Transects were always walked at a steady pace and without stopping, and all birds seen or heard within 100 m on either side were documented, along with distance from structure. For all transects, habitat type was recorded as well as characteristics of each individual structure (Table 4).

Table 4: Variables used to quantify the effect various structures on the density of breeding birds recorded on transects and point counts in lowland Iceland.

Variable	**Unit**	**Definition**
Bird density	Birds/ha (Transect counts) Birds/point (Point counts)	Number of birds recorded in each point (~12.5 ha) or interval of each transect (1 ha)
Interval	From 1 to N	50 m distance bands on transects, from closest (1) to furthest (N) from the studied structure
Transect	Transect number	Individual transect
Transect length	Maximum length of transect	Plantation forests = 700 m Power lines = 500 m Roads = 400 m

Habitat	Poor heathland/rich heathland/grassland/ semi-wetland/wetland	Classification of transect habitat (Gísladóttir *et al.*, 2014)
Direction	To/from	Transects were walked towards or from the plantation edges/power lines
	Plantation forestry additional factors	
Forest width	m	Distance between two outermost trees on plantation edges, recorded from aerial photos (Icelandic forest service 2014) or in the field with a range finder
Forest area	m^2	Area of forest, extracted from aerial photos
Forest height	0-2 /2-5 / 5-10 />10 m	Tallest visible point of plantation, measured with a range finder
Forest type	Mixed/conifer/broadleaf	Predominant tree type (coniferous, broadleaved or both)
Forest density	Sparse/dense	Interior (up to 50 m) of plantation visible (sparse) or not (dense) from edge
	Summer houses additional factors	
House density	Houses/point	No houses (0); points that had a single house (1); low house density (2-5 houses) and high house density (6-35 houses).
Area lost	m^2	Area covered with infrastructure (houses, tracks, decks and parking spaces) where our focal species are presumed not to generally nest or feed
	Power lines additional factors	
Line/pylon height	m	Height of the pylon or line, measured with a range finder from the ground
Voltage	Lower/higher	Voltage of the power line (Landsnet, 2019) categorized as higher (220kV) or lower (66 kV or 132 kV)
Pylon type	Wood or Metal	Pylons construction material
Number of cables	3-8	Number of electric cables running between pylons
	Roads additional factors	
Traffic	Number of cars/day in summer	Extracted from The Icelandic Road and Coastal Administration (Vegagerðin, 2019)

For the summer house dataset, birds were counted on points where the observer stood still for 5 minutes and documented all birds seen within a 200 m radius. Sites with one or more summer house were chosen from known locations, and between 2-8 points were counted in each site. The points within each site were distributed so they would capture the variability in house density, with a control point where there were no houses, points which had a single house, and points with varying house density (range 2-35). All birds seen or heard within the allocated time frame were recorded, along with the number of houses, habitat type and if trees were present surrounding the houses.

2.2 Statistical analysis

2.2.1 Transect data

All transects were separated into 50 m intervals (blocks of 1 ha) and the density of birds within each interval calculated and used as a response variable in GLMMs (generalized linear mixed models). Distance from structure was used as the explanatory variable in all models and transect identity as a random factor, as intervals within each transect are not independent of each other. All models were performed on a species level and for all species combined, with various environmental factors and structure characteristics included (See materials and methods in **Paper I, II and IV** for details). From these models, estimates on how much birds of each species increase/decrease in number with each 50 m increment from the beginning of the transect can be extracted, along with which factors influence this relationship.

2.2.2 Point counts

Point counts were only obtained for the study on the effect of houses (**Paper III**). Points were divided in to four groups, control points (0 houses), points with a single house, points with low house density (2-5 houses) or high house density (6-35 houses). The boundaries between the groups with low and high house density were chosen so that number of points between groups would be balanced. Generalized linear mixed models (GLMM) with a Poisson distribution were constructed with bird abundance as the response variable and house density and habitat as fixed effects, and site as a random effect to account for possible non-independence of points within the same site.

2.3 Effects of plantation scenarios on bird density

To identify how far from plantation edges and roads bird density was affected, segmented linear regression was applied, which identified a breaking point in bird numbers at a certain distance from forest, after which bird numbers plateau. This breaking point was then used to separate an “affected area”, closer to the plantation/road edge where bird numbers show the largest change in density, and an “unaffected area” where bird numbers remain stable.

The breaking point surrounding plantations was used to estimate potential change in bird abundance that will result from new plantations being placed in the Icelandic lowlands, by applying bird numbers from this study to the following equation:

Equation 1:

Change in number of birds = No of patches (Change in numbers in forest area + Change in numbers in affected area)*

$\Delta N = P^* (\Delta D_T + \Delta D_A)$

$\Delta N = P^* (T^*(D_T - D_U) + A^*(D_A - D_U))$

where N = number of birds, P = number of plantation patches, T = plantation area, A = affected area, D_T = average bird density in plantation area (assumed to be 0 for open-nesting species), D_A = average bird density in affected area, D_U = average bird density in unaffected area.

Using the affected area, and assuming a circular shape (giving the most conservative estimate of affected surrounding area) and no overlap of affected area between plantations, it was estimated how bird abundance changes would vary with 1000 ha forest being planted in varying number of patches, ranging from 1 to 1000 (see **Paper I** for a more detailed analysis).

2.4 Habitat loss vs house presence

To examine if the effects of houses on bird density exceeded the effect of the habitat lost due to houses and accompanying infrastructure, area lost in each point was calculated manually in the 251 (out of 292) points for which recent aerial photographs could be obtained. The amount of available area (*area with infrastructure subtracted from total area of point*) was then calculated and included as an offset in a GLMM on the subset of points to see if this would change the results (See **Paper III** for a more detailed analysis).

2.5 Cumulative effects of studied structures

2.5.1 Species specific vulnerability index

To assess how individual species are being affected by the introduction of anthropogenic structures in the Icelandic lowlands, results for all species were combined and categorized as showing significant negative (↓), significant positive (↑) or non-significant neutral effects (0). A vulnerability index was calculated by scoring the species on a scale from -4 (negative effects of all 4 studied structures) to +4 (positive effects of all studied structures). Using this index, it is possible to identify which of our study species are likely to be most vulnerable to anthropogenic expansion in the Icelandic lowlands, and which may benefit.

2.5.2 Assessment of local population trend

Although long-term monitoring data on waders in Iceland is lacking, with systematic counts being established locally in 2006 (Skarphéðinsson *et al.*, 2016), ground-nesting birds have been surveyed on the same points along roads and tracks in the southern lowlands of Iceland for the last 11 years (for detailed methods see Gunnarsson *et al.* (2017) or Gunnarsson and Þórisson (2019)). However, in the first year (2011) there was a volcanic eruption in Iceland, which has been shown to depress breeding success significantly (Gunnarsson *et al.*, 2017; Katrínardóttir *et al.*, 2015) and thereby affect bird density, and this year was thus excluded from the dataset. The counts from 2012-2021 were analysed using a GLMM with a Poisson distribution with bird density (birds/point) as the response variable and year and traffic as explanatory variables to study how the density of birds has changed throughout these years and account for any variance due to the traffic volume rising with increased tourism after 2008 (Jóhannesson & Huijbens, 2010), and then decreasing due to the Covid-19 pandemic in 2019-2021. Point identity was included as a random effect to account for non-independence of the same points between years and account for new points which were added in 2016.

2.5.3 Assessing current status of anthropogenic influence in the Icelandic lowlands

In an effort to estimate how much of the lowlands are currently under the influence of anthropogenic structures, 100,000 random points were created in the Icelandic lowlands (< 300 m a.s.l.). Using GIS and two layers from the National Land Survey of Iceland (transportation infrastructure and housing infrastructure) and one layer from the Icelandic Forest Service (forest plantations), the distance from the random points to these structures was measured (Icelandic Forest Service, 2021; Landmælingar Íslands, 2020a, 2020b). From the results of individual chapters, a disturbance distance where bird densities change surrounding our structures was defined, and this disturbance distance was subsequently used to classify the random points as being affected by aforementioned structures or not.

3 Results

3.1 Forest plantations

Out of 3,713 birds counted in 161 transects, nine study species were identified which had more than 60 individuals (excluding gulls), and were used for the subsequent analysis (Table 5). Overall bird density did not change significantly with distance from forest. However, five of the study species (Whimbrel, Golden plover, Godwit, Dunlin and Oystercatcher) were found in significantly lower densities closer to the forest edge, two were found in higher densities (Snipe and Redwing), and one showed no change in density with distance from the forest edge (Meadow pipit). Redshank did not show a linear relationship with distance from plantation edges, however redshank densities were lowest close to the plantation edge (≤150 m), showing an approximately twofold increase in subsequent intervals (>150 m) (Figure 2 in **Paper I**). This relationship was generally not dependent on forest characteristics (See **Paper I** for details).

3.1.1 Effects of plantation configuration scenarios on bird density

As no plantation characteristics had a consistent effect on the study species, it is assumed that all forests, regardless of size, density or tree type, will have similar effects on density of ground-nesting birds in the vicinity. To quantify the effects of varying planting configuration scenarios on bird density, species were separated into two groups, ground-nesting species in open habitats that do generally not nest in forests (Whimbrel, Golden plover, Godwit, Dunlin, Redshank and Oystercatcher) and species which frequently nest in forests (Snipe and Redwing). No estimates were created for Meadow pipit, as their nesting densities (if any) inside plantations are unknown. For the open-nesting species, a breaking point in the data was identified at 200 m away from the forest edge where bird densities were significantly lower before plateauing (Figure 3 in **Paper I**). The combined densities of these six non-forest nesting species in our study was on average 17 birds/km^2 in the first interval (0-50 m from the forest edge), 29 birds/km^2 in the second interval (51-100 m), 30 birds/km^2 in the third interval (101-150 m) and 51 birds/km^2 in the fourth interval (151-200 m) compared to 67 birds/km^2 in subsequent intervals. By adding these numbers to *Equation 1*, it is estimated that planting 1000 ha of forest in 1 large patch would result in only a fraction (~750 birds) of the declines of planting it in 1000 smaller (1 ha) patches (~7000 birds) (Figure 4 in **Paper I**). Average size of plantation forests in our study (where size of forest could be estimated from recent aerial photos) was approximately 37 ha, which would result in 27 patches covering 1000 ha (see **Paper I** for detailed calculations).

For Snipe and Redwing, a breaking point was estimated to be at a 50 m distance from the forest edge, but their combined densities in the first interval (0-50 m) was 114 birds/km^2, compared to 55 birds/km^2 in subsequent intervals (see **Paper I** for detailed calculations).

3.2 Power lines

On 85 transect surveys, 1,067 individual birds were identified, and eight of the most numerous species (Meadow pipit, Snipe, Whimbrel, Godwit, Redwing, Dunlin, Redshank and Golden plover) used in subsequent analysis (Table 5). Total number of birds increased with distance from power lines, as well as individual densities of Redshank and Whimbrel. No effects of power lines characteristics were identified as having effects on total number of birds or individual species (See **Paper II** for details).

3.3 Summer houses

At 71 sites in the Icelandic lowlands, birds were counted on 292 points, resulting in 2,819 individuals (Table 5). Of the total number of individuals, 89% comprised of seven species that were used in the analysis. Total bird density did not change with house presence or density, but the species-specific models revealed that five of the study species (Meadow pipit, Whimbrel, Godwit, Redshank and Golden plover) were found in lower densities in points with more houses. Snipe showed no effect and Redwing increased with house presence (See **Paper III** for details).

3.3.1 Habitat loss vs. house presence

When area lost due to infrastructure was included as an offset in the models exploring bird abundance in relation to house density, no significant changes to the results were identified. This suggests that the effect of houses on densities of ground-nesting birds are primarily driven by the presence of houses and associated factors, as opposed to habitat occupied by infrastructure.

3.4 Roads

In total 1,894 individuals were counted on 122 transects spanning two years, with the eight most numerous species (Meadow pipit, Snipe, Whimbrel, Dunlin, Godwit, Golden plover, Redwing and Redshank) retained for analysis (Table 5). Total bird density increased linearly with distance from the road. On a species level, four species (Meadow pipit, Whimbrel, Dunlin and Golden plover) showed a negative effect, being found in lowest densities closer to roads, and the four remaining species (Redwing, Godwit, Redshank and Snipe) showed no effect. For Dunlin, this effect depended on traffic volume (See **Paper IV** for details).

Table 5: Number of counted individuals in each part of the project, ranked by total abundance, along with total numbers recorded. Species are ranked by the number of individuals counted from 1-N for each respective part of the project and this number is shown in parenthesis. The species that were retained for analysis in each part of the project are shown shaded in grey.

Species	***Latin name***	**Paper I** (Plantation forests)	**Paper II** (Power lines)	**Paper III** (Summer houses)	**Paper IV** (Roads)	**Total**
Meadow pipit	*Anthus pratensis*	926 (1)	465 (1)	639 (3)	722 (1)	**2,752**
Common Snipe	*Gallinago gallinago*	719 (2)	159 (2)	695 (1)	391 (2)	**1,964**
Redwing	*Turdus iliacus*	476 (3)	49 (5)	682 (2)	100 (7)	**1,307**
Whimbrel	*Numenius phaeopus*	364 (4)	97 (3)	154 (4)	141 (3)	**756**
Black-tailed Godwit	*Limosa limosa*	202 (7)	67 (4)	135 (5)	106 (5)	**510**
European Golden plover	*Pluvialis apricaria*	246 (5)	44 (8)	86 (7)	102 (6)	**478**
Redshank	*Tringa totanus*	208 (6)	46 (7)	107 (6)	93 (8)	**454**
Dunlin	*Calidris alpina*	82 (8-9)	47 (6)	21 (13-14)	107 (4)	**257**
Lesser black-backed gull	*Larus fuscus*	62 (10)	30 (9)	32 (10-11)	11 (14)	**135**
Oystercatcher	*Haematopus ostralegus*	61 (11)	6 (12)	33 (9)	26 (9)	**126**
Greylag goose	*Anser anser*	59 (12)	5 (14)	32 (10-11)	17 (11)	**113**
Black-headed gull	*Chroicocephalus ridibundus*	82 (8-9)	1 (20)	20 (15-16)	4 (18)	**107**
Arctic tern	*Sterna paradisaea*	42 (13)	2 (17)	55 (8)		**99**
Common raven	*Corvus corax*	32 (14)	23 (10)	27 (12)	5 (17)	**87**
Arctic skua	*Stercorarius parasiticus*	28 (15)	6 (13)	16 (17)	24 (10)	**74**
Rock ptarmigan	*Lagopus muta*	25 (16)	2 (18)	20 (15-16)	6 (16)	**53**

Whooper swan	*Cygnus cygnus*	15 (18)	2 (19)	15 (18)	10 (15)	**42**
Mallard	*Anas platyrhynchos*	18 (17)	1 (21)	3 (22-23)	14 (13)	**36**
Red-necked phalarope	*Phalaropus lobatus*	12 (20)	5 (15)		15 (12)	**32**
Redpoll	*Acanthis flammea*			21 (13-14)		**21**
Eurasian wigeon	*Anas penelope*	10 (21)	7 (11)	2 (24)		**19**
White wagtail	*Motacilla alba*	6 (23)		12 (19)		**18**
Great black-backed gull	*Larus marinus*	7 (22)	3 (16)	3 (22-23)		**13**
Ringed plover	*Charadrius hiaticula*	13 (19)				**13**
Common shelduck	*Tadorna tadorna*	2 (26-28)		4 (20-21)		**6**
Harlequin duck	*Histrionicus histrionicus*	5 (24-25)				**5**
Northern wheatear	*Oenanthe oenanthe*	5 (24-25)				**5**
Starling	*Sturnus vulgaris*			4 (20-21)		**4**
Eurasian teal	*Anas crecca*	2 (26-28)				**2**
Northern fulmar	*Fulmarus glacialis*	2 (26-28)				**2**
Blackbird	*Turdus merula*	1 (29-30)				**1**
European Herring gull	*Larus argentatus*	1 (29-30)				**1**
Short-eared owl	*Asio flammeus*			1 (25)		**1**
Total		**3713**	**1067**	**2819**	**1894**	**9493**

3.5 Cumulative effects of studied structures

3.5.1 Species specific vulnerability index and assessment of local population trends

The combined results of the four independent datasets revealed that Whimbrel and Golden plover showed the strongest negative effects from anthropogenic structures (significant negative effects of 4 and 3 structure types, respectively), followed by Godwit, Dunlin, Redshank and Meadow pipit which showed negative effects of 2 types of structures (although they varied in which ones), and Oystercatcher which was only found in large enough numbers surrounding plantation forests to identify any pattern. Both Snipe and Redwing only showed positive (from 1 and 2 structure types, respectively) or neutral effects (Table 6, Figure 4).

Table 6: Vulnerability index calculated from the respective results of single structures on the density of the study species, along with the population trend in the past 10 years in point counts performed in the last 10 days of June each year along road transects in the Icelandic lowlands (Gunnarsson & Þórisson, 2019).

	Plantation forest	**Power lines**	**Summer houses**	**Roads**	**Vulnerability index**	**Trend***
Whimbrel (*Numenius phaeopus*)	↓	↓	↓	↓	**-4**	Declining
Golden plover (*Pluvialis apricaria*)	↓	0	↓	↓	**-3**	Declining
Godwit (*Limosa limosa*)	↓	0	↓	0	**-2**	Declining
Dunlin (*Calidris alpina*)	↓	0	NA	↓	**-2**	Declining
Redshank (*Tringa totanus*)	0	↓	↓	0	**-2**	Declining
Meadow pipit (*Anthus pratensis*)	0	0	↓	↓	**-2**	Declining
Oystercatcher (*Haematopus ostralegus*)	↓	NA	NA	NA	**-1**	Declining
Snipe (*Gallinago gallinago*)	↑	0	0	0	**+1**	No trend
Redwing (*Turdus iliacus*)	↑	0	↑	0	**+2**	Increasing

**Data from a 10 year series of point counts. Estimates from models are shown in Appendix A.*

When comparing these results to the points counts from the Icelandic southern lowlands, all seven species which showed negative effects of structure presence were found to be decreasing, Snipe showed no trend and Redwing is increasing (Table 6, Table A1, Figure 4).

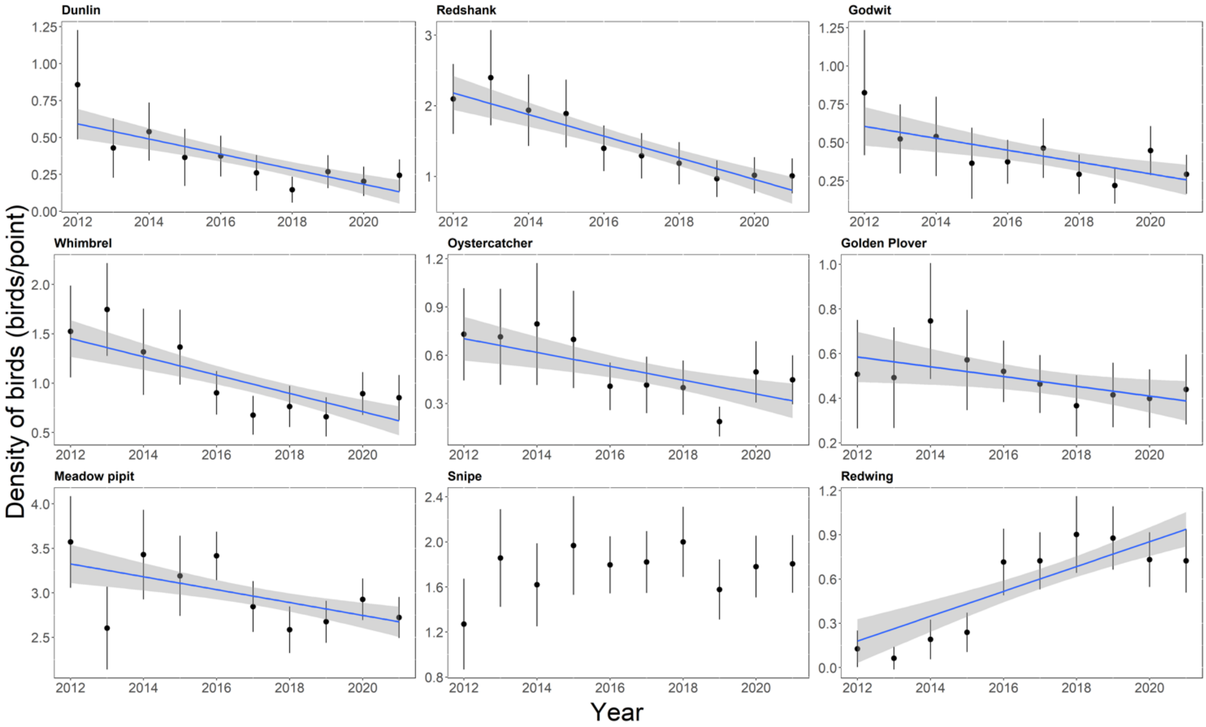

Figure 4: Densities of the study species (±SE) in point counts from the southern lowlands over a course of 10 years, along with a regression line (±SE). Points were counted in the last 10 days of June each year. Data obtained from Gunnarsson and Þórisson (2019).

3.5.2 Assessing current status of anthropogenic influence in the Icelandic lowlands

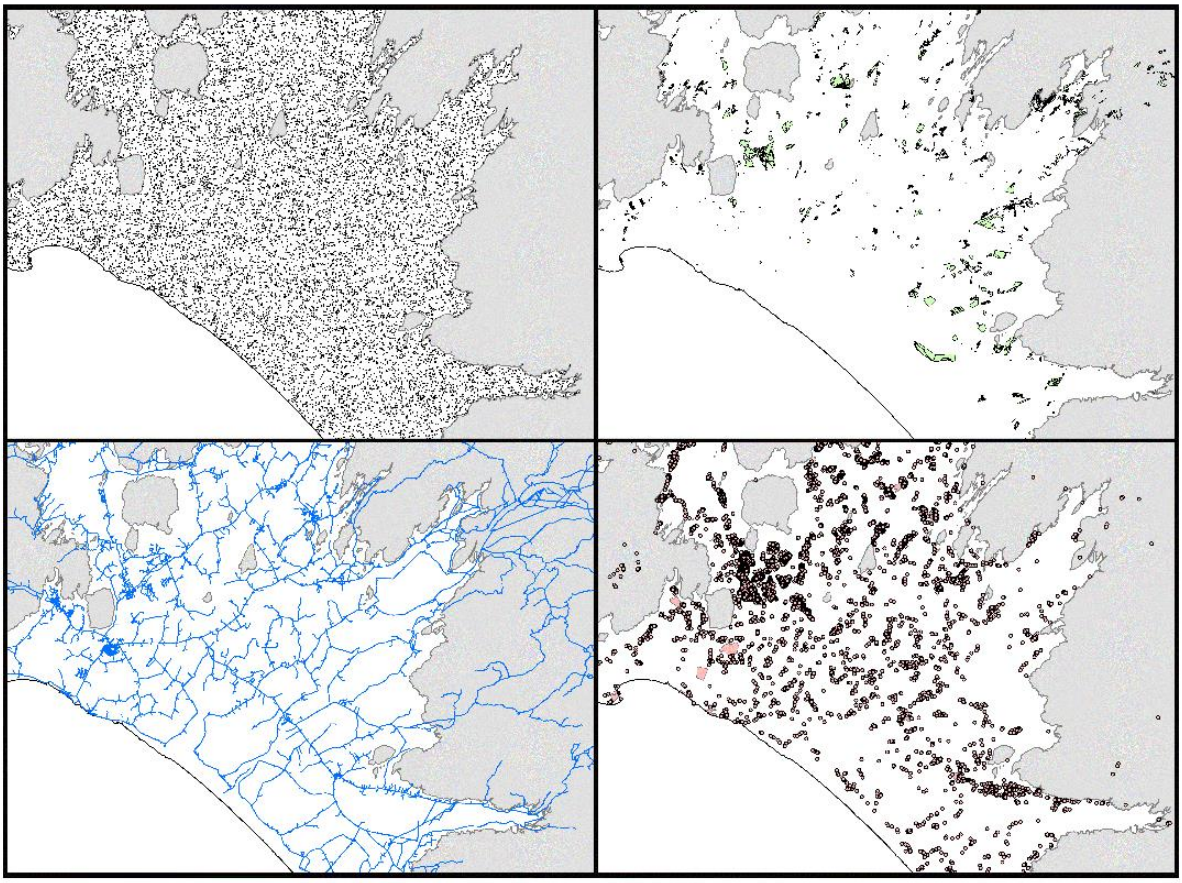

Figure 5: An example from the southern lowlands of the distribution of random points generated (top left), plantation forests (top right), roads (bottom left) and housing infrastructure (bottom right).

