Introduction of summer houses into semi-natural habitats: impacts on ground-nesting birds

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Abstract

Degradation of natural and semi-natural habitats is often initiated and facilitated by expansions in anthropogenic infrastructures. Identifying and reducing the impact of anthropogenic structures on the wildlife that these habitats support is vital for biodiversity conservation. In Iceland, the number of summer houses has increased over the past two decades, from ~10,000 to 15,000, and > 7,000 additional plots for summer house construction have been approved. Most of this housing infrastructure development is in the Icelandic lowlands, which support internationally important populations of several ground-nesting bird species. To explore the effects of summer house infrastructure on the distribution of ground-nesting birds, we conducted surveys at 292 points within 71 sites with varying density of houses and associated infrastructure (tracks, decking, etc). Significant reductions in abundance with increasing housing density occurred in five (Golden Plover (*Pluvialis apricaria*), Black-tailed Godwit (*Limosa limosa*), Redshank (*Tringa totanus*), Whimbrel (*Numenius phaeopus*) and Meadow pipit (*Anthus pratensis*)) of the seven study species, while one species (Snipe (*Gallinago gallinago*)) showed no change and one (Redwing (*Turdus iliacus*)) increased. The differences in abundance between plots with no houses and plots with high house densities (> 0.5 houses/ha) ranged from 34-95%, despite the housing infrastructure covering only ~6% of the area of these plots. These findings suggest that even relatively low densities of anthropogenic structures in natural or semi-natural areas can have substantial impacts on wildlife in the surrounding areas and highlight the urgent need for effective planning regulations to limit the expansion of anthropogenic structures into currently undisturbed habitats, particularly in areas of high biodiversity value.

Keywords: Anthropogenic change, conservation, edge effects, human infrastructure, wader, shorebird, developement

Introduction

The global human population has grown from 2.5 billion in the 1950s to an estimated ~8 billion at present (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 and associated levels of resource exploitation and consumption has been accompanied by introductions and subsequent expansions of anthropogenic infrastructures into natural and semi-natural areas, and in rural areas becoming increasingly urbanised. The transformation of natural areas into urban landscapes can have drastic effects on the abundance and species composition of animals within these landscapes (Koellner & Scholz, 2008; McKinney, 2008; Torres et al., 2016). While urbanised environments can provide the resources needed for some species to persist (typically generalist species), other previously abundant species often decline and may even disappear (Caula et al., 2010; Croci et al., 2008). In general, overall species richness and biodiversity tend to be depressed in areas with very high levels of urbanisation (Koellner & Scholz, 2008; McKinney, 2008), but most urbanisation studies have focused on areas where infrastructure is well established and extensive, and the habitat is strikingly different from natural areas. Much less is known about the initial impacts of relatively low-density infrastructure development in semi-natural and natural areas of high biodiversity value (Chace & Walsh, 2006; Miller et al., 2001).

The effects of urbanisation on birds have been studied extensively, often through comparisons of communities in areas with varying levels of urbanisation (Marzluff et al., 2001). These studies have revealed negative effects of anthropogenic structures on wildlife, through processes such as habitat loss, collision, cat predation, electrocutions and by introducing barriers in the landscape (Lepczyk et al., 2004; Loss et al., 2015; Morelli et al., 2014). However, there can also be benefits for some species through processes such as protection from natural predators, higher and more stable food supplies and increased nesting opportunities (Chace & Walsh, 2006; Gering & Blair, 1999; Jokimäki et al., 2016; Mainwaring, 2015; Morelli et al., 2014). Bird 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 resources provided by humans, along with cavity-nesting species which may find increased nesting opportunities (Chace & Walsh, 2006; Croci et al., 2008; Jokimäki et al., 2016; McKinney, 2002). On the contrary, ground-nesting birds are rare in urban areas, possibly due to a lack of suitable vegetation cover and/or increased numbers of mammalian nest predators (Jokimäki et al., 2016; McKinney, 2002). How species respond to and are affected by anthropogenic structures can thus be a combination of factors related to the previous habitat conditions, how much remains of those habitats, and the life history traits of the species (Chace & Walsh, 2006; Croci et al., 2008; Ludlow et al., 2015; Morelli et al., 2014).

The initial stages of urbanisation, during which low densities of housing infrastructure occur within areas that may have large amounts of natural habitats still present (Marzluff et al., 2001), are often characterised by the introduction of one or a few houses followed by rapid increases in housing density, facilitated by the availability of associated infrastructure (e.g. access roads, facilities). Thus, local intensification of urbanisation often precedes extensification. However, in the case of summer houses which are not permanently occupied, but used for recreational visits, practical limitations arising from local environmental conditions, regulatory constraints, landowner will or occupant desire for space and access to nature, may influence both the density and extent of these developments. Little is known about how bird communities respond to low density housing and housing clusters in natural habitats, the speed with which effects become apparent and how they change as housing density increases. The importance of identifying and understanding the impact, if any, of low-density housing infrastructure on wildlife in surrounding natural habitats cannot be underestimated, as these are often the last remaining areas of significant biodiversity value. Evidence is accumulating that a wide array of single anthropogenic structures, such as houses (van der Vliet et al., 2010), roads (Kociolek et al., 2011), power lines (D'Amico et al., 2018; Pálsdóttir, Gill, Pálsson, et al., 2022) and wind farms (Fernández-Bellon et al., 2018), can have negative effects on densities of ground-nesting birds in the surrounding habitat, and these effects may be detected over much wider areas than those structures occupy (Benítez-López et al., 2010; Dinkins et al., 2014; Fernández-Bellon et al., 2018; Liebezeit et al., 2009; Morán-López et al., 2017; Thompson et al., 2015; van der Vliet et al., 2010). The introduction of such structures into previously natural or semi-natural habitats will inevitably decrease the amount of remaining habitat, and may induce additional changes to the surrounding area, such as in vegetation and predator distribution and assemblage which can affect species distribution and/or demography (Chace & Walsh, 2006; Ludlow et al., 2015; Yoo & Koper, 2017).

Iceland is sparsely populated, and still retains large areas of open semi-natural landscapes which are important breeding areas for very large numbers of migratory, ground-nesting birds (Jóhannesdóttir et al., 2014; The World Bank, 2020). Summer house construction is increasing in Iceland, from just over 10,000 in 2005 to approximately 15,000 in 2022 (Registers Iceland, 2023), and over 7,000 summer house plots, where houses are planned but have yet to be constructed, have been registered in Iceland (Registers Iceland, 2022). 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 holds large proportions of the global populations of several 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 anthropogenic structures in natural habitats (Pálsdóttir, Gill, Pálsson, et al., 2022; 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 structure, predation pressure, microclimate) and the presence of humans and associated non-native predators such as domestic cats. Breeding waders typically have very high breeding site-fidelity (Méndez et al., 2018) and any impact of anthropogenic infrastructure on local demography can potentially also influence local population abundances. In addition, the visual obstruction caused by summer houses and the increased traffic of people and/or vehicles that often occur with the establishment of anthropogenic structures (Ditchkoff et al., 2006; Hovick et al., 2014) could make these areas less attractive to recruiting individuals and increase the risks and costs of breeding in these areas.

Here we use surveys of bird abundance along a gradient of summer house density in semi-natural habitats to assess (1) the relationship between housing density and abundance of ground-nesting bird species and (2) whether any changes in breeding bird abundance exceed those expected from the loss of the area occupied by the infrastructure.

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 at least 1 km away from urban settlements such as villages and towns, and ranged in housing density from 0-35 houses/point. At each site, between two and nine point count surveys were conducted, resulting in a total of 292 surveys with varying numbers of houses within each survey area. The number of point count surveys in each site depended on the size of the summer house area, with more surveys (up to nine) being conducted in larger areas (Registers Iceland, 2023). All point count surveys within each site were conducted on the same day, and at a time where most houses were unoccupied. At each location, the observer initiated the count immediately upon arriving at the point, standing still and identifying all birds within a 200 m radius (12.5 ha) for 5 minutes. A Bushnell laser rangefinder 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 anthropogenic structures (besides the summer houses and associated infrastructure) or modified habitats (major roads, forest plantations or agriculture fields) within the survey area.