Out of 100,000 points generated, 24% were within 200 m from any of the structures in this studiy, 6.6% were within 200 m from two structures and 1.2% from all three (plantation forests, housing infrastructure and roads; Figure 5, Table 7).

Table 7: The number and proportion of 100,000 random points (generated in ArcGIS) in the Icelandic lowlands that are within the affected area (defined by the results from our study as ≤200 m distance) of three structure types, forest plantations, housing infrastructure and roads.

Structure	**Points < 200 m from structure**	**% of all points**
Housing infrastructure	5,531	5.5
Roads	20,151	20.1
Plantation forests	6,262	6.3
Types of structures (plantation forest, housing infrastructure and roads) within 200 m		
1 structure	17,548	17.5
2 structures	5,428	6.6
3 structure	1,180	1.2
Total	24,156	24.2

4 Conclusions

The expansion of anthropogenic impacts has been considered a main cause for loss of biodiversity across the globe (Dirzo *et al.*, 2014). The introduction of structures and alterations of natural habitats for resource production will inevitably decrease the amount of native vegetation and habitats, along with secondary effects through changes to the surrounding landscape. These changes may influence the demography of bird populations in the vicinity, along with behavioural effects which may influence the distribution of individuals surrounding these structures. Here, strong, negative effects of structures on the density of ground-nesting birds in the vicinity in the Icelandic lowlands were identified for seven species. This thesis consists of four parts, which examine the effect of structures on nine (forest plantations), eight (summer houses and roads) and seven (power lines) individual species (Table 5), totalling 32 species-structure assessments. In sixteen (50%) of these 32 assessments, significantly lower densities occurred closer to structures, while significantly higher densities were only identified in three (9%) assessments, and only for two species, Redwing and Snipe (Table 6). Significantly lower densities were recorded at distances up to ~200 m from roads and forests (the structures around which the most extreme changes in bird density occurred). This distance is relatively short compared to other studies in Europe, where distances with effects have been identified ranging from 50 m (single trees) to over 3,000 m (roads with high traffic volume) (Reijnen *et al.*, 1996; Stroud *et al.*, 2009; van der Vliet *et al.*, 2010; Wilson *et al.*, 2014). The distance over which reduced bird density occurs may depend on an array of factors, and on the drivers underlying such patterns, which are currently unknown. Iceland holds several avian predators that prey on bird nests such as Ravens (*Corvus corax*), Arctic skua (*Stercorarius parasiticus*), various gull species (*Larus sp.*) and two mammalian predators, Arctic fox (*Vulpes lagopus*) and American mink (*Neovison vison*) (Bonesi & Palazon, 2007; Sillero-Zubiri *et al.*, 2004), as well as domestic cats (Bonnington *et al.*, 2013). Predators may use trees, houses and power lines for nesting and perching, and studies have found mammalian predators to travel along roads (Seiler, 2001). Little is known exactly about if and how predators use these structures in Iceland but, if they do, their presence may increase actual or perceived predation risk in the surrounding habitats, potentially prompting individuals to avoid nesting close to structures and/or directly altering the risk of mortality for eggs, chicks or adults. The three structure types which showed the largest effect on bird densities (roads, houses and plantation forests) are those most likely to constrain visibility (the majority of roads in the Icelandic lowlands are elevated), suggesting that the view-obstructing properties of structures may be particularly important components of their impact on ground-nesting birds.

The two species that showed the most consistent reduced densities close to structures in the Icelandic lowlands were Whimbrel and Golden plover, which showed negative effects from four and three structure types, respectively. Generally the nests of these species are not well-concealed (Laidlaw *et al.*, 2020), and individuals may rely on other anti-predatory behaviours which may be compromised with the presence of structures. Populations of these two species may therefore be particularly vulnerable to increased human influence in the Icelandic lowlands and, considering that Iceland holds approximately 40-52% of their populations, these effects should not be ignored and rather considered an important part in future landscape development. Out of seven wader species showing negative effects of structure presence, most individuals were identified of these two species and Godwit, in all studies combined (Table 5). A larger sample size increases the chances of detecting slight effects but when studying waders, which have large home ranges, encounter rates can be low which makes it difficult to detect changes in density. This raises the question whether a larger sample would increase the effects detected on species in which fewer individuals were found but have similar life histories. Previous studies on Golden plovers have shown a negative effect of both wind farms and tracks on density up to 200 m (Pearce-Higgins *et al.*, 2009), but results vary on their response around forest edges, being either neutral (Hancock *et al.*, 2009) or negative (Amar *et al.*, 2011; Buchanan *et al.*, 2017; Stroud *et al.*, 2009; Wilson *et al.*, 2014). The effects of these structures on Whimbrel have been less studied, but a preference of open and tree-less areas has been documented (Ballantyne & Nol, 2011; Katrínardóttir *et al.*, 2015).

Godwit densities were lower adjacent to summer houses and plantation forests, Dunlin densities adjacent to plantation forests and roads, and Redshank densities adjacent to power lines and summer houses. These three species all breed in vegetated habitats such as wetland and grasslands (Jóhannesdóttir *et al.*, 2014), and the nests are generally very well-concealed (Laidlaw *et al.*, 2020). It is therefore possible that these species are less influenced by compromised visibility surrounding the nest than Golden plover and Whimbrel, which nest in open habitats and may rely more on early detection of predators (Laidlaw *et al.*, 2020). Previous studies have shown that Godwit and Dunlin occurrence is negatively correlated with the presence of trees in surrounding landscapes (Holmes *et al.*, 2020; Żmihorski *et al.*, 2018). Additionally, Dunlin has been shown to occur in lower abundances close to forest edges (Hancock *et al.*, 2009; Stroud *et al.*, 2009; Wilson *et al.*, 2014) and Redshank occurrence to be negatively associated with proximity to buildings (Żmihorski *et al.*, 2018). The drivers behind these patterns are often hard to identify, but studies on nest survival of Dunlin and Redshank have been contradictory, with some revealing no clear fitness benefits from nesting further away from trees and structures (Holmes *et al.*, 2020; Laidlaw *et al.*, 2015; Ottvall *et al.*, 2010) while other identify a lower nest survival close to forest edges, due to a higher predation rate (Kaasiku *et al.*, 2022).

Meadow pipit is the only passerine in our study that nests exclusively in open habitat. Meadow pipits showed negative effects of roads and houses. Being the most common species in our study, with just under 3,000 individual counted, these result should be able to identify any effects of structures on Meadow pipit density. Previous studies have shown no effect of proximity to transmission lines on Meadow pipit density and a small affected area surrounding wind farms (100 m) (Pearce-Higgins *et al.*, 2009). Meadow pipits have smaller home ranges than the wader species in this study and will likely not be as vulnerable to increased anthropogenic effects, provided there is still enough breeding habitat remaining.

Snipe was found in higher density close to forest edges but no other effects were identified. Previous studies on Snipe have been inconsistent, but they have been shown to be negatively affected by closeness to forest edges, wind farms and tracks, while showing no effects of transmission lines (Amar *et al.*, 2011; Pearce-Higgins *et al.*, 2009) and their densities increase with vegetation height (Buchanan *et al.*, 2017). Snipes are the only wader species in Iceland known to nest in forests (Halldórsson *et al.*, 2008) and are found in all major habitat types, although they are in the highest densities in wetlands (Jóhannesdóttir *et al.*, 2014). Snipe being found in higher numbers closer to forest edges, may be because they prefer to hide their nest in higher vegetation which is often found in and around forest edges. However, Snipe did not show negative effects of any anthropogenic structures in this study, suggesting that Snipe is not of high conservational concern when it comes to the effects of structures in open habitats, except for the habitat lost.

Redwing showed positive effects of proximity to forests and summer houses. The majority of summer houses in Iceland have some trees planted around them which may contribute to increased Redwing density. The Redwing population in Iceland is likely to increase with increased forestry and urbanization, as they are also known to nest in forests (Skarphéðinsson *et al.*, 2016) and urban areas. There are already signs of localised increases of Redwings, with model estimates from point counts showing on average a 12% increase in Redwing numbers each year (Table A1). In addition to Redwings, it is also possible that certain species which were uncommon in our datasets will become more numerous surrounding anthropogenic structures, but citizen science in Iceland has shown that Redpoll (*Acanthis flammea),* Starling (*Sturnus vulgaris),* Goldcrest (*Regulus regulus*), Rock dove (*Columba livia*), Ravens, Eurasian wrens (*Troglodytes troglodytes*), Blackbirds (*Turdus merula*) and Fieldfares (*Turdus pilaris*) all occur frequently in urban settlements (Einarsson, 2021). These species were rarely, if ever, seen in our study areas (Table 5). The process of urbanization and increased human presence in natural habitats will inevitably change bird communities in these areas, which are expected to become more homogenised (Devictor *et al.*, 2007). Species that are common in urban and forested areas in Iceland generally have larger populations globally and are currently of less conservational concern than the most common open-habitat species in this study (IUCN, 2022; Stroud *et al.*, 2006).

There is a consistency between the population trends attained from the point count data and the combined results from densities of ground-nesting birds surrounding structures. For all species that were found in significantly lower densities surrounding at least one of the structures, significant decreases were identified from the point counts (Table 6). For the two species (Snipe and Redwing) for which abundances either did not vary with distance from structure or increased closer to structures, point count data indicate stable and increasing trends, respectively. Considering that a quarter of the 100,000 random points in the Icelandic lowlands were currently defined as being affected by these structures, it is not surprising that evidence of localised abundance changes is becoming apparent. It is also important to consider that the lowlands contain many areas which are not suitable for nesting by these species such as lakes, rivers, slopes and un-vegetated areas (Figure 1). However, the point counts used here were performed in areas in the southern lowlands which are currently under considerable anthropogenic influence and, although representative of localised changes in abundance, they may not necessarily represent population-scale changes in Iceland (point counts from other less developed areas do not show consistent negative trends for these species; (Lárusdóttir *et al.*, 2019; Náttúrufræðistofnun Íslands, 2019; Náttúrustofa Norðausturlands, 2018).

Anthropogenic impacts are increasing at a rapid pace in Iceland, with the ongoing expansion of among other, houses, wind farms, power lines, roads and plantations forests in the lowlands (EEA, 2018; Wald, 2012). Funding to the Icelandic forestry service has been raised for carbon sequestration (Ministry for the Environment and Natural Resources, 2018) and already 7,000 summer house plots have been approved with houses yet to be built (Registers Iceland, 2022b). These structures and habitats are generally accompanied by roads and power lines, which will then likely increase. In addition to these structures, there are plans for increased wind farm construction in Iceland (Orkustofnun, 2015) and according to a survey from 2014, more than half (63%) of farmers in Iceland intended to expand their agricultural areas (Jóhannesdóttir *et al.*, 2017), which may contribute to an altered landscape for ground-nesting birds. Habitat loss for ground-nesting birds in the Icelandic lowlands, which are currently composed of a mosaic of natural open habitats along with low-intensity agricultural patches, forestry and low density of anthropogenic structures (Gunnarsson *et al.*, 2006a), due to structure placement in the coming years is therefore expected to be considerable. The affected area, here defined as ~200 m surrounding these structures, may than even further exacerbate this effect and increase the negative effects on these bird species. Habitat degradation has been identified as the primary driver behind the recent global decline of waders (International Wader Study Group, 2003; Ławicki *et al.*, 2011). Attempts at restoring lost breeding bird habitat or increase current densities in available habitats after population declines in other countries have often proved unsuccessful, with restored sites holding lower nesting densities than reference sites (Bentzen *et al.*, 2018; Melman *et al.*, 2008). The negative effects of these structures on densities of ground-nesting birds documented here, along with a negative trend of these species in yearly counts, emphasizes the need for preserving the breeding habitats of these species, and not allow anthropogenic expansion into currently unaffected areas.

Appendix A

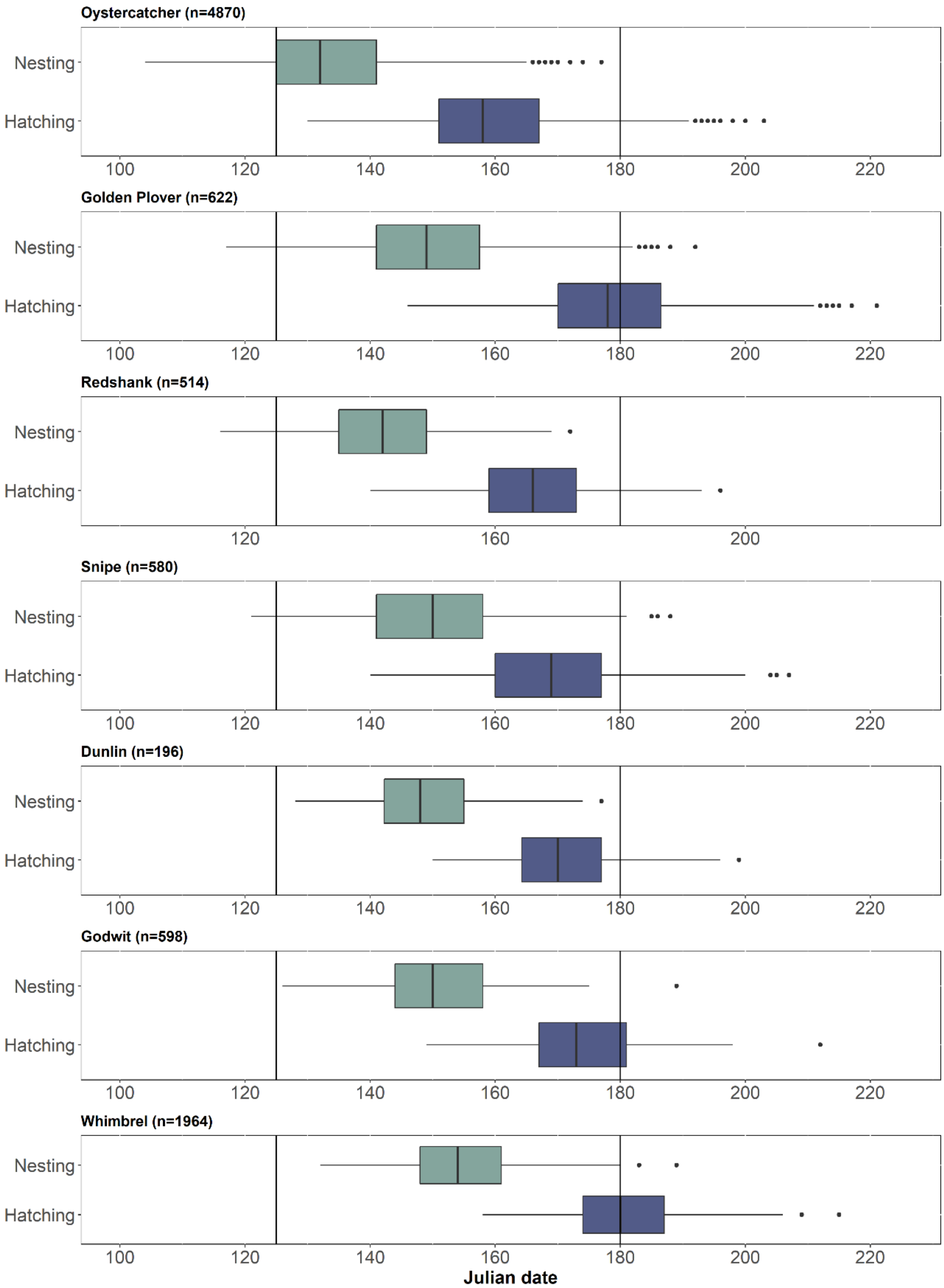

Figure A1: Boxplot showing the average timing of initiation of nesting (first egg laid; calculated by flotation tests) and hatching (Cramp and Simmons (1983) used as reference for incubation period) of 9,344 nests of waders in Iceland measured between the years 2011-2021. The vertical lines show period where bird counts were conducted in this study (1st of May to 30th of June).

Table A1: Estimates from the GLMM models on log scale of the influences on densities of nine species and the combined abundance of year and traffic. Data obtained from Gunnarsson and Þórisson (2019) and significance represented by letters (A, B and C).

Full model: Bird abundance (birds/point) ~ year + traffic (1000 cars/day) + (1|pointID)

Variable	**All birds**	**Meadow pipit**	**Snipe**	**Redwing**	**Whimbrel**	**Godwit**	**Golden plover**	**Redshank**	**Dunlin**	**Oystercatcher**
Intercept	2.39(±0.04)	1.23 (±0.06)	0.37 (±0.08)	-2.13 (±0.21)	-0.12 (±0.14)	-1.17 (±0.20)	-0.77 (±0.16)	0.13 (±0.12)	-1.38 (±0.26)	-1.23 (±0.20)
Year	-0.03(±0.01)^{A}	-0.03 (±0.01)^{A}	0.01 (±0.01)	0.12 (±0.02)^{A}	-0.05 (±0.01)^{A}	-0.06 (±0.02)^{B}	-0.04 (±0.02)^{C}	-0.07 (±0.01)^{A}	-0.10 (±0.02)^{A}	-0.05 (±0.02)^{B}
Traffic	-0.01 (±0.02)	-0.03 (±0.04)	0.07 (±0.05)	0.36 (±0.12)^{B}	-0.28 (±0.10)^{B}	-0.24 (±0.16)	-0.14 (±0.11)	0.15 (±0.07)^{C}	-0.64 (±0.24)^{B}	-0.18 (±0.14)

Significance: ^{A} p<0.001; ^{B} p<0.01; ^{C} p<0.05

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Paper I

Subarctic afforestation: effects of forest plantations on ground-nesting birds in lowland Iceland

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Abstract

1. Planting forests is a commonly suggested measure to mitigate climate change. The resulting changes in habitat structure can greatly influence the diversity and abundance of pre-existing wildlife. Understanding these consequences is key for avoiding unintended impacts of afforestation on habitats and populations of conservation concern.
2. Afforestation in lowland Iceland, primarily involving plantations of non-native tree species, has been gaining momentum in recent years and further increases are planned. Iceland supports internationally important breeding populations of several ground-nesting, migratory bird species that mostly breed in open habitats. If afforestation impacts the distribution and abundance of these species, the consequences may be apparent throughout their non-breeding ranges across Europe and Africa.
3. To quantify the effects of plantation forests on the abundance and distribution of ground-nesting birds (in particular waders, *Charadriiformes*), surveys were conducted on 161 transects (surrounding 118 plantations) perpendicular to forest edges throughout Iceland. The resulting variation in density with distance from plantation was used to estimate the likely changes in bird numbers resulting from future afforestation plans, and to explore the potential effects of different planting configuration (size and number of forest patches) scenarios.
4. Of seven wader species, densities of five (Golden Plover (*Pluvialis apricaria*), Whimbrel (*Numenius phaeopus*), Oystercatcher (*Haematopus ostralegus*), Dunlin (*Calidris alpina*) and black-tailed Godwit (*Limosa limosa*)) in the 200 m surrounding plantations were just around half of those further away (up to 700 m). Redshank (*Tringa totanus*) showed no variation with distance, Snipe (*Gallinago gallinago*) densities were 50% higher close to plantations (0-50 m) than further away (51-700 m), and no consistent effects of plantation height, diameter, density or type were identified. Plantations are typically small and widespread, and simulated scenarios indicated that total declines in bird abundance resulting from planting trees in one large block (1000 ha) could result in only ~11% of the declines predicted from planting multiple small blocks (1 ha) in similar habitats.
5. *Synthesis and application:* The severe impact that planting forests in open landscapes can have on populations of ground-nesting birds emphasizes the need for strategic planning of tree-planting schemes. Given Iceland's statutory commitments to species protection and the huge contribution of Iceland to global migratory bird flyways, these are challenges that must be addressed quickly, before population-level impacts are observed across migratory ranges.

Introduction

Loss and degradation of habitats that support wildlife is one of the major drivers of global biodiversity decline (Dirzo *et al.*, 2014). These changes often result from land conversion due to human activities, such as the development and expansion of housing, roads and agriculture; processes which reduce the overall amount of natural habitat and increase fragmentation of the landscape, creating smaller and more isolated habitat patches (Foley *et al.*, 2005; Torres *et al.*, 2016). During the initial stages of land conversion, habitat loss and fragmentation are often characterized by the introduction of novel structures such as roads, electric pylons, trees and wind turbines (Amar *et al.*, 2011; D'Amico *et al.*, 2018; Hovick *et al.*, 2014; Sutherland *et al.*, 2012). Structures can have direct effects such as increased collision risk and changes in foraging and breeding opportunities, and indirect effects such as changes in microclimatic conditions or altered predator-prey and host-parasite relationships on local populations, processes which can subsequently influence mortality, productivity and recruitment rates (Ewers & Didham, 2006; Fernández-Bellon *et al.*, 2018; Fischer & Lindenmayer, 2007; Hovick *et al.*, 2014; Pearce-Higgins *et al.*, 2009; Prugh *et al.*, 2009). The presence of novel structures may also affect the distribution of individuals in the surrounding landscape through changes in demographic factors such as altered rates of survival or recruitment or through behavioural change with individuals changing their temporal and/or spatial activity patterns by avoiding or choosing to be close to these structures (Dinkins *et al.*, 2014; Ditchkoff *et al.*, 2006; Jameson & Willis, 2014; Łopucki *et al.*, 2017; Wang *et al.*, 2015), potentially reducing local population sizes.

In recent decades, climatic amelioration at higher latitudes has facilitated rapid forestry development in areas where tree growth was previously limited by harsher environmental conditions (Halldórsson *et al.*, 2008). Afforestation at these latitudes can lead to loss and fragmentation of the open habitats that dominate these landscapes, with potentially important impacts on pre-existing biodiversity (Brockerhoff *et al.*, 2008; Halldórsson *et al.*, 2008). While afforestation may benefit species that use forest habitats, species that require open landscapes may decline, particularly if the landscape surrounding forests supports fewer individuals (Halldórsson *et al.*, 2008). Previous studies have reported lower densities of some open-nesting (i.e. nesting in open, non-forested habitats) bird species close to forest edges (Hancock *et al.*, 2009; Holmes *et al.*, 2020; Stroud *et al.*, 2009; Wilson *et al.*, 2014). Lower densities of open-nesting birds could reflect demographic effects such as increased distances between locations needed for foraging, breeding and chick rearing increasing travel costs and associated risks; or increased predation rates because predator activity is concentrated around forests (Berg *et al.*, 1992; Macdonald & Bolton, 2008; Svobodová *et al.*, 2010; Wilcove *et al.*, 1986), or behavioural effects (e.g. avoidance of areas in which visibility is impeded). Several studies have found ground-nesting waders to nest significantly further away than expected from man-made structures and trees, without clear fitness benefits (Bertholdt *et al.*, 2017; Holmes *et al.*, 2020; Wallander *et al.*, 2006).

In Iceland, which has been largely treeless for ~1000 years, afforestation could have widespread deleterious effects on the ecological communities of currently abundant open landscapes that support internationally important biodiversity. Icelandic forestry is still in its infancy and currently forests cover ~1.9% of the land area (~190,000 ha; (Eysteinsson, 2017)). Downy birch (*Betula pubescens*) is the only tree species to naturally form continuous forests in Iceland (Eysteinsson, 2017) and plantation forests typically contain non-native species such as sitka spruce (*Picea sitchensis*), larch (*Larix spp.*), lodgepole pine (*Pinus contorta*) and black cottonwood (*Populus trichocarpa*), along with the downy birch (Brynleifsdóttir, 2018). In 2018, the Icelandic government provided additional funding to the Icelandic forestry service to increase the number of trees planted, with a goal of enhancing carbon sequestration (Ministry for the Environment and Natural Resources, 2018). As forestry primarily operates through government grants to private landowners to plant trees within their land (Halldórsson *et al.*, 2008), plantations typically occur as numerous small patches in otherwise open landscapes. These features make Iceland an ideal location in which to quantify the plantation effects on densities of birds in the surrounding habitats, and identify afforestation strategies that might reduce these effects.

The ongoing expansion of plantation forestry in Iceland is mostly in the vegetated lowlands, which are also the most important habitats for most ground-nesting bird populations

(Gunnarsson *et al.*, 2006; Jóhannesdóttir *et al.*, 2014; Skarphéðinsson *et al.*, 2016). The most common ground-nesting species in Iceland are Meadow pipit, (*Anthus pratensis)*, and several species of wader (Jóhannesdóttir *et al.*, 2014). Several avian predators that commonly prey on bird nests also breed in lowland Iceland, including ravens (*Corvus corax*) (Þórisson, 2013) which have begun nesting in trees in Iceland, although this is still relatively rare (K.H. Skarphéðinsson, personal communication, November 2, 2018). Iceland also has two mammalian nest predators: arctic fox (*Vulpes lagopus*) and American mink (*Neovison vison*), which is a non-native species (Bonesi & Palazon, 2007; Sillero-Zubiri *et al.*, 2004), in addition to domestic cats which are common and likely to be occasional nest predators (Bonnington *et al.*, 2013). While little is currently known about how predators in Iceland use plantations, any perceived risks of predator presence and/or reduced visibility may influence densities of birds in the surrounding landscape (Amar *et al.*, 2011; van der Vliet & Wassen, 2008; Wilson *et al.*, 2014). Here we use surveys of open-nesting birds in lowland Iceland to assess (a) whether densities are reduced in the landscape surrounding plantations; (b) whether these effects vary among plantations with differing characteristics; and (c) the potential impact of differing future afforestation plans for lowland Iceland.

Methods

Study sites

The study was conducted in south, west and north Iceland (Figure 1). Forests that were at least 30 m in diameter, surrounded by homogenous semi-natural habitat and >100 m from houses or agricultural land (70% of forests were >200 m from these features) were selected from aerial photos and known locations. As all forests included in the study contained or were exclusively made up of non-native species, they are hereafter referred to as plantations. Afforestation primarily takes place within semi-natural habitats which were classified using the farmland database *Nytjaland* as: wetland, semi-wetland, rich heathland, poor heathland or grassland (Gísladóttir *et al.*, 2014).

Bird censuses

In total, 161 surveys of bird distribution and density were undertaken surrounding plantations between May and June 2017, spanning the majority of the nesting and chick-rearing period of ground-nesting species in Iceland (Alves *et al.*, 2019; Gunnarsson *et al.*, 2017). To ensure that detectability of target species was as consistent as possible counts were conducted between 8 am and 10 pm, to avoid peaks in bird activity early in the morning and reduced activity levels later in the evening (Davíðsdóttir, 2010), in wind speeds < 7 m/s and avoiding periods of heavy rainfall (Hoodless *et*

Figure 1: Location of 118 plantations around which transects were conducted in the summer of 2017 in areas below 300 m a.s.l. (shown in grey) in Iceland.

al., 2006). To avoid systematic bias arising from possible "push effects" of corralling birds in front of the surveyor, surveys were conducted along transects that started either at the edge of the plantation with the observer moving away (79 transects), or started away from the plantation with the observer walking towards it (82 transects). Each transect was surveyed once but, when sufficiently large blocks of homogenous habitat were available on both sides of a plantation (43 out of 118 plantations), two separate transects in opposite directions were conducted from the same plantation, each on different sides of the plantation. Transects were conducted within a single habitat type, and transect length ranged between 300 and 700 m (mean length = 581 ± 133 SD) depending on the homogeneity of the landscape and the presence of obstructions such as lakes or rivers, resulting in a total distance covered of 93 km. All transects were preceded by a 5-minute period in which the observer stood still to allow birds to settle, after which the transect was walked at a steady pace without stopping. All birds seen or heard within a 100 m range on either side of the transect were recorded when first seen, and their distance from the plantation documented. If there was any doubt that this was the first time the bird was seen, the individual was not documented for a more conservative estimate. Subsequently, transects were divided into 50 m distance intervals (1 ha in area) from the forest edge, and the number of birds recorded within each interval was calculated (Figure B1).

Plantation characteristics

For each plantation, a suite of characteristics was recorded (Table 1). As plantation diameter and area were strongly correlated (Pearson's $r = 0.84$, $n = 76$, $p < 0.001$), only diameter was included in subsequent models (Table 1). Coniferous, broad-leaved and mixed plantations were comparable in diameter, height and density (Table B1) and sampling of all plantation characteristics occurred throughout the survey period and the daily survey times.

Table 1: Variables and model structure used to quantify the effect of forests on the density of breeding birds recorded on transects through the surrounding landscape in lowland Iceland.

Variable	Unit	Definition
Bird density	Birds ha^{-1}	Number of birds recorded in each 1 ha interval of each transect
Interval	1-14	50 m distance bands from closest (1) to furthest (14) from the plantation edge
Transect	Transect number	Individual transect (one or two per plantation)
Direction	To/from	Transects were walked towards or from the plantation edge
Plantation diameter	m	Distance between two outermost trees on plantation edges, recorded from aerial photos (Icelandic Forest Service, 2014) or in the field with a rangefinder
Plantation area	m^2	Area of forest, extracted from aerial photos
Plantation height	0-2 /2-5 / 5-10 /> 10 m	Tallest visible point of plantation, measured with a rangefinder
Plantation type	Mixed/conifer/broadleaf	Predominant tree type (coniferous, broadleaved or both)
Plantation density	Sparse/dense	Interior (up to 50 m) of plantation visible (sparse) or not (dense) from edge
Habitat	Poor heathland/rich heathland/grassland/ semi-wetland/wetland	Classification of transect habitat (Gísladóttir *et al.*, 2014)
Plantation	Plantation number	Individual plantations (one or two transects per plantation)
Full model	Bird density (birds/ha) ~ Interval + Height + Width + Type + Forest Density + Habitat + Direction (where applicable) + (1|Plantation/Transect)	

Effects of plantation configuration on bird density

To explore the magnitude of effect on waders of different future plantation configurations, segmented linear regression was used to identify the 'breaking point' distance from the plantation edge at which the most extreme change in bird densities occurs, and thus separate the 'affected area' within which densities differed from the remaining 'unaffected area'. Mean densities in affected and unaffected areas were used to estimate the changes in abundance of these species resulting from scenarios of planting 1000 ha as one large up to 1000 small (1 ha) plantations, combining the change in bird numbers in the forested area (assuming complete loss for open-nesting species (Halldórsson *et al.*, 2008)) and the affected area (altered density) within each distance band, as;

Equation 1:

Change in number of birds = No of patches (Change in numbers in forest area + Change in numbers in affected area)*

$$\Delta N = P^* (\Delta D_T + \Delta D_A)$$

$$\Delta N = P^* (T^* (D_T - D_U) + A^* (D_A - D_U))$$

where N = number of birds, P = number of plantation patches, T = plantation area, A = affected area, D_T = average bird density in plantation area (assumed to be 0 for open-nesting species), D_A = average bird density in affected area, D_U = average bird density in unaffected area. All plantation patches were assumed to be circular (giving the most conservative estimate of affected surrounding area) and have an individual affected area with no overlap between patches. Confidence intervals for the change in numbers of birds were then calculated by bootstrapping the observed variation in bird density per area and repeating the equation 1000 times. To assess how much of the Icelandic lowlands is currently within the affected area of forest plantations, the distance from plantation forests to 100,000 randomly located points was calculated using a GIS layer from the Icelandic forest service (Icelandic Forest Service, 2021).

Statistical analyses

In order to assess the change in density of birds with distance to plantation, we constructed a generalized linear mixed effect model (GLMM) with a Poisson distribution and a log-link function, with bird density as the response variable, accounting for zero inflation when appropriate by using the R package glmmADMB (Fournier *et al.*, 2012). First, models were constructed to assess the effect of direction of transects (direction, interval and their interaction as explanatory variables) with transect identity nested in plantation identity included as a random factor to account for non-independence of intervals within the same transect and surrounding the same plantations. Second, models exploring the effects of interval, distance from plantation, habitat and plantation characteristics were explored for each individual species (Table 1), with direction of transect included for the three species for which counts differed significantly with direction and transect nested in plantation identity included as a random factor. For plantation type, broadleaved, which most closely resembles the native birch forest, was used as the reference, and 2-5 m category as the reference height and grassland as reference habitat which were the most numerous categories Starting with a full model, sequential deletion of non-significant predictors (plantation factors and habitat removed in an order of increasing significance as determined by a priori test) (Table B2) was used to find minimum models by removing a single factor at a time, and comparing the resulting model to the previous more complex model with a chi-square test (backward stepwise regression). If removal of a given predictor resulted in a significant change in the model, it was retained in subsequent models (Harrison *et al.*, 2018). In addition to backward stepwise regression, sequential adding of factors to the null model (forward stepwise regression), and subsequent comparison of the AIC values was performed to verify the model selection. All statistical analyses were undertaken in RStudio 1.0.153 (R Core Team, 2017; RStudio Team, 2016) with R packages "segmented" used to estimate break points in density changes over distance intervals (Muggeo, 2008).

Results

Relationships between distance to plantation and bird density

On the 161 transects conducted across lowland Iceland, 3713 individual birds of 30 species were recorded The nine most common species (excluding gulls which do not breed in the focal habitats) used in subsequent analyses were seven waders; Oystercatcher, Golden Plover, Dunlin, common Snipe (hereafter Snipe), Whimbrel, black-tailed Godwit (hereafter Godwit), Redshank; and two passerines: Meadow pipit and Redwing (*Turdus iliacus*). These species comprised 88% of all birds recorded. Of the seven waders, Snipe was the only one found in significantly higher numbers closer to plantations, with density decreasing on average ~6% per 50 m increment (Table B3, Figure 2). Snipe density declined by approximately 50% between the first (0-50 m) and second (50-100 m) distance intervals, suggesting a highly localized effect

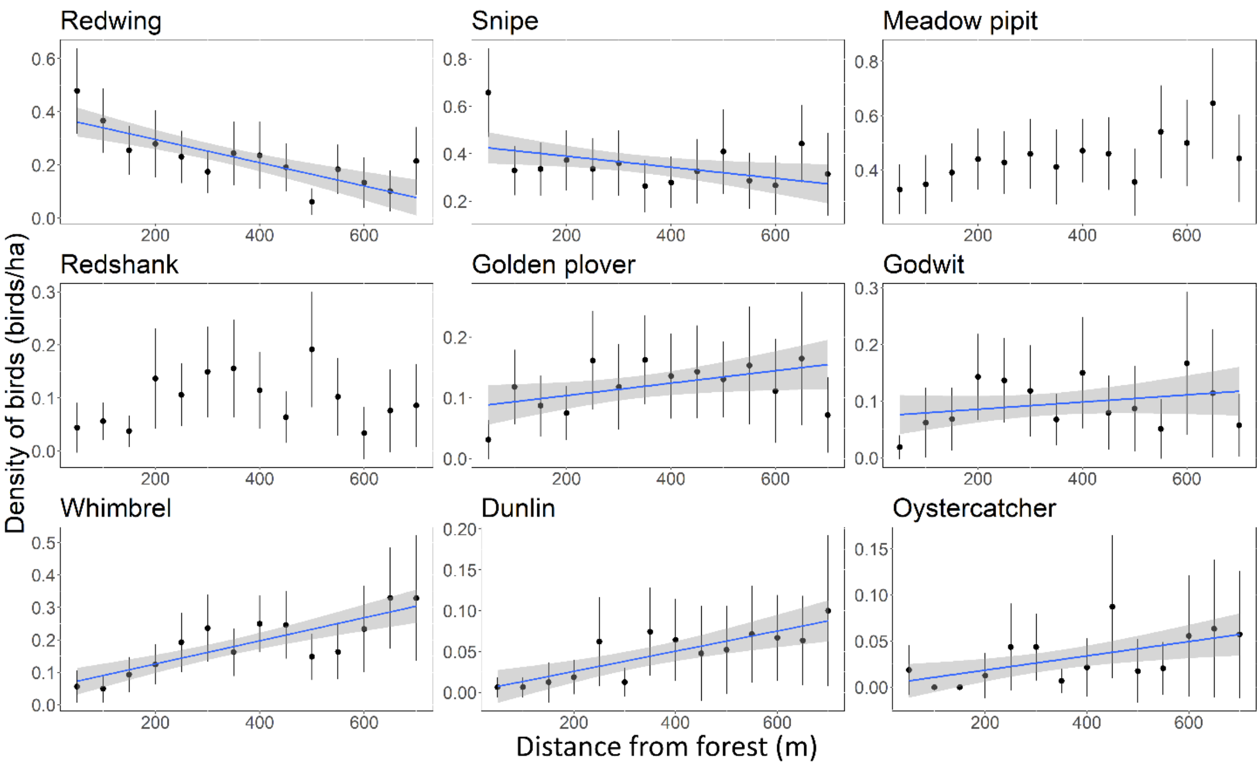

Figure 2: The mean (± SE) density of nine species with distance from plantations in 50 m intervals along transects. Regression lines (± SE) are shown for significant relationships.

of plantations. Densities of Golden Plover, Whimbrel, Oystercatcher, Dunlin and Godwit all increased significantly with increasing distance from all plantations (Table B3, Figure 2). Dunlin and Oystercatcher showed the largest effect (~15% increase per 50 m), followed by Whimbrel (~12%), Godwit (~7%) and Golden Plover (~4%) (Table B3, Figure 2). Although Redshank did not show a linear relationship with distance from plantation edges, Redshank densities were significantly lower in the first three intervals compared to the rest of the transects (Table B4). For the two passerines, Redwing density decreased by ~12% per 50 m increment, and Meadow pipit showed no change in density with distance from plantations (Table B3, Figure 3) For Redwing, Snipe and Meadow pipit, the change in density with distance varied significantly with direction of transect, with lower densities being recorded in the first 50 m from the plantation when walking towards the plantation edge, rather than away from it (Figure B2, Table B3).

Effects of plantation characteristics on bird density

Golden plover, Whimbrel and Snipe were found in lower densities in the area surrounding the tallest plantations (over 10 m) compared to the 2-5 m tall plantations (Table B3). Density of Redwings increased with increasing plantation diameter and thereby size and Dunlins were found in higher densities surrounding broadleaved plantations than mixed and coniferous (Table B3). Plantation density had no significant effect on the density of any of the species, or on the relationship between bird density and distance from plantation.

Effects of plantation configuration on bird density

The effect of plantation configuration on bird densities was quantified for six wader species, five which increased linearly with distance from plantations (Oystercatcher, Golden Plover, Dunlin, Whimbrel and Godwit) along with Redshank, which does not nest in forested areas in Iceland (Halldórsson *et al.*, 2008) and was found in the lowest density within 150 m from the forest edge (Table B4, Figure 3A), and separately for Snipe and Redwing which are known to nest within forests and were found in higher densities close to the plantation edges (Figure 3B). No estimates were created for Meadow pipit, as their nesting densities inside plantations are unknown. The breaking point was estimated to be in interval 5 (200-250 m from the forest edge), and the affected area for the open-nesting waders defined as the first 4 intervals (0-200 m) from the plantation edge. The mean density of the six species within each distance band within that area was, A1 (0-50 m): 17 birds/km^2; A2 (51-100 m): 29 birds/km^2; A3 (101-150 m): 30 birds/km^2; A4 (151-200 m): 51 birds/km^2 compared to 67 birds/km^2 in the remaining area (201-700 m). Consequently, the densities in the affected and unaffected areas were applied to equation 1 to estimate the change in bird numbers of these six open-nesting species resulting from different future plantation scenarios in vegetated open habitats in lowland Iceland (Figure B3).

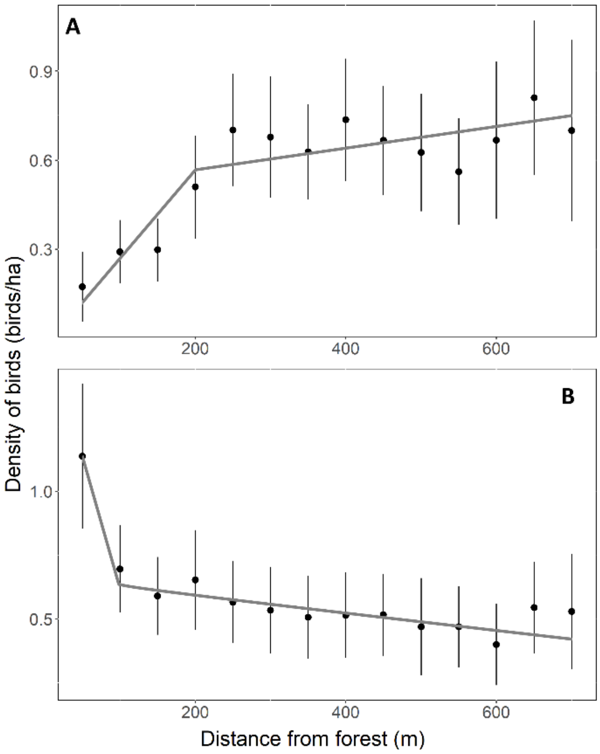

Figure 3: Combined density of A: six open-nesting wader species (Oystercatcher, Golden Plover, Dunlin, Whimbrel, Godwit and Redshank) at different distances from plantations and B: two forest-nesting species (Snipe and Redwing). The regression lines are from a segmented linear regression, indicating a rapid increase in open-nesting species density until the breaking point between 200-250 m, and rapid decrease of forest-nesting species until the breaking point between 50-100 m.

Change in number of birds=

= No of patches (Plantation area *(Density in plantation area – Density in unaffected area) + Affected area*(Density in affected area – Density in unaffected area))*

*=No of patches * (Forest area (km^2) * (-67 birds/km^2) + Affected area A1 (km^2) *(- 50 birds/km^2)) + Affected area A2 (km^2) *(- 38 birds/km^2)) + Affected area A3 (km^2) *(- 37 birds/km^2)) + Affected area A4 (km^2) *(- 16 birds/km^2))*

Using this equation, we can estimate likely changes in abundance resulting from planting 1000 ha of plantation in different planting scenarios. Planting 1000 ha of forest in one large patch instead of 50 smaller patches (20 ha each) would approximately halve the resulting decline in abundance (Figure 4). This effect increases even further as the patches become smaller, such that planting one 1000 ha forest patch would result in only a fraction (~11%) of the decline in overall abundance compared to planting 1000 small (1 ha) patches. The analysis of the random points revealed that 6.3% of the Icelandic lowlands (<300 m a.s.l.) is currently within the affected area (≤200 m) from forest plantations.

For the combined density of Redwing and Snipe, the breaking point was estimated to be in interval 2 (51-100 m) away from the forest edge. The mean density of these species was 114 birds/km^2 in the first interval (0-50 m) compared to 55 birds/km^2 in subsequent intervals (51-700 m), suggesting a twofold increase in Snipe and Redwing numbers immediately adjacent to plantations, in addition to any breeding of individuals within those plantations.

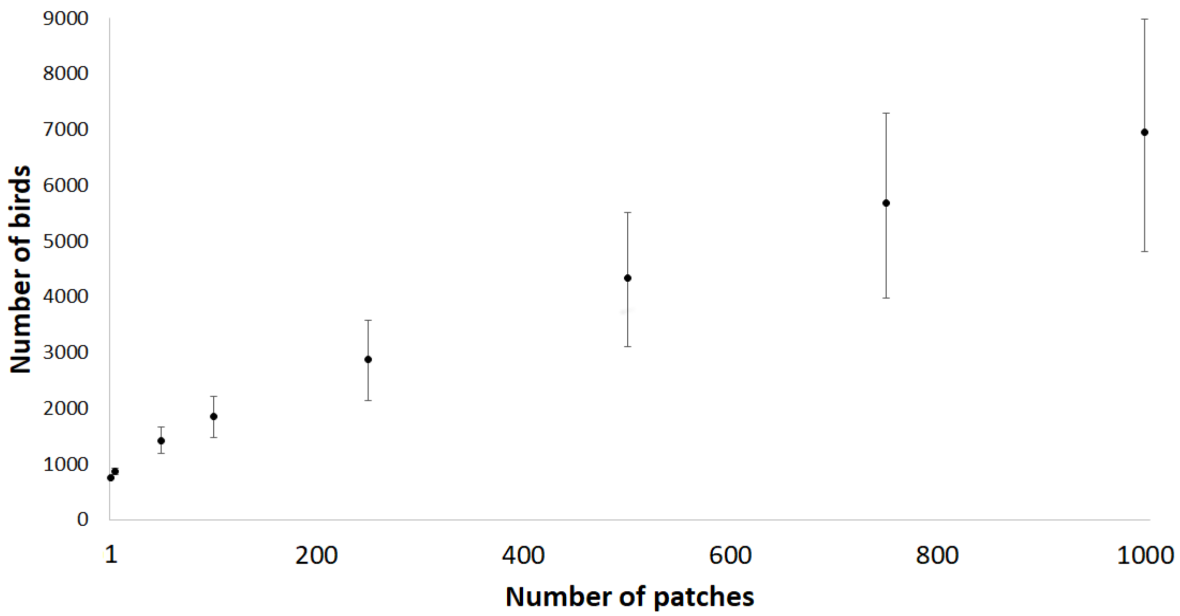

Figure 4: Estimated declines in numbers (means ± 95% Cis) of open-nesting birds (Oystercatcher, Golden Plover, Dunlin, Whimbrel, Godwit and Redshank) in future afforestation scenarios in which 1000 ha are planted in differing numbers of equal-sized patches, as a consequence of both complete loss of birds within the plantations and reduced numbers in the affected area (within 200 m) surrounding each plantation.