Bird counts

Bird counts were conducted between 6:30 am and 7 pm, as previous studies in Iceland have shown the target species to be active throughout this time period (Davíðsdóttir, 2010), 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 to one of four groups: no houses (control, n=103); single house (n=43); low house density (2-5 houses, n=77) and high house density (6-35 houses, n=69) within the 12.5 ha survey area. To eliminate any bias due to time of day, points from each group were counted at all times of the day (Figure S1). For each survey point, habitat type was classified according to the Icelandic farmland database *Nytjaland* (Gísladóttir et al., 2014) as: semi-wetland, grassland, rich heathland and poor heathland, and the presence or absence of trees was recorded, as these factors have been shown to influence ground-nesting bird densities in Iceland (Jóhannesdóttir et al., 2014; Pálsdóttir, Gill, Alves, et al., 2022).

Quantifying extent of infrastructure

Areas with summer cottages typically have associated anthropogenic infrastructure, such as tracks, decks and parking spaces, all of which directly remove potential breeding 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, 2022), the total area of anthropogenic infrastructure (houses, tracks, decks and parking spaces) within the 12.5 ha survey area was calculated (Figure 2). Anthropogenic features in both points with houses (houses, tracks etc) and control points (tracks) were outlined using www.map.is and the area they covered was calculated (Figure 2).

Statistical analysis

To explore how bird abundance varies with house density, GLMMs with a Poisson distribution and a log-link function were constructed with count (for each species and all species combined) as the response variable, house density (in four categories) and habitat type (in four categories) as fixed effects (Table S1), and site was included as a random effect to account for non-independence of point counts within the same site. To compare bird abundance between points with houses (control points excluded), a post-hoc analysis was performed using package emmeans (Lenth, 2019). An interaction between house density and habitat type was explored but lacked the power to allow convergence as not all species were recorded in all habitats/house combinations (Table S2) and was therefore not retained. Rich heathland was set as a reference group as it was the habitat in which most surveys points occurred (Table S1).

To explore whether the abundance of birds within the available area exceeds that expected from direct habitat lost to infrastructure, the same GLMM models were run on a subset of data (251 of the 292 points) for which it was possible to estimate area occupied by housing infrastructure, and an offset of available area (i.e., excluding the area occupied by housing infrastructure) was included (Figure 2). All statistical analyses were performed using R software (R Core Team, 2017; RStudio Team, 2016). The package lme4 was used for models and ggplot2 for graphing (Bates et al., 2014; Wickham, 2016). Package performance was used to check that all model assumptions were met (Lüdecke et al., 2021).

To explore whether detectability of birds changed with increasing numbers of houses, for example if houses or surrounding trees obstructed the observers view and reduced the detectability of more distant individuals, an additional GLMM was constructed with bird numbers (in points at which the relevant species was recorded) as the response variable, number of houses (in the four categories) and distance from observer (in three distance bands, 0-50 m, 51-100 m and 101-200 m) as fixed factors with their interaction. As in the previous models, site was included as a random factor and the area of each distance band set was included as an offset.

Results

Effects of housing infrastructure on bird abundance

In total 2,819 birds were counted on 292 survey points, of which 89% belonged to seven species: two passerines; Meadow pipit and Redwing and five wader species; Golden Plover, Snipe, Redshank, Whimbrel and Black-tailed Godwit (hereafter Godwit), and these species were retained for analyses (Table S3). 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 abundances were highest in poor heathland and rich heathland, respectively (Table S1). There was no evidence that birds further away from the observer were less likely to be seen in points with higher house density (Table S4), indicating that the presence of houses and trees did not alter the detectability of birds in the surrounding landscape.