Discussion

Planting new forests may provide potential benefits in terms of carbon sequestration, habitat for forest-dwelling species and physical protection of human settlements and infrastructure from adverse weather conditions. However, afforestation in open landscapes can have considerable impacts on the biodiversity those landscapes support. Iceland is considered one of the most important areas for breeding waders in Europe (Thorup, 2004), and holds large proportions of the global nesting populations of Golden Plover (52%), Whimbrel (40%), Redshank (19%), Dunlin (16%) and black-tailed Godwit (10%) (Gunnarsson *et al.*, 2006). The effects of rapid and widespread afforestation in Iceland are already becoming apparent, with five of the seven wader species in our study occurring in the lowest densities close to plantations, and areas surrounding plantations (up to 200 m) supporting just over half the number of birds that occur in the same habitats further away from the plantations. There are currently hundreds of plantations throughout lowland Iceland, many of which (including the 118 used in this study) are located within semi-natural habitats. For the 76 study plantations for which recent area estimates area could be accurately measured (from aerial photographs within ±1 year of survey year) total plantation area is ~2,800 ha and the total amount of semi-natural habitat in the surrounding 200 m of them is ~3,600 ha. Using the equations reported here (Figure 4), we estimate that these 76 plantations could potentially have resulted in losses of ~3000 breeding waders, and thus the total losses resulting from all current plantations are likely to already be in the tens of thousands. While the abundance of breeding waders in forested areas prior to the presence of plantations is unknown, previous studies in Iceland have shown much higher densities of waders (~123-276 birds/km^2, depending on the habitat type; (Jóhannesdóttir *et al.*, 2014)) than we recorded in the unaffected area around plantations (63-187 birds/km^2). Thus, the estimated losses are likely to be conservative and the low overall densities in areas with plantations suggests that these are real losses rather than local redistributions away from plantations. While larger-scale redistributions cannot be ruled out, these migratory species are typically highly faithful to breeding sites (Newton, 2010), likely because of the importance of re-locating mates (Gunnarsson *et al.*, 2004) and the benefits of local site-knowledge for nesting safely and raising chicks. Even if redistribution did occur, the surrounding habitats might eventually become saturated, and productivity and/or survival could be reduced through impacts on availability of key resources. Even if redistribution did occur, the surrounding habitats might eventually become saturated If they are not already, which would be suggested by the high densities of waders in the Icelandic lowlands and evidence of density dependence in large-scale studies of Icelandic waders (Gunnarsson *et al.*, 2005; Katrínardóttir *et al.*, 2015). This underlines the urgent importance of strategic planning when it comes to afforestation (planting fewer, larger forests), along with protection of areas of great importance. Should future planting continue in the current format of many small plantations, the consequences will be far more severe than planting the same area in a smaller number of large blocks.

The changes in density of waders in open habitats surrounding forest plantations in Iceland was species-specific, with Snipe (which are known to nest in forests) being found in higher numbers closer to plantations and Redshank showing no effect with distance from plantations. The five species which were found in lower densities closer to plantations included species that typically nest in open landscapes such as heathland or grassland and with nests that are generally not well-concealed (Oystercatcher, Whimbrel and Golden Plover), and species that require tall vegetation in which to conceal their nests (Godwit and Dunlin) (Laidlaw *et al.*, 2020), suggesting that effects of plantations will be apparent across all of lowland Iceland's semi-natural habitats. Species such as Snipe (ground-nesting; (Laidlaw *et al.*, 2020)) and Redwing (tree- and ground-nesting; (Meilvang *et al.*, 1997)) that can nest within plantations could benefit from afforestation, but their potential breeding densities within plantations are not currently known.

Effects of plantation characteristics on bird density

Two wader species (Golden Plover and Whimbrel) were found in significantly lower densities in areas surrounding the tallest plantations (>10 m high) compared to the reference group (2-5 m high). Taller trees may provide avian predators with more or better perches (Andersson *et al.*, 2009), and visibility (e.g. of approaching predators) is likely to be reduced in areas surrounding taller forests. Forest height can also be an indicator of forest age, which could impact bird density in the surrounding habitat, as any reduction in productivity, recruitment and/or survival will take some time to manifest, particularly for long-lived species with high breeding site fidelity, such as waders (Halldórsson *et al.*, 2008; Méndez *et al.*, 2018). The number of predators using forests may also be greater in older, more established forests, and thus actual or perceived predation risks for breeding birds in the surrounding habitat may be greater (Hancock *et al.*, 2020). However, it should be noted that the majority of the plantations in this study are relatively young compared to other countries, with the Icelandic Forestry Association being officially founded in 1930 and forestry only gaining momentum in recent decades (Eysteinsson, 2018).

Plantation density and diameter had no additional effect on the species that were in lower densities closer to the plantations, suggesting that the mere presence of plantations induces the observed changes in abundance, and that these effects will not increase in magnitude around larger plantations. In this study, plantations all had a minimum edge length of 30 m (i.e. 900 m^2 in area, assuming a square shape), but it is possible that this effect may operate at even smaller scales. For example, some studies have shown the presence of single trees to have an effect on breeding densities of waders in the surrounding areas (Berg *et al.*, 1992; Żmihorski *et al.*, 2018).

Reduced densities of open-nesting species in areas surrounding trees and forests have been recorded elsewhere, with effects ranging from 50 up to 700 m in studies from the UK and the Netherlands (Stroud *et al.*, 2009; van der Vliet *et al.*, 2010; Wilson *et al.*, 2014). Our results suggest that reduced densities of ground-nesting waders surrounding plantations in Iceland typically reach approximately 200 m from the edge. The extent of this effect could be influenced by composition of the predator community and the associated predation risks. No mammalian predators were seen during the course of this study but ravens were seen on numerous occasions, and a third (13 out of 35) of these raven sightings were within 50 m of the forest edge (areas within 50 m totalled 9% of the total surveyed area), indicating that ravens may be more abundant close to forests in lowland Iceland. Changes in the distribution and number of predators can be an important consequence of introducing plantations into open habitats (Hancock *et al.*, 2020), and should be considered when planning future forest expansion.

Effects of plantation configuration on bird density

Estimates of the consequences of differing future planting scenarios highlight the strong potential for designing forest configurations that reduce the impact on biodiversity in the surrounding landscapes. As plantations in Iceland often appear as small patches of trees in otherwise open landscapes, rather than large forests, the total amount of affected area is considerably higher than it needs to be. The magnitude of the reduction in bird abundance close to forests is such that planting trees in few large blocks rather than many small ones could reduce total declines in abundance by more than 90%. To reduce the impact of tree planting on bird abundance, initiation of new forests should be concentrated on areas with the potential for large plantations, many of which still exist, rather than planting on smaller private lands (Ministry of Finance and Economic Affairs, 2022). Plantation size is not the only parameter that could be considered; shape can also make a difference. Wilcove *et al.* (1986) suggested that, in an effort to reduce the proportion of forest edge to forest interior, making forest plantations circular should be encouraged, and the same applies to reducing the proportion of the forest edge to the surrounding habitat. Future forestry planning should also consider the natural habitat on which planting takes place, given the large variation in bird density between habitats (Jóhannesdóttir *et al.*, 2014). Ideally, plantations should be located where bird numbers are naturally low, such as in sparsely or non-vegetated areas, at higher altitudes and on slopes (Skarphéðinsson *et al.*, 2016; Whittingham *et al.*, 2002), and surveys of breeding birds prior to planting would also help to identify and avoid areas of high breeding densities. Although heathland habitats supported the lowest overall densities of birds in this study, densities of some open-nesting species are high in these habitats, making them of high conservation value (Jóhannesdóttir *et al.*, 2014; Katrínardóttir, 2012). Currently, the majority of plantation forests in Iceland have been placed in previously vegetated lowlands (dry habitats, such as heathlands and grasslands, drained wetlands and wetlands) (75%), and less in un-vegetated areas (19%) and natural forests (6%) (Traustason, 2021). However, the Icelandic Forest Service has announced that wetlands will not be prioritized when it comes to future forest planting, which is an important step towards protection of these habitats and the internationally important bird species they support (Traustason, 2021).

One of the assumptions underlying our calculations of density is that all birds within transects were detected. This is rather unlikely as the detectability of birds may vary with stage of breeding or behaviour (e.g. incubating individuals hiding on the nest). However, such detectability issues would only be a concern here if they varied with distance from plantations. Individuals very close to plantations could potentially move into the plantations and be under-recorded, but this is unlikely as none of the species for which densities increased with distance from plantation are known to occur in forests, and the reduced densities were apparent over hundreds of metres from plantation edges. Meadow pipit, Redwing and Snipe were found in higher numbers close to the forest edge when walking away from, rather than towards, the plantation, suggesting that these three species could move into plantations in response to an approaching observer, but none showed reduced densities closer to plantations (Figure 3).

Forestry in Iceland is an ongoing project, and planting is expected to increase even further on an annual basis, with a goal of countering human-induced climate change. However, planting forests in open landscapes can have severe impacts on biodiversity, particularly on populations of ground-nesting birds. This serves as an example of a trade-off between two major challenges facing humanity, with contributions towards solving one, climate change (via carbon sequestration), impacting the other, biodiversity loss (Sikora, 2021; United Nations, 2015; Veríssimo *et al.*, 2014). Although plantations may support breeding Snipe and Redwing, these species have larger global populations and ranges (and are thus less vulnerable) than the wader species that breed only in open habitats only in Iceland, some of which are also declining globally (International Wader Study Group, 2003; IUCN, 2022; Stroud *et al.*, 2006) and are therefore of high conservation value. Waders are highly site-faithful and long-lived (Méndez *et al.*, 2018) and displacement by forestry is likely to have significant fitness and population consequences. To identify the underlying drivers behind an altered bird abundance surrounding plantation forests, and better predict future impacts, before-after-control-studies of marked individuals in areas where forests are planted, where their behaviour and demography could be tracked would be idea. However, long-term tracking of displaced individuals and any subsequent changes to their fitness is very challenging, particularly in systems in which breeding success is often highly stochastic (Laidlaw *et al.*, 2020). Iceland holds large proportions of the global populations of several bird species, the five wader species found in lower densities close to plantation edges are all classified as focal species by the Icelandic Institute of Natural History (Vilmundardóttir *et al.*, 2019) and four (Godwit, Whimbrel, Dunlin and Oystercatcher) are decreasing worldwide according to the IUCN red list (IUCN, 2022). Iceland is a signatory to numerous international agreements such as AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds) and the Bern Convention on the Conservation of European Wildlife and Natural Habitats) committing it to protecting birds as well as their habitats, especially wetlands (Einarsson *et al.*, 2002; Schmalensee *et al.*, 2013). It is therefore imperative that strategic planning of tree-planting schemes in Iceland is developed and implemented, in order to reduce the effect on ground-nesting birds, by avoiding areas with high bird abundance and optimizing the size and shape of future forest plots.

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Appendix B

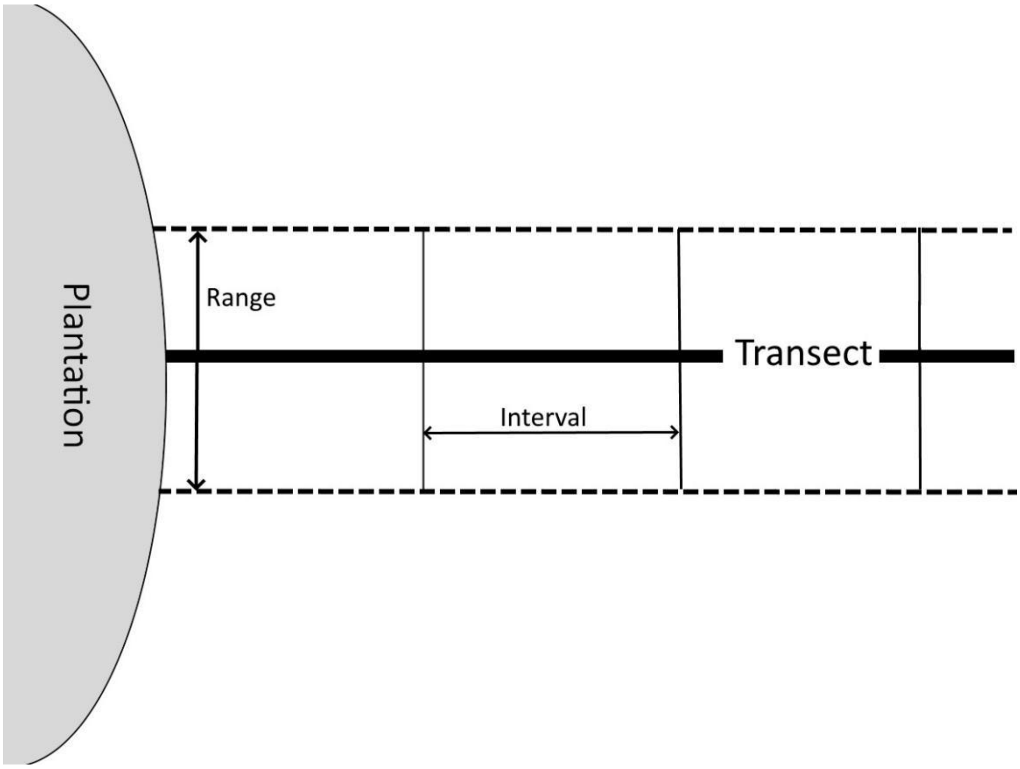

Figure B1: Transects ranging from 300-700 m long were walked either to or from plantation edges in which birds were counted within a 100 m range on each side. These transects were then divided into 50 m intervals (= area of 1 hectare) and bird densities were calculated within these intervals.

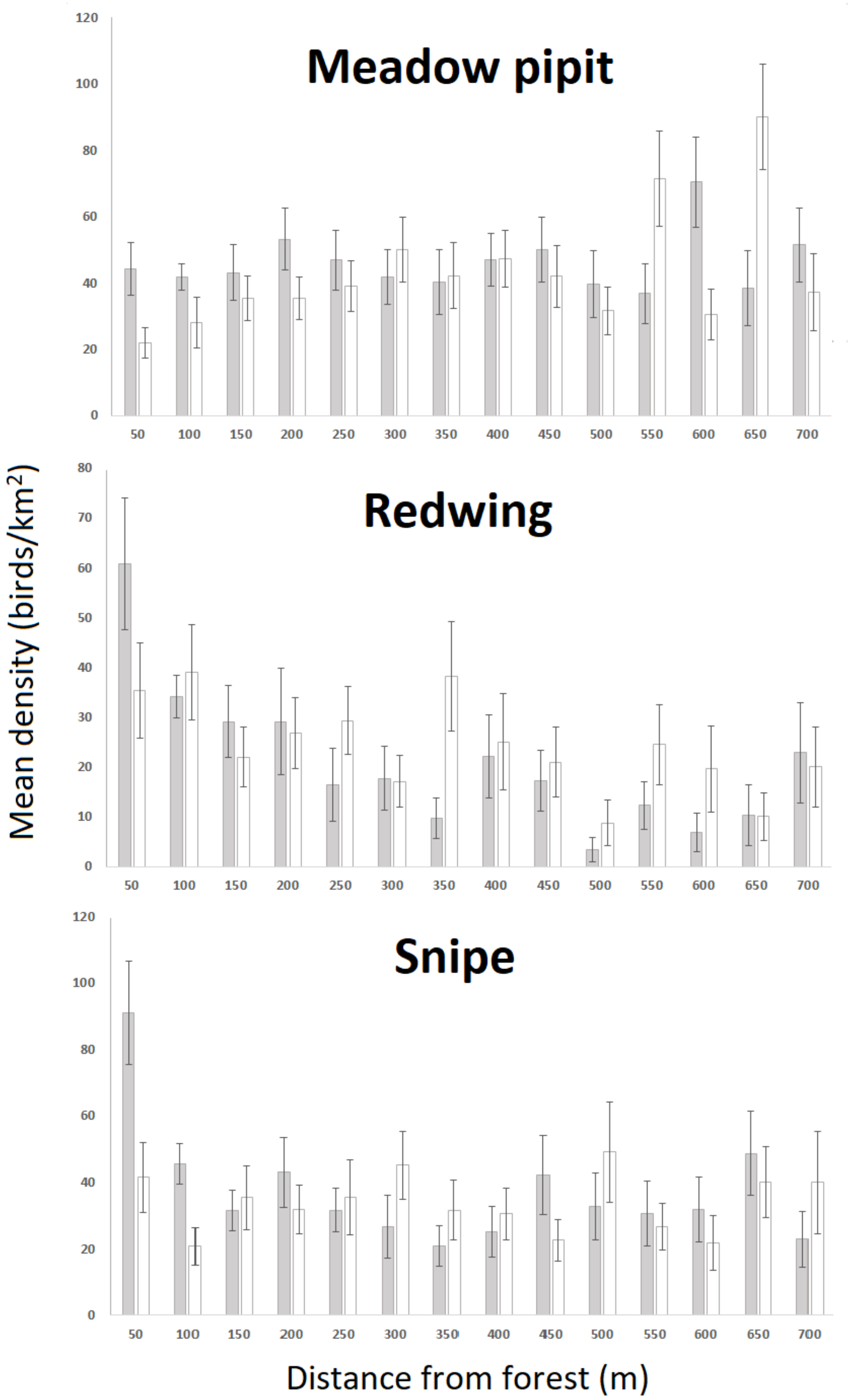

Figure B2: Variation in the mean density (± SE) of Meadow pipit, Snipe and Redwing with distance from plantations in 50 m intervals, on transects walked towards (white) or away from (grey) the plantation edge.

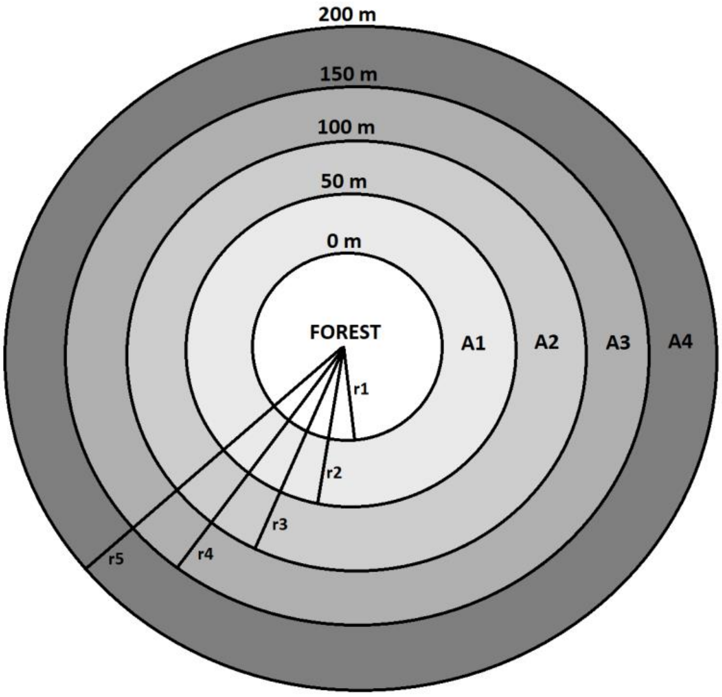

Figure B3: Plantation area shown in white and affected area in greyscale. Assuming a circular forest patch, (which is conservative as these have the least amount of affected area), these factors (r1-r5) can be used to calculate the area of each distance band (A1-A4) for a given amount of forest, and thereby estimate changes in bird numbers in forest and affected areas.

Table B1: The number, diameter (mean ± SE), and % of plantations in four height categories and two density categories (% of plantations) of broadleaved, coniferous and mixed plantations around which transects were conducted.

Plantation type	n	Diameter (m)	Height (%) 0-2 /2-5 /5-10 />10 m	Density (%) Dense/sparse
Broadleaved	59	556 (± 75)	7/59/25/9	59/41
Mixed	66	399 (± 67)	6/45/29/20	74/26
Coniferous	36	451 (± 81)	3/50/22/25	81/19

Table B2: Estimates from a priori test where individual factors were tested along with distance from forest and an interaction effect. Transect nested within plantation was a random factor in all models. Significant results are marked with an asteriks and in bold.

Full model: Bird density (birds/ha) ~ interval * direction + (1|plantation/transect)									
Variable	Redwing density	Snipe density*	Golden plover density	Whimbrel density	Dunlin density	Oystercatcher density	Godwit density	Redshank density	Meadow pipit density
Intercept	-0.76(±0.21)*	-0.90 (±0.14)*	-1.83 (±0.31)*	-2.16 (±0.27)*	-3.69 (±0.60)*	-5.71 (±1.62)*	-2.53 (±0.44)*	-1.69 (±0.40)*	-0.92 (±0.11)*
Interval	-0.14 (±0.02) *	-0.07 (±0.01) *	0.05 (±0.03)	0.10 (±0.02) *	0.16 (±0.04) *	0.10 (±0.07)	0.07 (±0.03)*	0.01 (±0.03)	0.01 (±0.01)
Direction	-0.37 (±0.25)	-0.43 (±0.18) *	0.00 (±0.34)	-0.28 (±0.31)	-0.63 (±0.69)	-1.19 (±1.00)	-0.35 (±0.47)	-0.63 (±0.44)	-0.48 (±0.16) *
Interval:direction	0.07 (±0.03)*	0.06 (±0.02) *	-0.01 (±0.04)	0.02 (±0.03)	-0.05 (±0.08)	0.09 (±0.10)	0.00 (±0.06)	0.04 (±0.05)	0.05 (±0.02) *
Full model: Bird density (birds/ha) ~ interval * height + (1|plantation/transect)									
Intercept^B	-0.93 (±0.23)*	-1.01 (±0.15)*	-1.82 (±0.30)*	-2.29 (±0.27)*	-3.89 (±0.65)*	-5.71 (±1.52)*	-2.91 (±0.53)*	-1.91 (±0.46)*	-1.04 (±0.12)*
Interval	-0.11 (±0.02)*	-0.04 (±0.01)*	0.07 (±0.03)*	0.13 (±0.02)*	0.16 (±0.05)*	0.12 (±0.07)	0.06 (±0.05)	0.00 (±0.04)	0.02 (±0.01)
0-2 m	-0.21 (±0.76)	0.03 (±0.51)	1.64 (±0.70)*	-0.17 (±0.85)	-2.73 (±2.84)	-1.15 (±2.41)	0.19 (±1.08)	1.39 (±1.06)	-0.60 (±0.43)
5- 10 m	0.16 (±0.34)	0.01 (±0.26)	0.16 (±0.42)	0.39 (±0.40)	0.22 (±0.83)	0.28 (±1.25)	0.68 (±0.63)	-0.28 (±0.56)	-0.09 (±0.20)
>10 m	-0.02 (±0.44)	-0.67 (±0.36)	-0.67 (±0.72)	-0.43 (±0.61)	0.13 (±1.11)	-0.35 (±2.12)	0.20 (±0.85)	0.21 (±0.64)	-0.49 (±0.26)
Interval:0-2 m	-0.11 (±0.10)	-0.01 (±0.05)	-0.14 (±0.09)	-0.05 (±0.09)	0.27 (±0.25)	0.26 (±0.23)	0.01 (±0.10)	-0.17 (±0.14)	0.05 (±0.05)
Interval:5-10 m	0.03 (±0.03)	-0.01 (±0.02)	-0.05 (±0.05)	-0.04 (±0.04)	-0.04 (±0.08)	-0.04 (±0.11)	0.01 (±0.06)	0.09 (±0.06)	0.03 (±0.02)
Interval: >10 m	-0.06 (±0,05)	0.01 (±0.04)	-0.12 (±0.11)	-0.08 (±.07)	-0.09 (±0.13)	-0.04 (±0.25)	0.07 (±0.10)	0.03 (±0.07)	0.03 (±0.03)
Full model: Bird density (birds/ha) ~ interval * diameter (km) + (1|plantation/transect)									
Intercept	-1.24 (±0.23)*	-1.01 (±0.16)*	-1.72 (±0.31)*	-2.48 (±0.28)*	-3.73 (±0.65)*	-6.11 (±1.66)*	-2.46 (±0.46)*	-1.75 (±0.41)*	-1.10 (±0.12)*
Interval	-0.09 (±0.02)*	-0.05 (±0.01)*	0.03 (±0.03)	0.12 (±0.02)*	0.14 (±0.05)*	0.09 (±0.07)	0.07 (±0.04)	0.02 (±0.04)	0.04 (±0.01)*
Diameter	0.64 (±0.26)*	-0.23 (±0.23)	-0.22 (±0.33)	0.38 (±0.32)	-0.45 (±0.81)	-0.44 (±1.24)	-0.42 (±0.61)	-0.50 (±0.54)	-0.10 (±0.18)
Interval:diameter	-0.04 (±0.02)	0.02 (±0.02)	0.03 (±0.03)	-0.02 (±0.03)	0.03 (±0.08)	0.10 (±0.11)	-0.01 (±0.07)	0.01 (±0.06)	-0.01 (±0.02)
Full model: Bird density (birds/ha) ~ interval * type + (1|plantation/transect)									
Intercept^C	-0.86 (±0.25)*	-1.17 (±0.18)*	-1.67 (±0.34)*	-2.25 (±0.31)*	-3.40 (±0.68)*	-6.26 (±1.74)*	-2.83 (±0.52)*	-1.95 (±0.45)*	-1.01 (±0.13)*
Interval	-0.09 (±0.02)*	-0.04 (±0.02) *	0.01 (±0.04)	0.10 (±0.03)*	0.06 (±0.06)	0.16 (±0.07)*	0.10 (±0.04)*	0.01 (±0.04)	0.02 (±0.02)
Broadleaved	-0.11 (±0.34)	0.31 (±0.26)	-0.40 (±0.42)	0.04 (±0.40)	0.01 (±0.74)	0.17 (±1.29)	0.11 (±0.63)	-0.12 (±0.54)	-0.08 (±0.19)
Conifer	-0.08 (±0.39)	-0.26 (±0.31)	-0.04 (±0.49)	-0.22 (±0.46)	-4.15 (±1.93)*	1.06 (±1.45)	0.54 (±0.68)	-0.04 (±0.63)	-0.54 (±0.24)*
Interval:broadleaved	-0.02 (±0.03)	-0.01 (±0.02)	0.09 (±0.05)	0.02 (±0.04)	0.09 (±0.08)	0.05 (±0.11)	-0.07 (±0.06)	0.01 (±0.06)	-0.01 (±0.02)
Interval:conifer	-0.04 (±0.04)	0.04 (±0.03)	-0.04 (±0.06)	0.02 (±0.05)	0.36 (±0.17)*	-0.25 (±0.15)	-0.07 (±0.08)	0.06 (±0.07)	0.06 (±0.03)*
Full model: Bird density (birds/ha) ~ interval * forest density + (1|plantation/transect)									
Intercept^D	-0.98 (±0.21)*	-1.07 (±0.14)*	-1.86 (±0.29)*	-2.34 (±0.25)*	-4.26 (±0.63)*	-5.82 (±1.64)*	-2.53 (±0.45)*	-2.16 (±0.41)*	-1.14 ± (0.11)*
Interval	-0.10 (±0.02)*	-0.04 (±0.01)*	0.04 (±0.03)	0.12 (±0.02)*	0.18 (±0.05)*	0.09 (±0.09)	0.05 (±0.04)	0.04 (±0.03)	0.03 (±0.01)*
Sparse	0.21 (±0.32)	-0.11 (±0.25)	0.12 (±0.40)	0.13 (±0.37)	1.09 (±0.75)	-0.28 (±1.25)	-0.40 (±0.56)	0.51 (±0.49)	-0.05 (±0.19)
Interval:sparse	-0.02 (±0.03)	-0.01 (±0.03)	0.02 (±0.05)	-0.02 (±0.04)	-0.10 (±0.08)	0.09 (±0.12)	0.05 (±0.06)	-0.04 (±0.05)	0.01 (±0.02)
Full model: Bird density (birds/ha) ~ interval * habitat + (1|plantation/transect)									
Intercept ^E	-1.32 (±0.29) *	-1.01 (±0.18) *	-2.74 (±0.33) *	-2.25 (±0.30)*	-3.66 (±0.71) *	-5.38 (±1.70) *	-2.49 (±0.47) *	-1.58 (±0.41)*	-0.99 (±0.14) *
Interval	-0.11 (±0.03) *	-0.04 (±0.02) *	0.02 (±0.04)	0.12 (±0.03) *	0.13 (±0.07)*	0.16 (±0.07) *	0.08 (±0.04)	0.02 (±0.04)	0.02 (±0.02)
Poor heathland	0.01 (±0.44)	-0.70 (±0.34) *	-0.20 (±0.54)	-0.28 (±0.52)	-0.73 (±1.90)	-2.35 (±2.38)	-0.67 (±1.06)	-0.80 (±0.82)	-0.68 (±0.27) *
Rich heathland	0.81 (±0.38) *	0.01 (±0.28)	0.17 (±0.45)	-0.29 (±0.45)	-0.19 (±0.89)	-1.79 (±1.71)	-1.10 (±0.85)	-0.59 (±0.61)	-0.13(±0.22)
Semi-wetland	0.93 (±0.45)*	0.07 (±0.30)	0.02 (±0.62)	0.29 (±0.50)	0.44 (±0.97)	0.16 (±1.42)	0.99 (±0.58)	-0.27 (±0.72)	0.06 (±0.25)
Wetland	0.72 (±0.62)	0.39 (±0.41)	0.81 (±0.88)	0.77 (±0.73)	1.12 (±1.13)	3.19 (±1.56)*	1.96 (±0.76)*	1.17 (±0.79)	-0.28 (±0.39)
Interval:Poor heathland	0.06 (±0.05)	0.02 (±0.03)	0.05 (±0.06)	-0.03 (±0.05)	-0.26 (±0.30)	0.04 (±0.21)	-0.21 (±0.16)	-0.11 (±0.12)	0.04 (±0.03)
Interval:Rich heathland	0.00 (±0.04)	-0.02 (±0.03)	0.06 (±0.5)	0.02 (±0.05)	0.05 (±0.09)	0.12 (±0.15)	0.03 (±0.10)	0.03 (±0.07)	0.01 (±0.02)
Interval:Semi-wetland	-0.03 (±0.05)	0.02 (±0.03)	-0.05 (±0.08)	-0.03 (±0.05)	0.04 (±0.11)	-0.02 (±0.13)	-0.01 (±0.07)	0.03 (±0.09)	0.01 (±0.03)
Interval:Wetland	-0.11 (±0.08)	0.03 (±0.04)	-0.20 (±0.14)	-0.10 (±0.09)	-0.04 (±0.12)	-0.43 (±0.23)	-0.07 (±0.08)	-0.01 (±0.08)	0.03 (±0.04)
Most numerous category always used as reference: ^A Away from, ^B 2-5 m, ^C Mixed forests, ^D Dense, ^E Grassland									

*Table B3: Estimates from the minimum glmmADMB models of the influence on densities of nine species of distance from plantation edge, tree height, tree type and width of plantation. Asterisks represent significance (p<0.05 *; p<0.01 **; p<0.001 ***)*

Full model: Bird density (birds/ha) ~ Interval + Type + Height + Width + Forest Density + Direction (where applicable) + Habitat + (1|plantation/transect)

Variable		Redwing	Snipe	Golden plover	Whimbrel	Dunlin	Oystercatcher	Godwit	Redshank	Meadow pipit
Interval		-0.13 (±0.02) ***	-0.06 (±0.02) ***	0.04 (±0.02) *	0.11 (±0.02) ***	0.14 (± 0.04) ***	0.14 (±0.05) **	0.06 (±0.03) *	0.02 (±0.03)	0.01 (±0.01)
Height	(Intercept)[a]	-1.13 (± 0.22)	-0.22 (±0.29)	-1.61 (±0.27)	-2.16 (±0.25)	-3.91 (±0.63)	-6.21 (±1.52)	-2.37 (±0.42)	-1.60 (±0.38)	-0.92 (±0.11)
	0-2 m		-0.25 (±0.38)	0.73 (±0.40)	-0.57 (±0.49)					
	5-10 m		-0.25 (±0.21)	-0.20 (±0.24)	0.07 (±0.25)					
	>10 m		-0.82 (0.28)**	-1.39 (±0.41) ***	-0.96 (±0.38) *					
Width	**km**	0.44 (±0.22) *								
Direction	Direction		-0.32 (±0.18)							-0.48 (±0.16) **
	Interval:direction	0.04 (±0.02)	0.05 (±0.02)*							0.05 (±0.02) **
Type	Broadleaved					0.80 (±0.38) *				
	Conifer					-0.68 (±0.56)				
Habitat	Poor heathland		-0.69 (±0.28)*			-2.41 (±1.08) *		-1.96 (±0.66) **	-1.43 (±0.51) **	
	Rich heathland		-0.25 (±0.22)			0.33 (±0.41)		-0.89 (±0.44) *	-0.36 (±0.37)	
	Semi-wetland		0.18 (±0.24)			0.90 (±0.45) *		0.95 (±0.38) *	-0.08 (0.42)	
	Wetland		0.63 (±0.32) *			0.97 (±0.57)		1.47 (±0.50) **	1.04 (±0.51) *	

[a] Reference height: 2-5 m; type: broadleaved; habitat: grassland, direction: away from

*Table B4: Estimates (on log-scale) from glmmAMDB models with a Poisson distribution with asterisks representing significance (p<0.05 *; p<0.01 **; p<0.001 ***) of the influence on Redshank densities of distance from plantation edge in two categories along with habitat. Transect nested within plantation was included as a random factor.*

Variable		**Redshank**
Intercept		-2.19 (±0.40)
Distance from forest in two categories (≤150 m (reference distance) and >150 m)		0.87 (±0.27) **
Habitat	Poor heathland	-1.44 (±0.51) **
	Rich heathland	-0.42 (±0.37)
	Semi-wetland	-0.14 (±0.42)
	Wetland	0.95 (±0.51)

Paper II

Effects of overhead power-lines on the density of ground-nesting birds in open sub-arctic habitats

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Abstract

Yearly electricity production has increased steadily in the world in recent decades and the associated overhead power lines are widespread and occur across urban and natural habitats, and often in remote areas where there is little other anthropogenic influence. Here we assessed the effects of overhead power lines on the density of ground-nesting birds in the Icelandic lowlands which host several populations of international importance. The combined breeding density of the eight study species increased significantly from ~112 birds/km^2 close (< 50 m) to the power lines to ~177 birds/km^2 away (450-500 m) from the power lines, with two of these species (Whimbrel (*Numenius phaeopus*) and Redshank (*Tringa totanus*)) increasing significantly with distance from power lines and six species (Golden Plover (*Pluvialis apricaria*), Snipe (*Gallinago gallinago*), Meadow Pipit (*Anthus pratensis*), Black-tailed Godwit (*Limosa limosa*), Dunlin (*Calidris alpina*) and Redwing (*Turdus iliacus*)) showing no changes. These findings suggest that power lines can influence the breeding density of ground-nesting bird species in their vicinity and that accounting for such effects when planning future infrastructure will be imperative.

Introduction

Human-driven land use change and infrastructure establishment are important drivers of habitat loss and degradation which can have substantial effects on native wildlife (Foley *et al.*, 2005). Introducing anthropogenic structures into open habitats can result in habitat loss for wildlife populations and also affect the surrounding habitat through changes in vegetation, predation risk and pathogen invasion (Becker *et al.*, 2015; Marzluff *et al.*, 2001; Prugh *et al.*, 2009; Runkovski & Pickering, 2015). These processes can cause changes in demographic parameters such as survival and/or productivity (Lepczyk *et al.*, 2004; Loss *et al.*, 2015). Additionally, the presence of anthropogenic structures, or the increase in human traffic which often accompanies them, may prompt individuals to alter their patterns of use of landscapes, by avoiding or being drawn to the structures (Barrueto *et al.*, 2014; Łopucki *et al.*, 2017; Silva *et al.*, 2010; Watts, 2017).

Annual electricity production, accompanied by electrical infrastructure, has increased steadily in the world in recent decades and further increases in production are anticipated (IEA, 2020). Electricity is typically generated in one area and transported to where it is used. This transportation usually goes through power lines which can be either overhead or underground (Fenrick & Getachew, 2012). With the growing demand for renewable energy, the distance electricity needs to travel from energy sources to consumers may increase further (Jorge & Hertwich, 2014), resulting in an increased number of power lines. Currently, the European power transmission grid contains 301,000 km of overhead lines (Jorge & Hertwich, 2014) which are widespread and found across urban, semi-urban, agricultural and natural habitats, and often in remote areas where there is little other anthropogenic influence.

The introduction of power lines in open habitats could potentially provide additional places for birds to nest, for example an estimated 25% of the population of Portuguese white storks (*Ciconia ciconia*) nest in transmission towers (Moreira *et al.*, 2017). However, collision with power lines can be an important source of bird mortality (Bevanger & Brøseth, 2001; Loss *et al.*, 2015). In addition, the presence of power lines may change the distribution of mammalian predators, for example through scavenging for carcasses under power lines and using towers as cover in open habitats, and power lines and towers can be used by avian predators for perching and hunting (DeGregorio *et al.*, 2014; Ponce *et al.*, 2010). Such changes in predator distribution and activity may alter predation pressure and perceptions of risk in surrounding areas (D'Amico *et al.*, 2018; DeGregorio *et al.*, 2014). The visual obstruction, noise, presence of humans during maintenance procedures and habitat loss in areas containing the power lines (Bevanger & Brøseth, 2001; D'Amico *et al.*, 2018) may also make these areas less attractive to ground-nesting species. Finally, power lines emit ultraviolet light (Engels *et al.*, 2014; Tyler *et al.*, 2014) and generate an electromagnetic field which has been shown to affect avian behaviour, physiology and development (D'Amico *et al.*, 2018; Fernie & Reynolds, 2005).

In Iceland, the vast majority of electricity is produced from hydropower (~70%) or geothermal (~30%) sources (Hjaltason *et al.*, 2020). Both hydro and geothermal power plants can only be established in locations where geothermal heat or large amounts of water are readily available, and the electricity produced needs to be transported to urban or industrial areas. Iceland has the highest electric power consumption per capita in the world (Bank, 2014), with most (70-80%) being used by companies that produce either aluminium or ferrosilicon (Orkustofnun, 2012; Samtök iðnaðarins, 2009), and ~3% being used in data centres (KPMG, 2018; Landsvirkjun, 2020). With a growing human population, electrification of various systems and increasing infrastructure, along with plans for linking Iceland to electric grids in other countries, the demand for electricity is increasing in the country (Landsvirkjun, 2014), and power lines in the Icelandic landscape are therefore likely to increase in the near future. Since agriculture in Iceland is not yet highly intensive or extensive and the density of anthropogenic structures is not high compared to the rest of Europe (Jóhannesdóttir *et al.*, 2019; Torres *et al.*, 2016), the Icelandic lowlands still contain large areas of relatively undisturbed semi-natural wetland, grassland and heathland habitats which support internationally important breeding populations of several ground-nesting bird species, particularly waders (Gunnarsson *et al.*, 2006; Jóhannesdóttir *et al.*, 2014; Skarphéðinsson *et al.*, 2016). Wader breeding densities are estimated to be, on average, between 123-276 birds/km^2, depending on the habitat type (Jóhannesdóttir *et al.*, 2014). Although little is currently known about the effects of power lines on birds in the Icelandic landscape, there are some recorded cases of birds colliding with power lines, mostly involving large species such as Whooper Swans (*Cygnus cygnus*) and White-tailed Eagles (*Haliaeetus albicilla*) (Hilmarsson & Einarsson, 2009; Schmalensee & Skarphéðinsson, 2021), but also smaller birds such as Golden Plovers (*Pluvialis apricaria*), Dunlins (*Calidris alpina*), Snipes (*Gallinago gallinago*) and Redwings (*Turdus iliacus*) (Snæþórsson *et al.*, 2018). Here we aim to assess the effect of overhead power lines on the density of ground-nesting birds in the Icelandic lowlands and identify which properties of these structures may influence these patterns.

Materials and methods

Bird counts

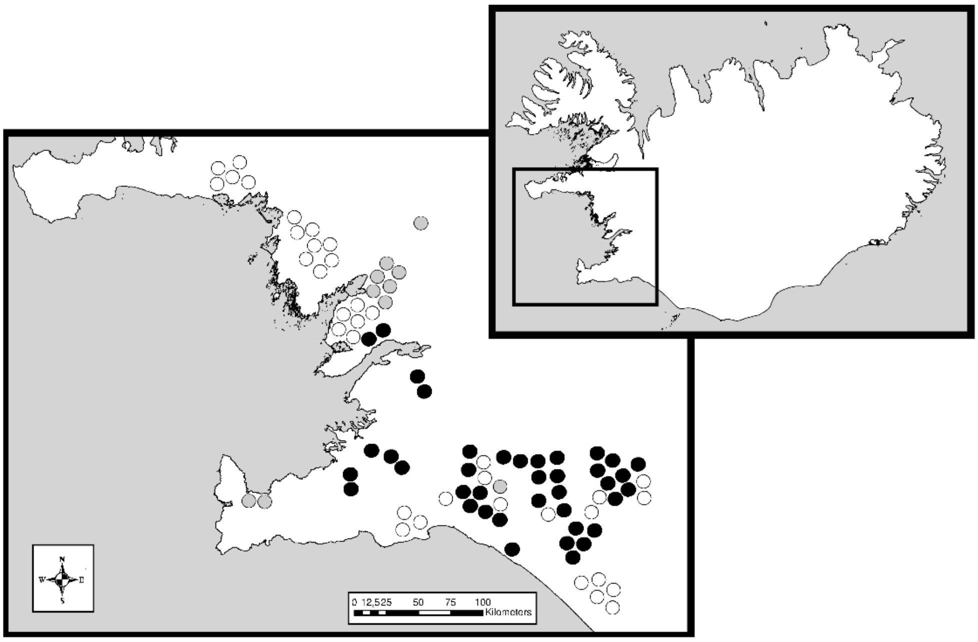

Figure 1: Locations in southwest Iceland of the 85 transects surveyed perpendicular to power lines of 66 kV (white), 132 kV (grey) and 220 kV (black) voltage.

This study was conducted in southwest Iceland between the 6th of May and the 20th of June 2019 by transect counts (Figure 1). Transects were not conducted in heavy rain or if wind was over 7 m/s due to low detectability of the study species (Hoodless *et al.*, 2006). Transects were chosen by selecting patches of homogenous habitat along power lines in the Icelandic lowlands. To eliminate any observer effect on the distribution of birds, transects were walked either to (n=40) or from (n=45) the power lines and this was included as direction of transect in the analysis. To minimise potential confounding effects, each transect was at least 100 m away from all other anthropogenic structures or habitats (houses, roads, agricultural fields and forest plantations). Before initiating each transect survey, the observer waited for 5 minutes at the starting position, or until all birds had settled, and then the transect was walked at a steady pace. Transect length varied between 300-500 m, depending on the area of homogenous habitat available (see Table 1 for habitat types). Birds were counted along 85 transects which were perpendicular to power lines (Figure 1), and evenly distributed between starting at pylons (n=42) or at the lines in between two pylons (n=43). All birds seen within 100 m in each direction of the transect were recorded where first seen (distance determined with a laser range finder), and distance from the power line recorded (determined from GPS). For each power line, we recorded the number of cables, material of pylons, height and voltage of the line (Table 1).

All power line characteristics were strongly correlated to voltage of line, with the largest lines which transported 220 kV had three or more cables, metal pylons and a mean height of 25 m (±7.4 SE), while lines that transported lower voltages (132 kV or 66 kV) always had three cables, most had wood pylons and their mean height = 11 m (±2.7 SE) (Table C1).

Table 1: The model variables and structure used to explore effects of power lines on breeding birds in lowland Iceland

Variable	Unit	Definition
Bird density	Birds/ha	Total number of birds counted per interval (1 ha)
Interval	1-10	Distance bands of 50 m on transects from closest (1) to furthest away (10) from power lines. Measured with a GPS tracker.
Transect	Transect number	Transect identity
Direction	Towards or Away	If the transect was walked to or away from the power line
Voltage	Low/high	Voltage of the power line (Landsnet, 2019) categorized as high (220kV) or low (66 kV or 132 kV)
Habitat	Poor heathland/rich heathland/grassland/ semi-wetland/wetland	Classification of transect habitat type, from the Icelandic farmland database (Gísladóttir *et al.*, 2014).
Distance to water	m	Distance from transects to water bodies extracted using ArcMap and hydrological data from the National Land survey of Iceland (Landmælingar Íslands, 2022)
Slope	Elevation difference/meter	Calculated from the elevation at each end of the transects, and length of transect

Model structure	
Model A	Bird density ~ slope + distance to water + (1|Habitat/Transect)
Model B	Bird density ~ Interval + slope + distance to water + (1|Habitat/Transect)
Model C	Bird density ~ Interval*Direction + slope + distance to water + (1|Habitat/Transect)
Model D	Bird density ~ Interval*Voltage + slope + distance to water + (1|Habitat/Transect)
Model E	Bird density ~ Interval*Voltage + Direction + Interval:Direction + slope + distance to water + (1|Habitat/Transect)

Statistical analysis

Each transect was divided into intervals of 50 m, each corresponding to 1 hectare (Table 1). The recorded density of birds within these intervals (for each species separately and all the study species combined) was calculated and set as the response variable in a generalized linear mixed model (GLMM) with a Poisson distribution, with distance from power line (in 50 m intervals) as an explanatory variable using the R-package glmmTMB (Brooks *et al.*, 2017). Most of the study species have large home ranges, and therefore the data contains multiple zeros, which have been accounted for in all models by adding a zero-inflation parameter (*ziformula=~1*) (Bolker, 2016). Transect number nested within habitat was included as random factor to account for non-independence of intervals within the same transect and varying bird abundances between habitat types. Distance to water (extracted from GIS layers (Landmælingar Íslands, 2022)) and slope of transects (calculated from the elevation difference between the beginning and end points of the transects) were included as fixed factors in the model to account for any effect of these landscape structure variables on breeding densities (Eglington *et al.*, 2008; Whittingham *et al.*, 2002). To explore the potential effects of structural difference of lines, voltage (in two categories: high, 220 kV and low, 132 kV and 66kV) was included as a fixed factor along with an interaction term. To account for the effect of the observer on the distribution of the birds along the transect, an additional interaction term between direction of transect and distance from power lines was included in the models. Five models were constructed with all possible combinations of aforementioned factors, along with a null model (Table 1, models A-E). These models were subsequently compared (for each species separately and all species combined), and the model with the lowest AIC value chosen, provided it gave a significantly better fit than a simpler model (ΔAIC<2) (Table C2). All data analyses were performed in RStudio (R Core Team, 2017; RStudio Team, 2016) and package ggplot2 (Wickham, 2016) used for graphs.