Total bird abundance did not differ between survey points with varying house density. However, at the species level, Redwing abundance increased with increasing numbers of houses, Snipe showed no change in abundance and the remaining five species had reduced densities in survey points with houses (Figure 3, Table 1A). Of these five species, three (Whimbrel, Godwit and Golden Plover) had significantly lower densities in all points with houses compared to control points, one (Redshank) had lower densities in low and high house densities compared to control points and one (Meadow pipit) had lower densities in points with high house density compared to control points (Figure 3, Table 1A). The abundance of Whimbrel and Golden plover also decreased significantly from single to high house density, and Godwit abundance decreased from single and low density to high house density (Figure 3, Table 1A).

Accounting for infrastructure area

For 251 survey points, it was possible to estimate the area of housing infrastructure from aerial photographs and calculate available area (the area of the survey point excluding all houses and associated infrastructure). In models with available area included as an offset, abundance of Golden Plover, Whimbrel and Redshank was lower in points with houses compared to control points (Table 1B). Points with low and high house density also had significantly lower abundance of Godwits than control points, and points with high house density had significantly lower abundance of Meadow Pipits than control points. Only Redwing had significantly higher abundance in points with houses (Table 1B, Figure 3). In addition, abundances of Whimbrel and Godwit decreased between single and high house density (Table 1B), while redwing abundance was highest in points with high house density compared to all other categories (Table 1B). The changes in abundance of these ground-nesting species (all study species excluding redwing) are considerable, with declines of ~34-95% in areas with high house density (6-35 houses/point) compared to points with no houses, while the housing infrastructure covered only ~6% of these areas (Figure 4).

Discussion

In lowland Iceland, summer houses are widespread, and their numbers are increasing rapidly. Here, we have identified significant negative impacts of even single summer houses on abundances of three wader species (Golden plover, Godwit and Whimbrel) and of small housing clusters (fewer than six houses) on Redshank abundance. Additionally for the two passerines, Meadow pipit was found in lower abundance in points with high house density while Redwing abundance increased with house density. Construction of houses and tracks in natural habitats inevitably results in the direct loss of some breeding habitat but the scale of declines in bird abundance greatly exceed the area covered by housing infrastructure, suggesting that the impacts go well beyond simple reductions in area of available breeding habitat (Figure 4). The presence of summer houses and associated infrastructure thus has substantial impacts on the abundance of ground-nesting birds in the surrounding landscape, even though that landscape remains largely unchanged.

The causes of these large changes in bird abundance in areas with summer houses are currently unknown. The presence of summer house infrastructure could potentially increase local predator activity, for example by providing shelter or perching opportunities (Liebezeit et al., 2009; McGuire et al., 2023; Morelli et al., 2014), which could make these areas less attractive as breeding locations and/or could reduce local productivity and recruitment. Most summer cottages in Iceland are used frequently during the breeding season and the presence of humans, vehicles and pets (in particular domestic cats, which are known predators of ground-nesting birds (Loss et al., 2015)) could influence numbers of nesting attempts, likelihood of nest loss or desertion and/or parental care of chicks (Chace & Walsh, 2006). Although the habitat surrounding most summer cottages in Iceland generally remains unchanged for some time after the introduction of cottages, most houses have trees planted around them, often as wind shelter. As ~77% of all survey points with houses had some trees present, while none of the points with no houses had trees (Table S5), it is possible that tree presence is also contributing to the reduced densities, as has been shown in previous studies (Holmes et al., 2020; Pálsdóttir, Gill, Alves, et al., 2022; Wilson et al., 2014). The Arctic fox population in Iceland is increasing after a historical low in the late 1970s (Unnsteinsdóttir, 2021). Arctic foxes are a major predator of the eggs of ground-nesting birds in Iceland but it is unclear whether the expansion of summer houses has influenced their population expansion or the extent to which they use areas with summer houses. More detailed studies of nest success and predator distribution are needed to understand the contribution of nest predation to the reduction in bird densities around summer houses. If declines in productivity and recruitment are contributing to the reduced abundances in areas with houses, the true scale of the impact may take some time to become apparent, as approximately one third of the houses in our study areas were constructed within the last 20 years (Registers Iceland, 2023). Such ongoing impacts may be particularly apparent among breeding waders, which can live for >10-20 years (Méndez et al., 2018) and unsustainable breeding populations can therefore persist for considerably periods of time. In addition, numbers of summer houses are still increasing in most areas (Registers Iceland, 2023), which is likely to compound these impacts further.

Only Redwing occurred at higher densities in areas with summer houses, with abundances in areas with high house density being approximately double those in areas with no houses. Redwings nest both in forests and on the ground in open habitats in Iceland (Skarphéðinsson et al., 2016), and thus the trees that accompany many summer houses may facilitate increases in Redwing abundance. Two other tree-nesting passerine species (Starling, *Sturnus vulgaris*, and Redpoll, *Acanthis flammea*) occurred rarely on our surveys but only ever in areas with houses (Table S3), suggesting an important role of trees around summer houses. Thus, while a few species may benefit from summer house development in these open landscapes, these are likely to be generalist species (Chace & Walsh, 2006; Croci et al., 2008; Devictor et al., 2007), which are already common and abundant in urban areas in Iceland (Einarsson, 2021; Skarphéðinsson et al., 2016).

Across much of the world, populations of waders have been in severe decline in recent years, primarily as a result of habitat loss and degradation (International Wader Study Group, 2003; Pearce-Higgins et al., 2017; Rosenberg et al., 2019). Iceland is one of the most important remaining areas for breeding waders in Europe, with an estimated 1.5 million breeding pairs of which ~85% occur in the lowlands. The lowland landscapes of Iceland are largely comprised of a mosaic of open, semi-natural habitats (Gunnarsson, 2020; Gunnarsson et al., 2006; Skarphéðinsson et al., 2016) and also contain the majority of summer houses. An additional ~7,000 summer houses are currently planned in Iceland (Registers Iceland, 2022) and were these houses to be constructed in areas with no other houses, substantial reductions in breeding densities could occur in an additional ~900 km^2 of Iceland, potentially resulting in the loss of tens of thousands of breeding waders (given typical current breeding densities; Jóhannesdóttir et al. 2014). For Iceland to meet its international commitments to protect these species (Schmalensee et al., 2013), it is vital that future developments should be both limited and restricted to areas with existing anthropogenic infrastructure, rather than allowing expansion into currently undeveloped areas. Here, overall bird abundance was highest in semi-wetland and lowest in poor heathland (Table S1) which corroborates results from previous studies in Iceland (Jóhannesdóttir et al., 2014; Pálsdóttir, Gill, Alves, et al., 2022). Therefore protecting these habitats is key but currently only around ~7,800 km^2 (~7-8%) of Iceland is considered as wet- or semi-wetland habitat (Ottósson et al., 2016) due to extensive draining in the 20^{th} century, much of which took place in the Southern lowlands (Þóra Ellen Þórhallsdóttir, 1998), where summer house construction is concentrated (Registers Iceland, 2023). However, there are also priority species for which protection of other habitats from development will be important, such as Golden plovers for which Iceland holds around 50% of the global population (BirdLife International, 2023; Skarphéðinsson et al., 2016) and was found in the highest abundance in poor heathland (Table S1). Understanding the role of nest predators in different habitats and how these relationships are influenced by housing infrastructure is likely to be very important in identifying priorities for protection and management of the remaining semi-natural areas in lowland Iceland.

Despite Iceland's small human population, the land area exposed to anthropogenic surfaces and infrastructure is increasing at a rapid pace, with ongoing, widespread construction of houses, wind farms, power-lines, roads and plantations forests (EEA, 2018; Wald, 2012). The impacts of houses on breeding bird densities documented here are similar to the demonstrated impacts of plantation forests and power-lines (Pálsdóttir, Gill, Alves, et al., 2022; Pálsdóttir, Gill, Pálsson, et al., 2022). These localized changes in abundance are therefore occurring over ever-increasing areas, and the expansion of anthropogenic structures (houses, wind farms, roads etc.) and habitats (agriculture and plantation forestry) is contributing to declines in breeding wader populations across Europe (Amar et al., 2011; Pearce-Higgins et al., 2017; Sutherland et al., 2012; van der Vliet et al., 2010; Żmihorski et al., 2018). Given the difficulties in restoring breeding bird populations after such widespread impacts (Bentzen et al., 2018; Melman et al., 2008), it is imperative that remaining areas that still support large breeding populations are protected and that effective planning regulations that recognise the need to preserve areas of high biodiversity value are enforced.