Results

In total, 1067 birds of 21 different species were recorded on the 85 transect surveys. The vast majority (~91%) belonged to eight species which were used in the subsequent analysis: Dunlin, Black-tailed Godwit (*Limosa limosa*), Golden Plover, Meadow Pipit (*Anthus pratensis*), Redshank (*Tringa totanus*), Redwing, Snipe and Whimbrel. For all eight species combined, the areas closest to the power lines (0-50 m) supported densities of ~112 birds/km^2 (±13 SE) which increased by approximately 58% to ~177 birds/km^2 (±24 SE), between 450-500 m away from the power lines (Figure 2). Estimates from the model for all species combined showed, on average, a 4% increase per 50 m increment from the power lines. At the species level, Redshank and Whimbrel density increased significantly with distance from power lines (18% and 10% per 50 m, respectively; Figure 2, Table C3), but no other significant effects of distance from power lines or voltage were found for other species (Table C3).

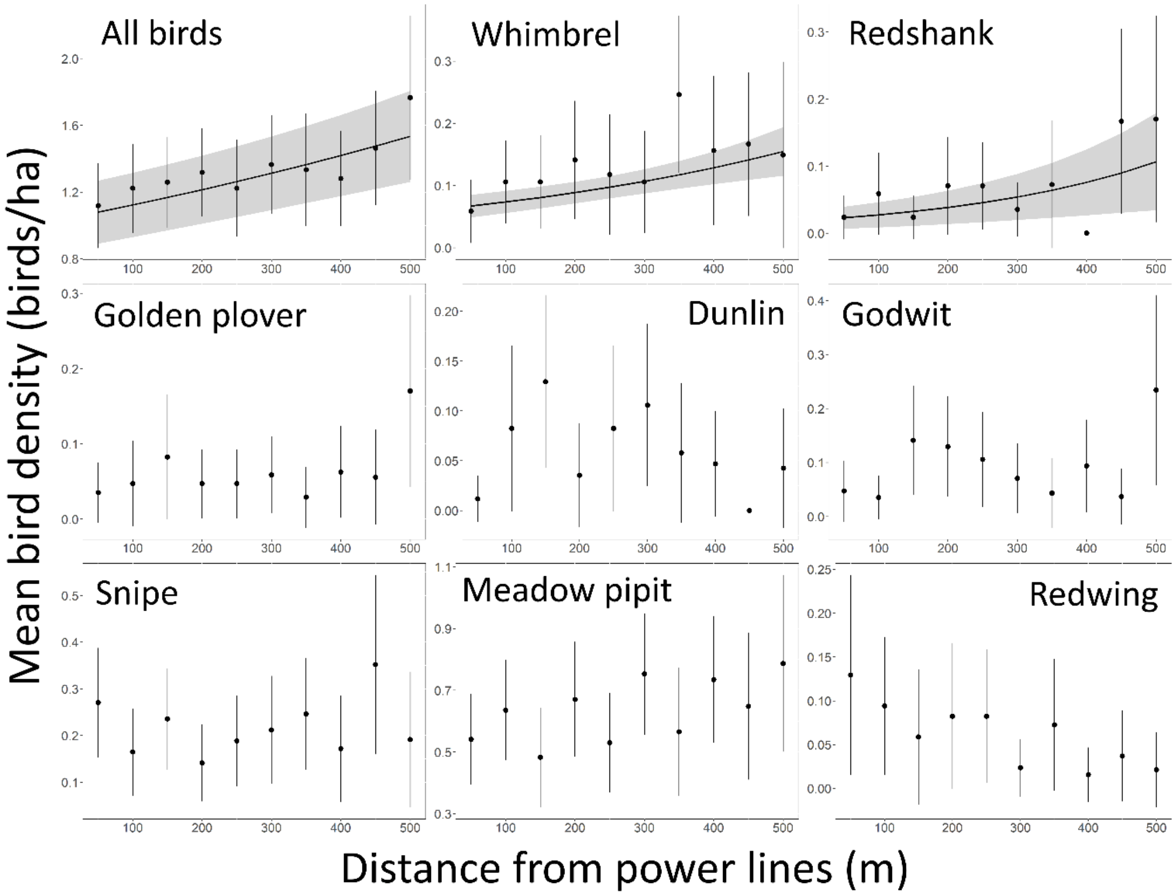

Figure 2: Mean bird densities per ha (±SE) at 50 m intervals with increasing distance from power lines for the eight most abundant species combined and individually. The horizontal lines represent model predictions, with the shaded interval as the standard error, and are shown for species with significant changes in density with distance from power lines (Table C2).

Discussion

The combined breeding density of the eight study species was lowest close to power lines and increased with distance, with two species (Whimbrel and Redshank) showing significant increases and the remaining species showing no changes. Power lines are expected to increase in frequency in Iceland, and the world, in future years and with bird density being on average ~58% higher at the end of transects (450-500 m) compared to the first 50 m surrounding the lines, the repercussions of long power lines, which can be thousands of kilometres and run through semi-natural habitats, may be considerable. Considering this depressed density of several ground-nesting bird species in the vicinity of overhead power lines, underground power lines may be more beneficial, even though this may cause a temporary disturbance to the ground.

Previous research on waders has shown that they are often found in lower densities close to anthropogenic structures (Fernández-Bellon *et al.*, 2018; Pearce-Higgins *et al.*, 2012; Żmihorski *et al.*, 2018). Overhead power lines differ from some of these structures as they do not introduce a physical barrier to the landscape, nor do they notably increase human traffic. It is possible that lower bird density in the proximity of power lines may be due to increased collision risk, but this is difficult to establish directly as carcasses are likely to be removed by scavengers (Ponce *et al.*, 2010). Another possibility is that predation risk increases close power lines, if they are used as perches by avian predators (DeGregorio *et al.*, 2014). Ravens, which are known nest predators in Iceland (Laidlaw *et al.*, 2020) were seen on pylons during the course of this study. This could cause an increase in actual or perceived predation rate close to the power lines which may affect the distribution of ground-nesting birds. Power lines may also cause disturbance due to noise, ultraviolet discharge or electromagnetic fields, which could potentially cause birds to avoid nesting close to power lines. Any noise originating from the power lines was not noticeable to the observer during the survey, but it is possible that birds sense low frequency sounds or electromagnetic currents stemming from the power lines, as well as detecting light frequencies (UV light) not noticeable to humans (Engels *et al.*, 2014; Plumb *et al.*, 2019; Tyler *et al.*, 2014). The reason why significant reductions in density close to power lines were apparent for Whimbrels and Redshanks but no other species is not clear, especially as previous studies have found breeding waders of several species in lower densities surrounding novel structures such as trees (Pálsdóttir *et al.*, In press; Żmihorski *et al.*, 2018) and anthropogenic structures (Pearce-Higgins *et al.*, 2009; Wallander *et al.*, 2006). It is possible that sample sizes were too low to detect effects in some species or that the distances over which it was possible to conduct transects within the same habitat was not long enough to detect effects. Breeding waders often occur at relatively low densities and, for some species, the small numbers of birds recorded on these transects (e.g. Golden Plovers for which a total of 44 birds, or ~1 bird per two transects, were recorded) is likely to have limited the power to detect effects of power lines. Increasing the number of transects would perhaps make these patterns clearer but the availability of suitable sampling sites was limited, as many power lines occur close to urban areas or parallel to roads and were thus not included in the study. For Golden Plover and black-tailed Godwit, densities in the furthest distance band from the power lines were higher than all other bands (Figure 2), which might suggest that effects could occur over larger distances than 500 m, but this remains to be assessed. It does not appear that effects of power lines vary depending on species' differences in nesting strategies, as Whimbrels nest in the open in areas with short vegetation (similar to Golden Plovers), while Redshanks conceal their nests (similar to black-tailed Godwits and Snipe) in more vegetated areas (Jóhannesdóttir *et al.*, 2014; Laidlaw *et al.*, 2020).

Most studies addressing the effect of power line presence on birds focus on collision risk, changes in predation pressure and secondary effects such as electromagnetic fields (D'Amico *et al.*, 2018; Fernie & Reynolds, 2005). Here we have identified reduced breeding densities of ground-nesting birds in the vicinity of power lines, however, the mechanisms driving these patterns are not yet known. Further studies quantifying demographic variation in relation to power-line presence (e.g. reductions in survival through collision risk and/or changes in breeding success as a consequence of predator use of pylons and overhead lines) may be informative, both in Iceland and other landscapes with power-lines and important ground-nesting bird populations. Additionally, as the human population grows, the amount of undisturbed land decreases (Torres *et al.*, 2016) and opportunities to quantify the communities and abundances that can be supported in large patches of open habitats become rarer. It is imperative to utilize current opportunities to identify the effects of structures such as power lines, and consider any identified effects in future infrastructure planning, before areas becomes saturated with anthropogenic developments.

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Appendix C

Table C1: Characteristics of the power lines from which the 85 transect surveys were conducted.

Voltage	66 kV	132 kV	220 kV
Number of cables	3	3	3-8
Pylon Type (no.) **Wood/Metal**	35/2	7/3	0/38
Mean height (±SD)	11 (± 2.7)	11 (± 2.7)	25 (±7.4)

Table C2: Table showing AIC values of models constructed for all study species combined and separately for each species. The model that had the lowest AIC value was considered to have best fit, but only if it ΔAIC ≥ 2 from a simpler model.*

Species	Model	AIC values
All species	A	2159.29
	B	**2151.02**
	C	2153.71
	D	2154.80
	E	2157.45
Meadow pipit	**A**	**1518.04**
	B	1517.01*
	C	1519.58
	D	1518.66
	E	1521.17
Snipe	**A**	**803.07**
	B	804.68
	C	804.89
	D	807.95
	E	808.11
Whimbrel	A	598.69
	B	**595.72**
	C	596.02
	D	594.36*
	E	595.30
Godwit	**A**	**417.00**
	B	418.47
	C	420.65

	D	420.42
	C	422.84
Redwing	A	341.51
	B	338.31
	C	**337.41**
	D	336.65
	E	335.48*
Dunlin	**A**	**320.74**
	B	322.62
	C	324.75
	D	325.23
	E	327.26
Redshank	A	329.12
	B	**323.34**
	C	325.75
	D	325.86
	E	327.77
Golden plover	A	332.49
	B	**331.87**
	C	334.15
	D	330.27*
	E	331.64

*Table C3: The effects (±SE) of distance from power line (interval), direction of transect and their interaction term, distance to water and slope on numbers of birds of eight species separately and all eight combined. Estimates from the GLMM models (Table 1) with the lowest AIC values (Table C2). Asterisks represent significance (p<0.05 *; p<0.01 **; p<0.001 ***).*

Species	**Individuals counted (n)**	**Best model**	**(intercept)**	**Interval**	**Direction**	**Interval:Direction**[ii]	**Distance to water**	**Slope**
All species	974	B	0.13 (±0.20)	0.04 (±0.01)**			0.01 (±0.07)	-0.99 (±0.55)
Golden plover	44	B	-4.57 (±0.83)	0.09 (±0.06)			0.67 (±0.23) **	0.99 (±1.92)
Redshank	46	B	-2.09 (±0.85)	0.17 (±0.06)**			-0.09 (±0.25)	-1.01 (±1.70)
Dunlin	47	A	-2.79 (±1.00)				-0.02 (±0.35)	3.20 (±2.43)
Redwing	49	C	-1.01 (±0.98)	-0.15 (±0.08)	-0.63 (±0.72)	-0.06 (±0.16)	0.30 (±0.23)	0.66 (±1.86)
Black-tailed Godwit	67	A	-2.32 (±0.98)				0.41 (±0.23)	1.08 (±1.30)
Whimbrel	97	B	-1.83 (±0.51)	0.09 (±0.04)*			-0.05 (±0.18)	-2.54 (±1.48)
Common Snipe	159	A	-1.98 (±0.33)				0.04 (±0.17)	0.65 (±1.21)
Meadow pipit	465	A	-0.32 (±0.17)				-0.11 (±0.10)	-1.80 (±0.77)*

[i]Reference voltage: lower

[ii]Reference direction: away from

Paper III

Fragmentation of semi-natural habitats with summer houses: effects on ground-nesting birds

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Abstract

The human population is increasing rapidly, accompanied by expansions in infrastructure, with introduction of anthropogenic structures into previously natural and semi-natural areas. The resulting changes can affect the abundance and species composition of pre-existing wildlife. Identifying and understanding the consequences of this introduction is vital for conservation of biodiversity. The number of summer houses in Iceland is increasing, from just over 10,000 in 2005 to approximately 15,000 in 2022. Additionally, over 7,000 summer house plots have been registered, where houses are planned but have yet to be constructed. The Icelandic lowlands, where the majority of summer houses are placed, support internationally important numbers of various populations of ground-nesting species. To explore the effects of single houses or low-density housing clusters, birds were counted in 292 points in the Icelandic lowlands with varying house density. Additionally, amount of habitat "lost", where the study species are generally not presumed to breed (houses, tracks and decks) was calculated from aerial photos, and its effect on densities of ground-nesting bird explored.

Out of seven study species, densities of five (Golden Plover (*Pluvialis apricaria*), black-tailed Godwit (*Limosa limosa*), Redshank (*Tringa totanus*), Whimbrel (*Numenius phaeopus*) and Meadow pipit (*Anthus pratensis*)) declined with increasing housing density, one species (Snipe (*Gallinago gallinago*)) showed no change and one (Redwing (*Turdus iliacus*)) increased. Accounting for habitat "lost" did not affect the results, suggesting that this decrease is not only driven by a reduction in suitable breeding area. The expansion of anthropogenic structures has been considered an important driver behind recent declines in wader abundance in Europe and it is imperative to conserve the current habitats of these species and prioritise generating and enforcing effective planning regulations that recognise the need to protect areas of high biodiversity value.

Introduction

The global human population has grown from 2.5 billion in the 1950s to an estimated ca. 8 billion at present time (Ritchie & Roser, 2018; Roser, 2013) and, according to UN projections, will peak at around 10.9 billion by the end of the century (Roser, 2013). This rapid increase in the human population has been accompanied by expansions in infrastructure, with introduction of anthropogenic structures into previously natural and semi-natural areas, and with rural areas becoming increasingly urbanised. Most urbanisation studies focus on areas where infrastructure is well established and extensive, but less is known about the impact of low-density infrastructure development in areas of biodiversity value (Chace & Walsh, 2006; Miller *et al.*, 2001). Previous studies have shown that transformation of natural areas into urban landscapes has drastic effects on the abundance and species composition of animals (Koellner & Scholz, 2008; McKinney, 2008; Torres *et al.*, 2016) and overall species richness and biodiversity tend to be depressed in areas with extreme levels of urbanization, such as urban core areas (Koellner & Scholz, 2008; McKinney, 2008). However, most studies have been conducted in areas where the human population density is high, and the habitat is strikingly different from natural areas while little attention has been given to the incremental effects of introducing houses into semi-natural areas which are the remaining areas supporting important biodiversity.

Studies on the effects of urbanization on birds have mainly involved comparisons of communities in areas with varying levels of urbanization (Marzluff *et al.*, 2001). Although the majority of studies have focussed on the negative effects of anthropogenic structures on wildlife, through processes such as habitat loss, collision risks, cat predation, electrocutions and by introducing a barrier in the landscape (Lepczyk *et al.*, 2004; Loss *et al.*, 2015; Morelli *et al.*, 2014), there may also be positive effects for some species such as the protection from natural predators, higher and more stable food supplies and increases in nesting opportunities (Chace & Walsh, 2006; Gering & Blair, 1999; Jokimäki *et al.*, 2016; Mainwaring, 2015; Morelli *et al.*, 2014). Although the urban environment may provide the resources needed for certain species to persist (typically generalist species), other previously abundant species may decline and even disappeared entirely (Caula *et al.*, 2010; Croci *et al.*, 2008). Studies have shown species that are frequently found in urban areas often possess certain traits such as being omnivorous or granivorous, possibly because they benefit from the presence of feeders provided by human, and cavity-nesting species which may find increased nesting opportunities in urban areas (Chace & Walsh, 2006; Croci *et al.*, 2008; Jokimäki *et al.*, 2016). How species respond to and are affected by anthropogenic structures will likely be a combination of factors related to the previous habitat, how much remains of that habitat, and the life history traits of the species (Chace & Walsh, 2006; Croci *et al.*, 2008; Ludlow *et al.*, 2015; Morelli *et al.*, 2014).

Although bird communities differ drastically between semi natural and urban areas, urbanization is a gradient, with certain areas in the initial stages containing low density of infrastructure, with large amounts of natural habitats still present (Marzluff *et al.*, 2001). Low-density housing in semi-natural landscapes are common in areas currently in the process of being transformed from natural to urban states, where initially one or more houses or anthropogenic structures are introduced and then their density increases with time. Additionally, this pattern may result from regulatory constraints which limit the number of houses in certain areas, practical limitations due to environmental conditions or the will of landowners. Little is known about how bird communities respond to newly established houses and housing clusters in semi-natural habitats. Do these effects appear immediately or does it take some time to manifest itself? The importance of identifying and understanding the impact, if any, of low density housing infrastructure on breeding birds in the surrounding habitats cannot be underestimated as these areas are often the last remaining areas of biodiversity value. Evidence is accumulating that a wide array of single anthropogenic structures can have a negative effect on densities of ground-nesting birds in the surrounding habitat, and this effect may be detected in a much wider area than what the structure occupies (Benítez-López *et al.*, 2010; Dinkins *et al.*, 2014; Fernández-Bellon *et al.*, 2018; Morán-López *et al.*, 2017; Thompson *et al.*, 2015; van der Vliet *et al.*, 2010). These structures include but are not limited to houses (van der Vliet *et al.*, 2010), roads (Kociolek *et al.*, 2011), power lines (D'Amico *et al.*, 2018) and wind farms (Fernández-Bellon *et al.*, 2018). The introduction of anthropogenic structures to previously natural habitats will inevitably decrease the amount of native habitat, and may induce changes to the surrounding area, which can affect species distribution and/or demographic parameters factors such as survival (Ludlow *et al.*, 2015) and productivity (Ludlow *et al.*, 2015; Yoo & Koper, 2017).

Iceland is sparsely populated, with large areas of open semi-natural landscapes which are important areas for breeding ground-nesting birds (Jóhannesdóttir *et al.*, 2014). Summer houses are increasing in Iceland, from just over 10,000 in 2005 to approximately 15,000 in 2022 (Registers Iceland, 2022b). Additionally, over 7,000 summer house plots have been registered in Iceland, where houses are planned but have yet to be constructed (Registers Iceland, 2022c). The majority of these summer houses and house plots are situated in the Icelandic lowlands which are also the most important areas for breeding birds (Jóhannesdóttir *et al.*, 2014; Skarphéðinsson *et al.*, 2016). Iceland is especially important for breeding waders (Charadrii), and it holds large proportions of the global populations of some species (Gunnarsson *et al.*, 2006; Jóhannesdóttir *et al.*, 2014). Previous studies have shown that the density of these species is often depressed in the vicinity of newly established anthropogenic structures in natural habitats (Pálsdóttir *et al.*, In press; Pearce-Higgins *et al.*, 2012; Reijnen *et al.*, 1997; van der Vliet *et al.*, 2010). Icelandic summer houses and the accompanying infrastructure may influence the density of ground-nesting birds primarily through habitat removal, and then via secondary factors, such as changes in the surrounding habitat (vegetation, predator pressure, microclimate) which can affect demographic parameters further reducing the density of local populations, given the high breeding site-fidelity of these species (Fischer & Lindenmayer, 2007; Miller *et al.*, 2001). In addition, the visual obstruction caused by summer houses and the increased traffic of people and/or cars that often occur with the establishment of anthropogenic structures (Ditchkoff *et al.*, 2006; Hovick *et al.*, 2014) could result in ground-nesting birds avoiding these areas.

Here we use surveys of bird abundance along a gradient of low-density recently established houses in semi-natural habitats to assess the relationship between housing density and abundance of different species and separately quantify the effects of housing density and (breeding) area lost on bird abundance.

Methods

Site characteristics

Birds were counted on 71 sites in the Icelandic lowlands (Figure 1) between May and June of 2018, a period which spans the majority of the nesting and chick-rearing of ground-nesting species in Iceland (Alves *et al.*, 2019; Gunnarsson *et al.*, 2017; Jóhannesdóttir *et al.*, 2019). Sites were chosen in areas that were at least 1 km away from urban settlements and where one or more summer cottages were present. At each site, between 2 and 8 point-counts were conducted, resulting in a total of 292 points. The location of point counts at each site was chosen with the aim of capturing the variability in housing density, (range=0-35 houses/point). At each point, the observer walked to the counting spot and initiated the count immediately, standing still and identifying all birds within a 200 m radius (approximately 12.5 ha) for 5 minutes. A laser range-finder was used to aid in the estimation of distance to the 200 m boundary. To avoid confounding effects on bird abundance, all counts were performed where there were no other anthropogenic structures or modified habitats (major roads, forest plantations or agriculture fields) within the survey area.

Bird counts

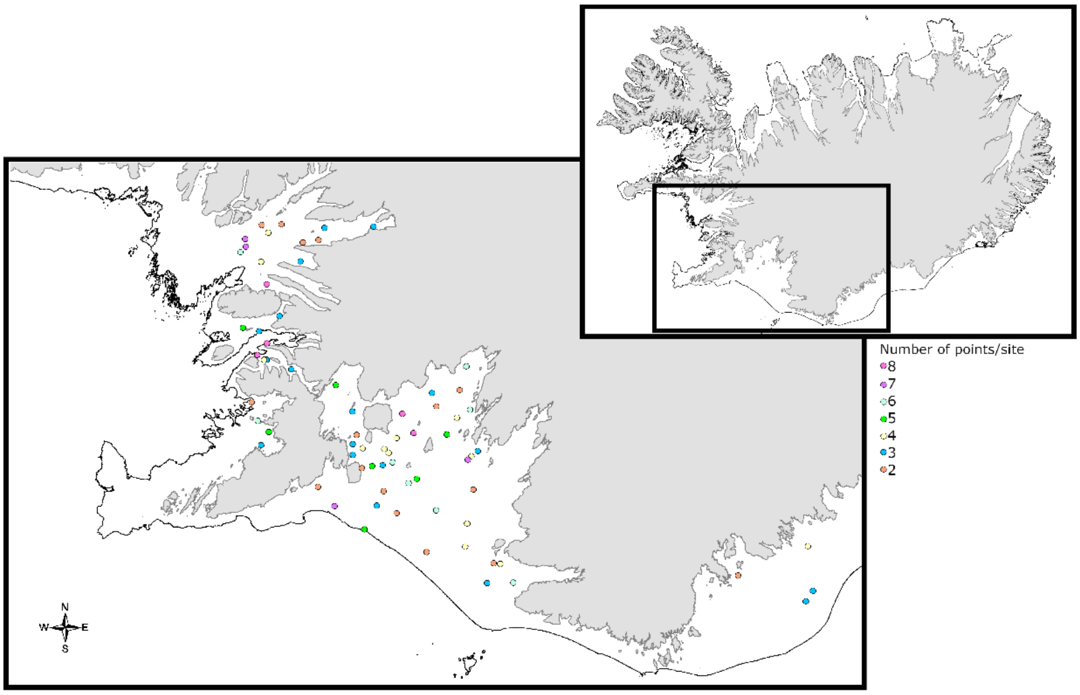

Figure 1: Location of 71 sites in lowland Iceland where between 2-9 point counts were conducted in areas below 200 m a.s.l. (shown in grey) in the summer of 2018.

Bird counts were conducted between 6:30 am and 7 pm, but not during times with heavy rainfall or wind speeds >7 $m.s^{-1}$, as this could affect the detectability of the target species (Hoodless *et al.*, 2006). Survey points were assigned into one of four groups: points with no houses; points with a single house; low house density (2-5 houses) and high house density (6-35 houses. For each survey point, habitat type (classified according to the Icelandic farmland database (*Nytjaland*) as: semi-wetland, grassland, rich heathland and poor heathland (Gísladóttir *et al.*, 2014; Jóhannesdóttir *et al.*, 2014)) and the presence or absence of trees was recorded.

Quantifying extent of infrastructure

In areas with summer cottages, anthropogenic infrastructure includes the houses, tracks, decks and parking spaces, all of which directly remove potential habitat for ground-nesting birds. For all points where recent (less than 2 years old) digitised aerial photos of sufficient resolution were available (251 out of 292 survey points) (Loftmyndir ehf, 2019) the total area of all infrastructure (houses, tracks, decks and parking spaces) was calculated (Figure 2). The amount of remaining available habitat was then calculated by subtracting the area of infrastructure from the total amount of area per point (125.664 m^2).

Figure 2: Example aerial photo of a survey point showing the boundary of the 200 m zone within which birds were counted (red line) and the area containing anthropogenic infrastructure (houses, roads and car parks; yellow line). Photos from www.map.is (Loftmyndir ehf 2019).

Statistical analysis

To explore how bird abundance varies with housing extent, GLMMs with a Poisson distribution and a log-link function were constructed with count (for each species in turn and all species combined) as response, house density (in four categories; no houses, single house, low house density or high house density) and habitat as fixed effects to account for varying bird densities between habitats (Table 1), and site included as a random effect (Table D1).

In an effort to separate the effects of habitat occupied by structures from the behavioural or demographic effect that house presence has on surrounding birds, we calculated how much area in each point was covered by infrastructure on a subset of points where aerial photos were available and houses and tracks visible. The same GLMM model was then run on this subset of data, now including an offset of available habitat (Table D1). All statistical analyses were performed using Rstudio (R Core Team, 2017; RStudio Team, 2016). The package lme4 was used for models and ggplot2 for graphing (Bates *et al.*, 2014; Wickham, 2016).

Results

Effects of housing infrastructure on bird abundance

In total 2,819 birds were counted on 292 survey points. Approximately 90% of the birds counted belonged to seven species: two passerines; Meadow pipit (*Anthus pratensis*), Redwing (*Turdus iliacus*) and five wader species; Golden Plover (*Pluvialis apricaria*), Snipe (*Gallinago gallinago*), Redshank (*Tringa totanus*), Whimbrel (*Numenius phaeopus*) and black-tailed Godwit (*Limosa limosa*: hereafter Godwit), and these species were retained for the analyses. The highest abundance of birds was recorded in semi-wetland and lowest in poor heathland habitats, for all seven species combined and for individual species, except for Golden Plover and Redwing for which abundance was highest in poor heathland and rich heathland, respectively (Table 1).

Table 1: Mean (± SE) numbers of seven bird species and houses recorded on survey points across four habitats in lowland Iceland in 2018.

Species	**Poor heathland (n=67)**	**Grassland (n=49)**	**Rich heathland (n=151)**	**Semi-wetland (n=22)**
Golden plover	0.4 (±0.1)	0.2 (±0.01)	0.3 (±0.05)	0.2 (±0.2)
Redwing	2.0 (±0.2)	2.2 (±0.4)	2.7 (±0.2)	1.1 (±0.4)
Snipe	2.1 (±0.2)	2.0 (±0.2)	2.4 (±0.2)	3.3 (±0.4)
Godwit	0.1 (±0.04)	0.6 (±0.2)	0.4 (±0.09)	1.5 (±0.4)
Redshank	0.1 (±0.03)	0.4 (±0.1)	0.4 (±0.06)	1.0 (±0.3)
Meadow pipit	1.9 (±0.2)	2.4 (±0.2)	2.2 (±0.1)	2.5 (±0.3)
Whimbrel	0.4 (±0.1)	0.4 (±0.1)	0.5 (±0.07)	0.9 (±0.3)
Total	6.9 (±0.4)	8.3 (±0.5)	9.0 (±0.3)	10.5 (±0.6)
Houses	2.7 (±0.5)	3 (±0.6)	4.2 (±0.5)	2 (±0.5)

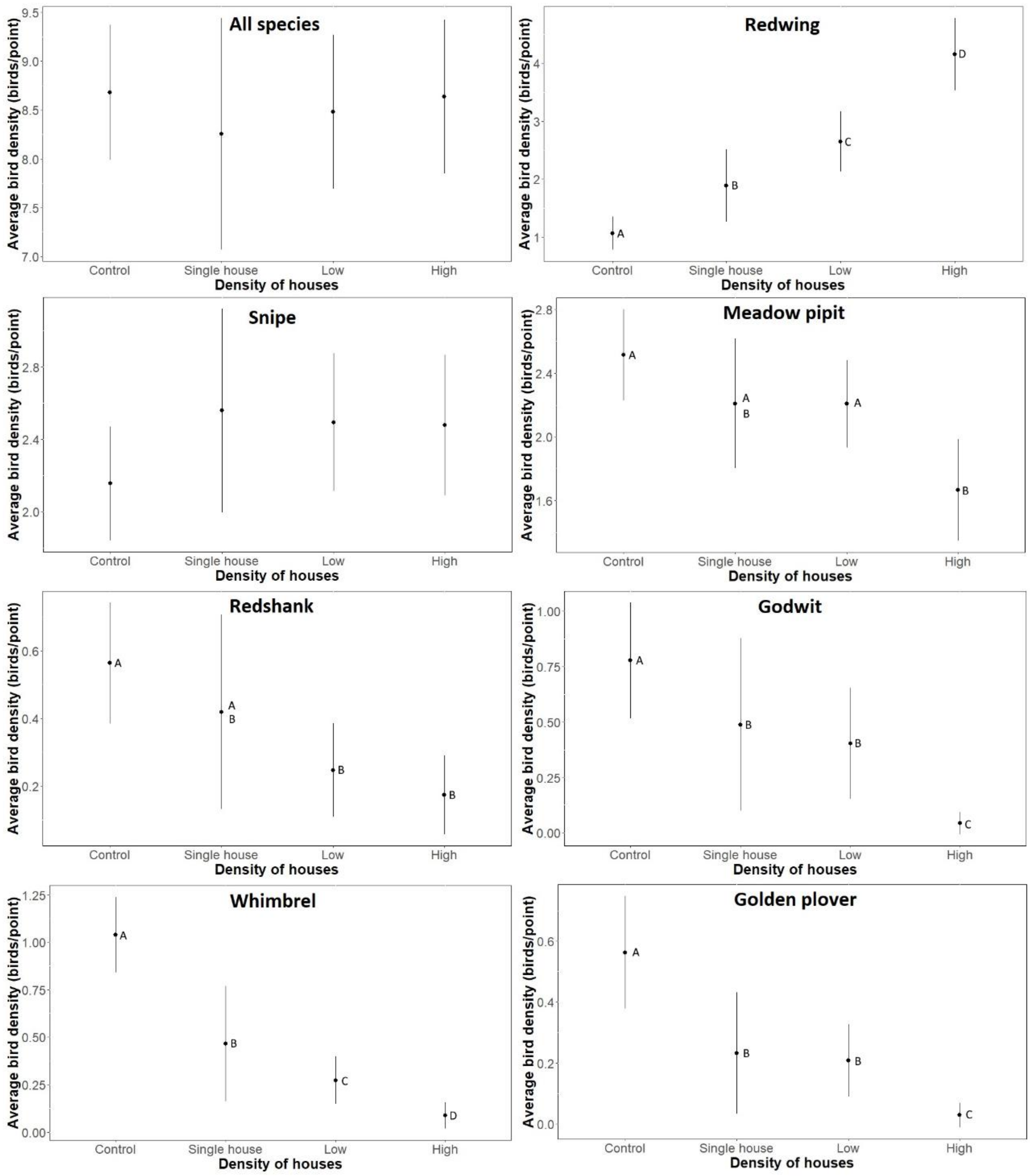

Figure 3: Mean (±SE) density of birds in survey points with no houses, single houses, low house density (2-5 houses) and high house density (6-30 houses). Letters indicate significant differences between categories.

Overall bird abundance did not differ between survey points with and without houses, but all species except Snipe did differ significantly in abundance. While Redwing abundance was higher with house presence, the remaining five species (Godwit, Golden Plover, Redshank, Whimbrel and Meadow pipit) all showed reduced abundance in survey points with houses (Table D1). Out of these five species, three (Whimbrel, Godwit and Golden Plover) showed significantly lower abundance in all points with houses compared to control points, one (Redshank) showed lower density in low/high house density compared to control points and one (Meadow pipit) showed decreased abundance in points with high house density compared to control points (Table D1, Figure 3).

Area covered by infrastructure

For 251 survey points, it was possible to calculate the area with housing infrastructure and the area of remaining habitat (Figure 4, Table 3). The results from these models were in large part the same as in the original models. Two changes were detected, Godwit, abundance did not vary significantly between control points and points with one house, contrary to previous result, and Redshank showed the opposite trend, with significantly lowered abundance in points with a single house compared to control points.

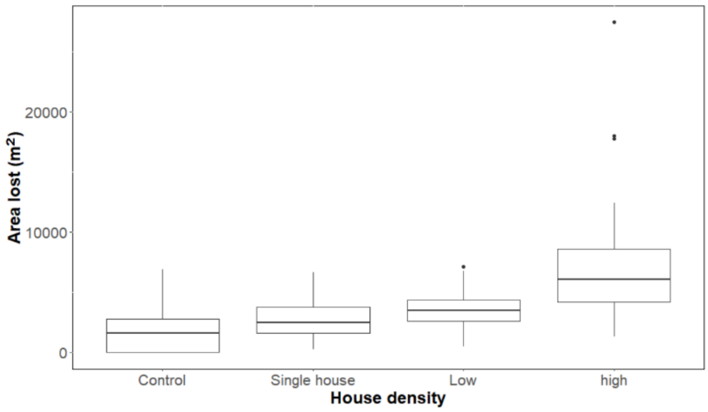

Figure 4: Boxplot of area that is covered by infrastructure in each of the housing categories in the 251 points where recent aerial photos were available. Total area of point is ~125,000 m^2.

Table 3: Percent change in bird abundance (±SE) between points with different house densities in relation to points with no houses. Only numbers in categories which were significantly different from control points in GLMM models are shown (Estimates presented in Table D1).

	Single house	Low house density	High house density
Area with infrastructure	2% (±0.2)	3% (±0.2%)	6% (±0.5%)
Golden plover	-59% (±19)	-63% (±15)	-95% (±11)
Whimbrel	-55% (±25)	-74% (±16)	-92% (±13)
Godwit	-37% (±32)[A]	-48% (±26)	-94% (±16)
Redshank	-26% (±23)[B]	-56% (±16)	-69% (±15)
Meadow pipit	-	-	-34% (±30)
Snipe	-	-	-
Redwing	+76% (±45)	+148% (±40)	+289% (±46)
All species	-	-	-

[A]Only significant in model without offset
[B]Only significant in model with offset

Discussion

In lowland Iceland, summer houses are widespread and increasing rapidly. Here, we have identified significant effects of single houses and small housing clusters (fewer than six houses), with four wader species (Golden Plover, Godwit, Whimbrel, Redshank) being found in lower densities where houses are present, and one passerine (Redwing) in higher densities. These effects became even more prominent as the number of houses increased and for another passerine (Meadow pipit) only had an effect at higher house density (> six houses). A certain amount of breeding habitat is lost when houses and tracks are placed in natural habitats, however including available area (removing area covered by infrastructure) as an offset did not change our overall results. In the remaining habitat, density of birds is visually lower in points with houses compared to control points (Figure 5). This decrease in abundance of our study species in the vicinity of houses is therefore much more than expected by the direct habitat area loss alone. The change in abundance of these ground-nesting species is considerable, with species declining on average between 36%-94% in areas with high house density (6-35 houses/point) compared to points with no houses, while the amount of habitat covered by infrastructure was on average 6% (Table 3). The point with the largest area covered by infrastructure had 20 houses and houses and tracks covered 27.469 m^2 of the total area of that point which is 125.664 m^2. This shows that even in the densest summerhouse areas, direct habitat loss never exceeded 22% of the total area, while the effects on birds are striking, suggesting that impacts go well beyond simple loss of area (Table 3).

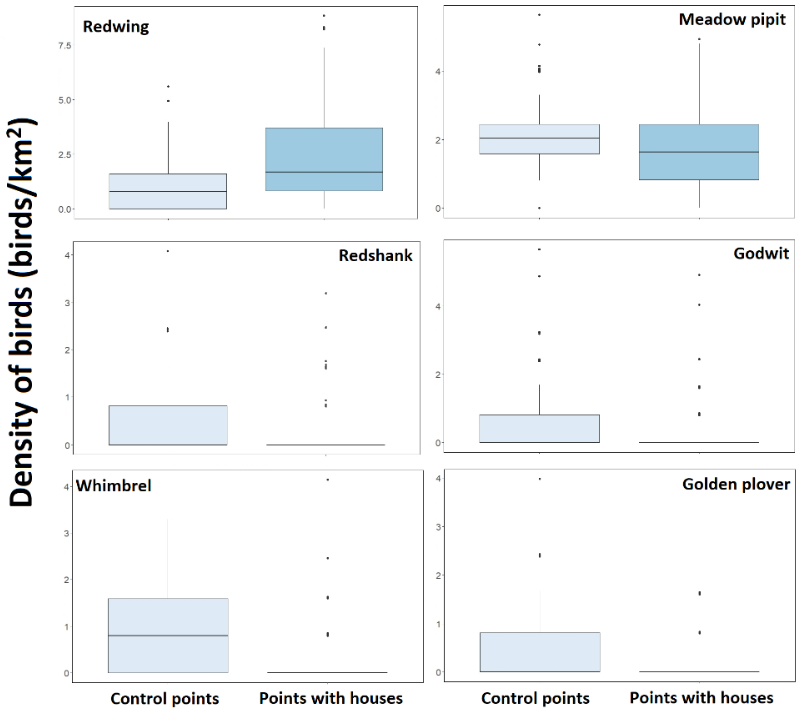

Figure 5: Boxplot showing density of birds for species which were affected by house presence, in available area (excluding area covered by infrastructure) in points with houses and control points which contained no houses.

The drivers behind the lower abundance of these bird species in areas with houses are currently unknown. Most summer cottages in Iceland are used frequently during the breeding season so humans, cars and cats (which are often predators of nesting birds) are common, and could influence levels of parental care of chicks and likelihood of nest desertion (Chace & Walsh, 2006). Although the habitat surrounding most summer cottages in Iceland generally remains unchanged after the introduction of cottages, most houses have trees planted around them, often to protect the house from wind. As ~77% of all points with houses had some trees present, and this was highly correlated with house density, it is impossible to disentangle the effect of houses from the effect of trees. Tree presence has been shown to induce lower densities of wader species in the surrounding area (Holmes *et al.*, 2020; Pálsdóttir *et al.*, In press; Wilson *et al.*, 2014), and trees may be a contributing factor to the patterns described here. Effects of summer houses on ground-nesting birds may take some time to become apparent, especially if they are driven by demographic factors rather than behavioural effects. The majority of houses in our study have been constructed in the last 20 years and, in most sites, house numbers are still increasing (Registers Iceland, 2022a). To identify the underlying drivers behind an altered bird abundance surrounding houses, before-after-control-studies of marked individuals through periods of construction, where their behaviour and demography were tracked would be needed. Redwing increased with housing density, with abundance being 2.3 times higher in points with high house density compared to points with no houses. Redwings nest both in forests and on the ground in open habitats in Iceland (Skarphéðinsson *et al.*, 2016). It is possible that the increase in tree growth that accompanies summer houses in Iceland may facilitate an increase in Redwing abundance where house density is high. Redwing are also known to vocalize from tall structures so they may even use houses and/or associated power lines for vocalization, thereby being drawn to more residential areas than some of the other ground-nesting species. In addition to Redwing, houses and associated features may be beneficial to other passerine species such as starling and redpoll, which are common in urban areas in Iceland (Einarsson, 2021; Skarphéðinsson *et al.*, 2016) and were only documented in points that had houses. However, bird communities in urban landscapes generally tend to be more homogenous and composed of generalist species (Chace & Walsh, 2006; Croci *et al.*, 2008; Devictor *et al.*, 2007). Even if some well adapted species will increase in abundance with the expansion of man-made surfaces, it may come at the cost of a lowered overall biodiversity and species richness in those areas. However, lowered species richness was not apparent in our data, with number of species seen in each of our housing categories being similar, but this pattern will probably become more apparent at higher urbanization levels.

Waders have been declining in the world in recent years, mostly driven by habitat degradation (International Wader Study Group, 2003). The Icelandic lowlands are composed of a mosaic of natural open habitats along with low-intensity agricultural patches, forestry and anthropogenic structures (Gunnarsson *et al.*, 2006). Iceland is considered one of the most important areas for breeding waders in Europe with an estimated 1.5 million pairs of waders nesting in Iceland, with ~85% of them in the lowlands (Gunnarsson, 2020), which is also the area in which the majority of summer houses are placed. Here we have shown that the effects of houses on the density of ground-nesting species in open habitats in lowland Iceland often become apparent with only a single house present. The Icelandic lowlands are around 33,000 ha (Gunnarsson, 2020), and if the 7,000 summer houses that are planned in Iceland would be placed in previously unaffected areas, assuming a 200 m radius affected area where densities of five of our study species are lower, this would accumulate to approximately 9.000 ha area where bird densities could be affected. Therefore, for Iceland to meet its international commitments in protecting these species (Schmalensee *et al.*, 2013), future developments should be primarily planned in areas which are already under anthropogenic influence rather than allowing expansion into currently undisturbed areas.

The conservation status of all of our study species in Iceland is currently classified as least concern (LC), except Redshank which is near threatened (NT) (Icelandic Institute of Natural History, 2018). However, long-term monitoring of ground-nesting bird populations in Iceland is in many cases lacking. Annual counts of meadow birds have only been systematically conducted since the year 2006 which makes it problematic to identify any long-term population trends (Skarphéðinsson *et al.*, 2016). The amount of anthropogenic surfaces in Iceland is increasing at a rapid pace, with the ongoing expansion of among other, houses, wind farms, power lines, roads and plantations forests (EEA, 2018; Wald, 2012). The negative effects of houses on wader density documented here, along with in similar studies in Iceland surrounding houses and power lines (Pálsdóttir *et al.*, In press), show that these species are already experiencing localized changes in density, and if this process goes on, it will eventually affect the population. The expansion of anthropogenic structures (houses, wind farms, roads etc.) and habitats (agriculture and plantation forestry) has been considered an important driver behind recent declines in wader abundance in Europe (Amar *et al.*, 2011; Pearce-Higgins *et al.*, 2017; Sutherland *et al.*, 2012; van der Vliet *et al.*, 2010; Żmihorski *et al.*, 2018) and attempts at restoring lost breeding bird habitat, or increase current densities in available habitats after population declines, have often proved unsuccessful, with restored sites holding lower nesting densities than reference sites (Bentzen *et al.*, 2018; Melman *et al.*, 2008). Therefore, it is imperative to conserve the current breeding habitats of these species and prioritise generating and enforcing effective planning regulations that recognise the need to protect areas of high biodiversity value.