Figures and tables

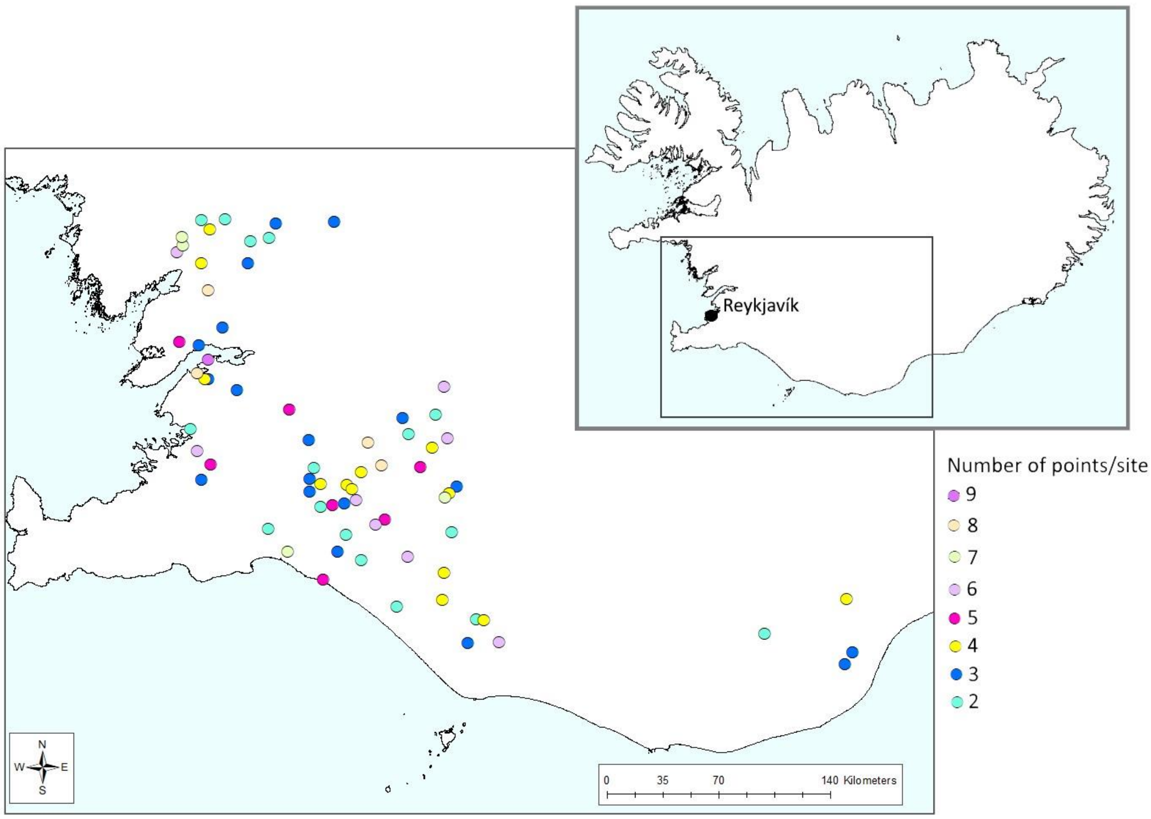

Figure 1: Locations of 71 sites at which point count surveys were conducted in lowland Iceland in 2018. Inset shows the location of the survey area.

Figure 2: Example 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, 2022).