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Appendix D

*Table D1: Estimates from the GLMM models of variation in abundance of birds in sites with varying numbers of summer houses. Site was included as a random factor in all models. Significance is indicated by asterisks (p<0.05 *; p<0.01 **; p<0.001 ***).*

Full model: Bird abundance (birds/point) ~ no. of houses + habitat									
Variable		**All birds**	**Golden Plover**	**Whimbrel**	**Godwit**	**Redshank**	**Meadow pipit**	**Redwing**	**Snipe**
Houses	(Intercept)[a]	2.08 (±0.07)	-1.38 (±0.40)	-0.38 (± 0.27)	-0.98 (±0.36)	-0.64 (± 0.32)	0.96 (±0.12)	-0.10 (±0.17)	0.54 (±0.14)
	1 house	-0.08 (±0.07)	-0.80 (±0.36)*	-0.69 (±0.26)**	-0.59 (± 0.29)*	-0.53 (± 0.31)	-0.15 (±0.12)	0.53 (±0.15)***	0.11 (±0.12)
	2-5 houses	-0.07 (±0.05)	-0.98 (±0.30)***	-1.34 (±0.25)***	-0.89 (±0.23)***	-1.02 (±0.28)***	-0.14 (±0.10)	0.90 (±0.12)***	0.07 (±0.10)
	6 or more houses	-0.03 (±0.06)	-2.85 (±0.73)***	-2.38 (±0.43)***	-2.73 (±0.60)***	-1.04 (±0.34)**	-0.44 (±0.12)***	1.19 (±0.12)***	0.14 (±0.11)
Habitat	Poor heathland	-0.16 (±0.09)	0.57 (±0.45)	-0.16 (±0.35)	-2.02 (±0.66)**	-2.11 (±0.62)***	-0.23 (±0.15)	-0.03 (±0.19)	0.12 (±0.17)
	Rich heathland	0.12 (±0.07)	0.46 (±0.40)	0.35 (±0.28)	-0.08 (±0.30)	-0.18 (±0.32)	-0.02 (±0.12)	0.20 (±0.15)	0.18 (±0.14)
	Semi-wetland	0.25 (±0.10)*	0.04 (±0.56)	0.61 (±0.37)	0.64 (±0.32)*	0.76 (± 0.40)	0.06 (±0.18)	-0.32 (±0.25)	0.45 (±0.18)*
Post hoc analysis									
Single house→low house density		0.01 (±0.07)	-0.18 (±0.43)	-0.65 (±0.33)*	-0.30 (±0.30)	-0.49 (±0.35)	0.01 (±0.13)	0.36 (±0.14)**	-0.04 (±0.13)
Single house→high house density		0.05 (±0.07)	-2.05 (±0.79)**	-1.69 (±0.48)***	-2.13 (±0.64)***	-0.51 (±0.42)	-0.28 (±0.15)	0.66 (±0.14)***	0.02 (±0.14)
Low→high house density		0.05 (±0.06)	-1.87 (±0.76)*	-1.04 (±0.47)*	-1.84 (±0.62)**	-0.02 (±0.40)	-0.29 (±0.13)*	0.30 (±0.11)**	0.06 (±0.12)
Full model: Bird abundance (birds/point) ~ no. of houses + habitat + offset(log(available area)									
Houses	(Intercept)[a]	-2.70 (±0.08)	-6.22 (±0.46)	-5.21 (± 0.29)	-5.64 (±0.38)	-5.51 (± 0.37)	-3.83 (±0.12)	-4.82 (±0.18)	-4.26 (±0.15)
	1 house	-0.07 (±0.07)	-1.08 (±0.42)*	-0.74 (±0.28)**	-0.44 (± 0.30)	-0.67 (± 0.34)*	-0.17 (±0.13)	0.52 (±0.16)**	0.17 (±0.13)
	2-5 houses	-0.07 (±0.06)	-0.86 (±0.32)**	-1.35 (±0.27)***	-1.13 (±0.29)***	-1.10 (±0.31)***	-0.11 (±0.11)	0.76 (±0.13)***	0.17 (±0.11)
	6 or more houses	-0.01 (±0.06)	-2.64 (±0.73)***	-2.15 (±0.43)***	-2.43 (±0.60)***	-1.18 (±0.41)**	-0.40 (±0.13)**	1.22 (±0.13)***	0.21 (±0.12)
Habitat	Poor heathland	-0.15 (±0.10)	0.77 (±0.50)	-0.16 (±0.38)	-1.84 (±0.69)**	-2.18 (±0.73)**	-0.17 (±0.16)	-0.01 (±0.21)	0.03 (±0.18)
	Rich heathland	0.11 (±0.08)	0.41 (±0.44)	0.36 (±0.30)	0.11 (±0.36)	-0.04 (±0.40)	-0.01 (±0.13)	0.19 (±0.17)	0.12 (±0.15)
	Semi-wetland	0.18 (±0.11)*	0.01 (±0.62)	0.71 (±0.40)	0.47 (±0.40)	0.83 (± 0.48)	0.01 (±0.19)	-0.69 (±0.30)*	0.46 (±0.20)*

[a]Reference group: Points with no houses; reference habitat: Grassland.

Paper IV

Effects of moderate to low-traffic roads on density of ground-nesting birds in subarctic habitats

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Abstract

Roads are one of the most widespread anthropogenic structures. The introduction of roads to open habitats will result in habitat loss along with increased disturbance and collision risk. Here we use transect counts, perpendicular to relatively low-traffic roads in Iceland, to estimate whether and which species of ground-nesting birds may be affected and how far from the roads this effect may extend. Out of eight species studied, four (Whimbrel (*Numenius phaeopus*), Golden Plover (*Pluvialis apricaria*), Dunlin (*Calidris alpina*) and Meadow pipit (*Anthus pratensis*) were found in lower densities near than further away from roads, and four (black-tailed Godwit (*Limosa limosa*), Redshank (*Tringa totanus*), Snipe (*Gallinago gallinago*) and Redwing (*Turdus iliacus*)) showed no change with distance to roads. For species that were negatively affected by roads, lower densities were detected up to a distance of 200 m. Total bird densities were approximately 20% lower within 200 m distance from roads, or 161 birds/km^2 close to roads (0-200 m), compared to 199 birds/km^2 further away (201-500 m).

Introduction

There is a growing body of evidence that roads can significantly alter the density and distribution of surrounding wildlife (Benítez-López *et al.*, 2010; Grilo *et al.*, 2020; Reijnen *et al.*, 1996; Yoo & Koper, 2017). Roads differ from many other anthropogenic structures as they are low and linear and do not necessarily occupy a large area, leaving substantial patches of the original habitat still present. However, roads decrease the amount of the native habitat to some extent and road placement may also induce changes to the surrounding habitats, e.g. through changes in hydrology, soil density and surrounding vegetation, along with various chemicals emitted by vehicles and particulate matter spreading from roads (Forman *et al.*, 2002; Seiler, 2001; Summers *et al.*, 2011). Roads may also introduce a barrier effect in the landscape, where individuals are unable or unwilling to cross the road and therefore remain isolated in a smaller habitat patch than before the road was placed (Seiler, 2001). Roads may also influence predator distribution in the surrounding habitat, either as a consequence of the barrier effect or due to predators travelling along roads (Seiler, 2001). In addition to the physical aspects of the road as a structure, road placement is usually accompanied by vehicle traffic. Collision risk by vehicles is considered an important cause of animal mortality (Benítez-López *et al.*, 2010; Grilo *et al.*, 2020; Seiler, 2001), and disturbance due to traffic may also affect animals in the surrounding landscape, especially species which rely on vocalizing, e.g. for establishment or maintenance of territories and for mating (Kociolek *et al.*, 2011; Rheindt, 2003). The placement of roads can also increase the accessibility of previously reclusive locations to humans, which may further facilitate the disturbance effect at a considerably larger scale.

Multiple studies have identified negative effects of roads on density of ground-nesting birds in the surrounding landscapes (Benítez-López *et al.*, 2010; Forman *et al.*, 2002; Kociolek *et al.*, 2011; Reijnen *et al.*, 1997). The primary driver behind this is considered to be increased collision risk and in both Europe and North America it is estimated that millions of birds die each year from collisions with cars (Loss *et al.*, 2015; Trombulak & Frissell, 2000). In addition to the higher mortality rate through increased collision risk, roads and vehicle traffic will increase the disturbance and alter the surrounding habitat, which can affect physical processes such as stress levels, survival, vigilance and reproductive success of these species (Kociolek *et al.*, 2011; Morán-López *et al.*, 2017; Trombulak & Frissell, 2000). How far this effect extends from roads may also vary between species (van der Vliet *et al.*, 2010) and road characteristics, but disturbance distances have been identified as small as 100 m from cycle paths and small roads, up to >2 km for highways (Thompson *et al.*, 2015; van der Vliet *et al.*, 2010). Although uncommon, examples of positive effects of roads on breeding birds have also been identified through processes such as reduced predation pressure and associated infrastructure used for perching, nesting and hunting (Morelli *et al.*, 2014). However, these processes are more likely to be beneficial to passerines and raptors, and are more commonly observed along unpaved roads or low traffic roads (Morelli *et al.*, 2014). For ground-nesting birds the majority of studies have been conducted in areas where roads are large and the traffic volume is high, and traffic intensity has also been shown to negatively affect breeding birds in the surrounding areas (van der Vliet *et al.*, 2010). A study from the Netherlands found that surrounding high traffic roads (>50,000 vehicles/day) the disturbance distance for ground-nesting birds was larger and more species showed a negative effect compared to low traffic roads (<500 vehicles/day) (Reijnen *et al.*, 1996). However, a meta-analysis found no effect of traffic volume on the reduction in bird populations close to roads (Benítez-López *et al.*, 2010) and it has been suggested that the negative effects of roads on breeding birds may be driven by vehicle velocity rather than traffic volume, which tends to be higher on high traffic roads.

The Icelandic lowlands are an important breeding area for a variety of ground-nesting birds and Iceland is a signatory to multiple international agreements where the country has committed to protect these species (Schmalensee *et al.*, 2013). The majority of ground-nesting birds in Iceland nest between May-June (Alves *et al.*, 2019; Gunnarsson *et al.*, 2017), which is also a time when people, both residents and tourists, tend to travel more within Iceland. Therefore, the breeding period of these species coincides with the highest traffic period of the year. The Icelandic transportation system is currently not extensive compared to the rest of Europe (Torres *et al.*, 2016) and traffic volume is much lower, with no roads surpassing 100,000 vehicles/day, and the majority of roads outside the capital region having fewer than 1000 vehicles/day (Vegagerðin, 2022). Traffic has been increasing steadily for the past years driven primarily by the increasing number of tourists along with a growing resident population. For example, traffic on the road leading Reykjavik to Keflavík international airport (the major international airport in the country) went from ~5,000 vehicles/day in 2006 to ~13,000 vehicles/day in 2018 (Vegagerðin, 2022). In Iceland, previous studies on the effect of roads on the density of birds have primarily focused on biodiversity censusing in areas prior to roads being placed, to estimate its possible effects (Albertsson *et al.*, 2004; Hreinsdóttir *et al.*, 2006). Therefore, much remains to be clarified regarding the effects of traffic on local biodiversity, particularly on ground nesting birds, which Iceland has agreed to protect at the international level.

Most studies on the effects of roads on ground-nesting birds in the adjacent habitat have focused on roads with high traffic volume. But far less attention has been given to tracks and low-traffic roads. Here we aim to study: a) if moderate to low traffic roads (<15,000 vehicles/day) have an effect on densities of ground-nesting birds in the surrounding areas; b) how far from roads does this potential effect extend; and c) explore how much of the Icelandic lowlands, currently with low density infrastructure and large open habitats, is within the area affected by roads.

Material and methods

Data collection

This study was conducted between May and June, which spans the majority of the breeding season of ground-nesting birds in Iceland, in the years 2018 and 2019. Sites surrounding low traffic roads were selected by searching the database of the The Icelandic Road and Coastal Administration (IRCA) for roads where the traffic volume was less than 15,000 vehicles/day in the summertime (Vegagerðin, 2019) and were surrounded by open habitats (Figure 1). Subsequently transects which were 400 m long and perpendicular to the roads were initiated at each chosen site, starting at the road edge and walked at a steady pace. All transect were limited to a single habitat type. All birds seen within 100 m in each direction were recorded when first seen, along with species and distance from the road. To avoid confounding effects of other structures, sites were chosen which were over 100 m away from other anthropogenic structures such as houses and power lines (Pálsdóttir *et al.*, In press; Pálsdóttir *et al.*, 2022). At each site, the habitat type was classified as wetland, semi-wetland, grassland, rich heathland and poor heathland according to the Icelandic Farmland Database (Gísladóttir *et al.*, 2014).

Figure 1: Location of 122 transects surrounding roads where bird surveys were conducted in areas below 300 m a.s.l. (shown in grey) in the summers of 2018 and 2019.

Statistical analysis

All transects were divided into intervals of 50 m and bird density, both in total and for each species, was calculated at each interval and used as a response variable in a generalized linear mixed model (GLMM) with a Poisson distribution. As bird density was low, the majority of intervals had a value of 0 and package glmmTMB was used to add a zero-inflation parameter to all models (*ziformula=~1*) (Brooks *et al.*, 2017). Four models were constructed, using all combinations of distance from roads (interval), traffic volume and an interaction term between them, along with a null model (Table 1). The constructed models were subsequently compared, and the highest ranking model identified using AIC values, assuming a better fit when AIC was significantly lower ($\Delta AIC \geq 2$) than a more parsimonious model (Table 1, Table E1). Transect nested in habitat was included as a random factor to account for varying density between habitats and non-independence of interval within the same transects.

To explore the magnitude of the effect of roads on density of ground-nesting birds, segmented linear regression was used to identify the distance from the roads at which bird numbers are altered before they plateau (Muggeo, 2008).

Table 1: Variables included in the models and structures of models testing various combinations of fixed factors, along with an intercept only model (Model G).

Variable	**Unit**	**Definition**
Bird density	Birds/ha	Total number of birds counted per interval (1 ha)
Interval	1-8	Distance bands of 50 m on transects from closest (1) to furthest away (8) from roads. Measured with a GPS tracker.
Transect	Transect number	Transect identity
Traffic	Vehicles/day	Traffic on the road (Range 39-14,612) corresponding to each transect (Vegagerðin, 2019).
Habitat	Poor heathland/rich heathland/grassland/ semi-wetland/wetland	Classification of transect habitat type, from the Nytjaland database (Gísladóttir *et al.*, 2014)
	Model structure	
Model A	Bird density (birds/ha) ~ Interval * Traffic + (1|Habitat/Transect)	
Model B	Bird density (birds/ha) ~ Interval + Traffic + (1|Habitat/Transect)	
Model C	Bird density (birds/ha) ~ Interval + (1|Habitat/Transect)	
Model D	Bird density (birds/ha) ~ 1 + (1|Habitat/Transect)	

Affected area in the Icelandic lowlands

In an attempt to estimate how much of the Icelandic lowlands are currently affected by roads, 100,000 random points were generated in the Icelandic lowlands (<300 m a.s.l.) using ArcGIS, and their respective distance from roads measured using a map layer from the National Land Survey of Iceland (Landmælingar Íslands, 2020) which contains all roads in Iceland.

Results

In total, 1,894 individuals were counted in 122 transects: 60 transects in 2018 and 62 in 2019 (Figure 1). Approximately 93% of individuals counted belonged to eight species: Redshank (*Tringa totanus*), Redwing (*Turdus iliacus*), Golden Plover (*Pluvialis apricaria*), black-tailed Godwit (*Limosa limosa*), Dunlin (*Calidris alpina*), Whimbrel (*Numenius phaeopus*), Snipe (*Gallinago gallinago*) and Meadow pipit (*Anthus pratensis*), which were retained for the statistical analysis.

Total bird density increased with distance from road by 6% per 50 m interval (Table E2, Figure 2). Four of the study species (Whimbrel, Golden Plover, Dunlin and Meadow pipit) increased with distance from roads, whereas the other four showed no effect (Godwit, Snipe, Redwing and Redshank) (Figure 2). Among species affected by the roads, Meadow pipit showed the smallest increase (4% increase per 50 m interval), and Whimbrel the largest (24% increase per 50 m interval) (Table E2). Additionally, Dunlin density was negatively affected by the traffic (Table E2).

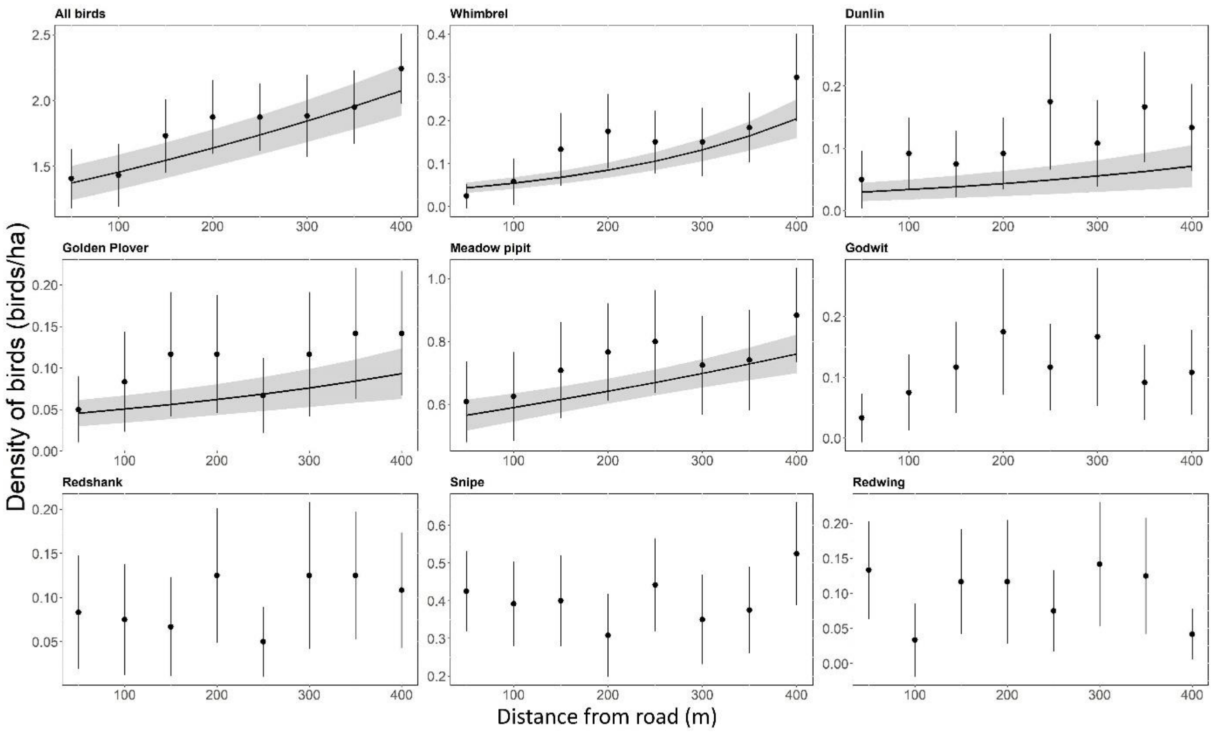

Figure 2: Mean bird density per ha (±SE) at 50 m intervals with increasing distance from roads for the eight most abundant species combined and individually. Lines represent model prediction (±SE) and are shown for species with significant changes in the GLMMs (Table 2).

Segmented linear regression indicated a breaking point in total bird density between 150-200 m away from the road, after which bird numbers plateaued. Mean density of birds within 200 m was 161 (±6) birds/km^2 compared to 200 (±7) birds/km^2 further away.

From the 100,000 random points generated in the Icelandic lowlands, exactly 20,151, or c.a. 20%, were within 200 m distance from roads.

Discussion

The amount of roads is ever increasing and expanding into areas previously unaffected by anthropogenic structures. The majority of roads in the Icelandic lowlands have relatively low traffic volume (<15,000 vehicles/day) compared to more densely populated countries (Vegagerðin, 2022). These moderate to low traffic roads have nonetheless a negative effect on density of birds in the surrounding habitat, and this effect was strongest in the first 200 m adjacent to roads. Bird density was on average ~20% lower in the first 200 m, compared to further away. At the species level, three waders (Dunlin, Whimbrel and Golden Plover), and one passerine (Meadow pipit), showed a negative effect of proximity to roads, and for Dunlin this effect was further induced by traffic volume. This reduced density, in addition to any bird loss in the area of the road, suggests that the cumulative effects of placing roads in open habitats will be significant. The effect detected here, along with similar studies on the effects of novel structures on breeding birds, reveals that low impact infrastructure such as single trees, houses and roads, can in fact have a considerable negative effect on ground-nesting birds in the surrounding landscape (Fernández-Bellon *et al.*, 2018; Pálsdóttir *et al.*, In press; Thompson *et al.*, 2015; van der Vliet *et al.*, 2010). Considering that densities of ground-nesting birds is ~20% lower in ~20% of the area of the Icelandic lowlands, we can assume that abundance of ground-nesting birds has decreased ~ 4% (0.2*0.2) due to current road placement. However, this percentage will depend on various factors such as previous densities in the habitat where roads were placed, along with size and structure of the road. To better explore how densities change with road placement, a before-and-after study would be ideal, where bird abundance is measured before the road is placed, and consistently for some years after the road is placed, but the latter part is often lacking.

A possible driver behind this lowered density of ground-nesting birds surrounding roads may be increased mortality. The main road in Iceland, which surrounds the island is 1,322 km long and the velocity is limited to 90 km/hour. This limit is often surpassed by drivers and vehicle speeds of ~100 km/hour have been shown to affect the behaviour of birds in the surrounding landscape (Legagneux & Ducatez, 2013). During the course of this study, bird carcasses were often encountered on the roads. Another driver could be reduced visibility surrounding the nests for breeding birds, but the Icelandic lowlands generally have large open habitats with low growing vegetation but roads are generally slightly elevated, and could be view obstructing to ground-nesting birds. Additionally, roads may alter the surrounding habitat, e.g. by drainage and protection from grazing which can encourage taller vegetation closer to roads.

Whimbrel and Golden Plover usually nest in open areas and the nest has little if any concealment (Laidlaw *et al.*, 2020). These species may therefore rely on visibility around the nest, which could explain their lower densities closer to roads as these structures are known to impair visibility. Redshank, Godwit and Snipe all conceal their nests, hence impaired visibility due to roads may not be relevant. Dunlins which have both open and concealed nests, appear to be particularly sensitive to roads, showing lower densities close to these structures and also being the only species negatively affected by traffic volume. This may be driven by negative impacts of roads and traffic on the display behaviour of Dunlin, but the underlying mechanism remains unknown. For the passerines, Meadow pipit might be found in lower densities closer to roads as they typically nest in open habitats (e.g. meadows), while Redwing may find suitable nesting places in trees and bushes which often occur at higher densities closer to roads.

Iceland has overall one of the lowest density of transportation infrastructure in Europe (Torres *et al.*, 2016), and low traffic volume with roads outside of the capital region rarely surpassing the single-track format. However, the majority of roads and other infrastructure is currently situated in the Icelandic lowlands, which are also considered the most important area for breeding waders, with the majority (~85%) of the estimated ~1.5 million pairs of waders that breed in Iceland, breeding there (Gunnarsson, 2020; Skarphéðinsson *et al.*, 2016). Currently 1/5 of the lowlands are within the disturbance distance from roads identified here (200 m) where bird densities are lower. As roads generally have the distinct purpose of connecting certain locations to one another, they cannot be strategically placed only in areas with low biodiversity. But given the large overlap shown here between infrastructure placement (i.e. roads) and areas which are of high conservational value, some consideration of these effects is necessary. Therefore, this study emphasizes the need for local small scale regulations of infrastructure where small patches of high biodiversity importance are protected, in addition to large scale regulations, where the cumulative effects and connectivity between multiple areas are taken in to account.

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Appendix E

*Table E1: Table showing AIC values of models constructed for all study species combined and separately for each species. The model that had the lowest AIC value was considered to have best fit, but only if it ΔAIC ≥ 2 from a simpler model**

Model	All birds	Whimbrel	Dunlin	Golden plover	Meadow pipit	Godwit	Redshank	Snipe	Redwing
Model A	3148.94	802.79	625.52*	652.17	2099.46	674.44*	592.38	1529.90	583.27
Model B	3147.97	802.21	**625.70**	650.29*	2098.05	677.67	591.50	1529.94	581.90
Model C	**3146.07**	**800.33**	631.99	**650.66**	**2096.11**	**676.07**	590.25*	1527.96	580.87
Model D	3175.32	831.38	638.41	654.04	2100.67	677.25	**590.33**	**1526.60**	**579.03**

*Table E2: Estimates from GlmmTMB models on the effects (±SE) of distance from roads (interval) and traffic on numbers of birds of eight species separately and all combined. Significant effects of factor on density of each species or bird group is indicated with an asterisk (p<0.05 *; p<0.01 **; p<0.001 ***)*

	All birds	**Whimbrel**	**Dunlin**	**Golden plover**	**Meadow pipit**	**Godwit**	**Redshank**	**Snipe**	**Redwing**
Model	C	C	B	C	C	C	D	D	D
Intercept	0.26 (±0.10)	-3.43 (±0.30)	-3.16 (±0.49)	-3.17 (±0.37)	-0.61 (±0.10)	-3.16 (±0.43)	-3.08 (±0.51)	-1.14 (±0.15)	-3.52 (±0.32)
Interval	0.06 (±0.01) ***	0.22 (±0.04)***	0.12 (±0.04)**	0.10 (±0.04)*	0.04 (±0.02)*	0.08 (±0.04)			
Traffic			-0.24 (±0.09)**						