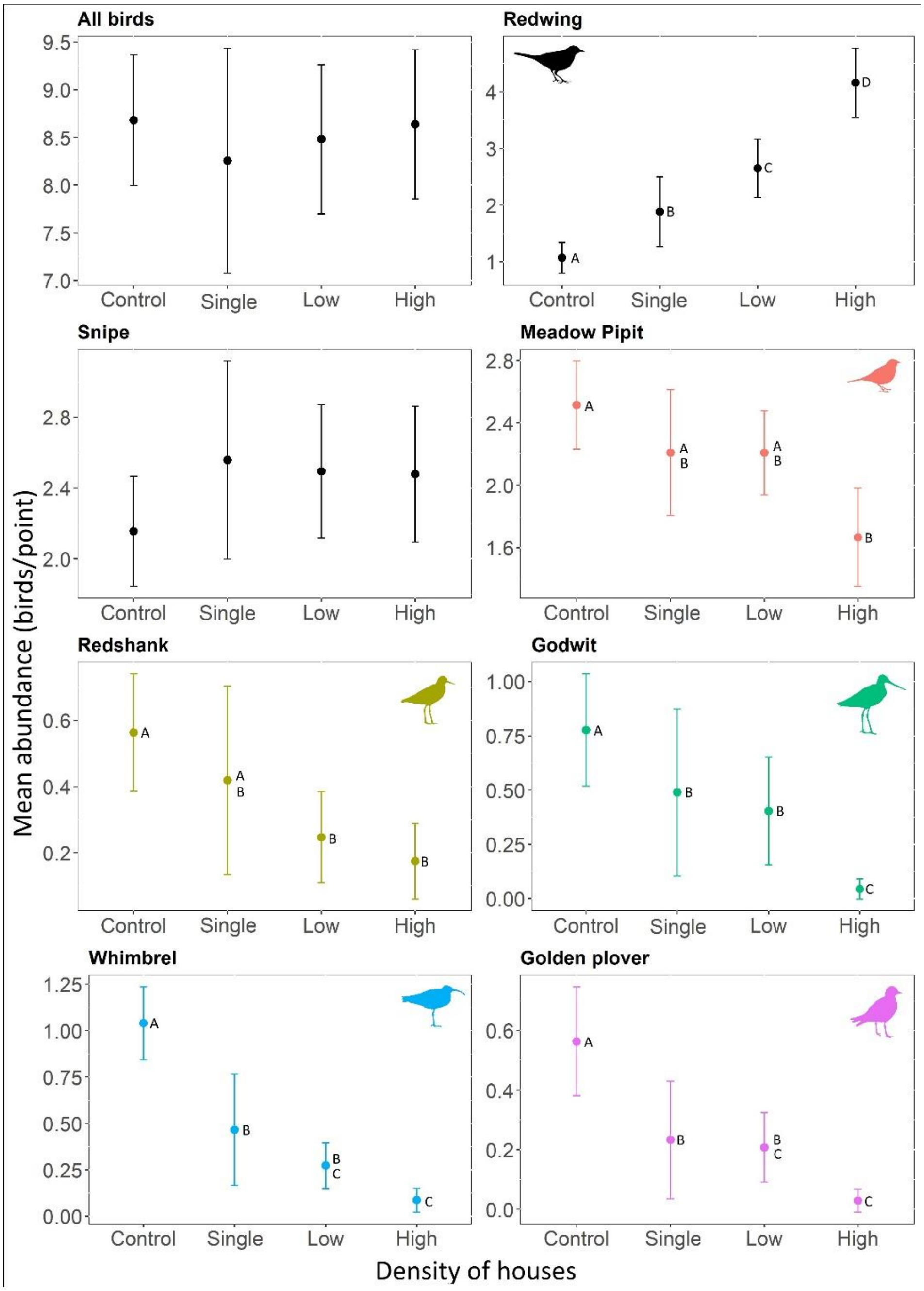

Figure 3: Variation in the abundance (±SE) of seven bird species (combined and separately) across survey points in lowland Iceland with differing densities of summer houses (control points = no houses, Single = one house, Low = 2-5 houses and High = 6-35 houses). Different letters indicate house density categories which differed significantly in bird density (Table 1A).

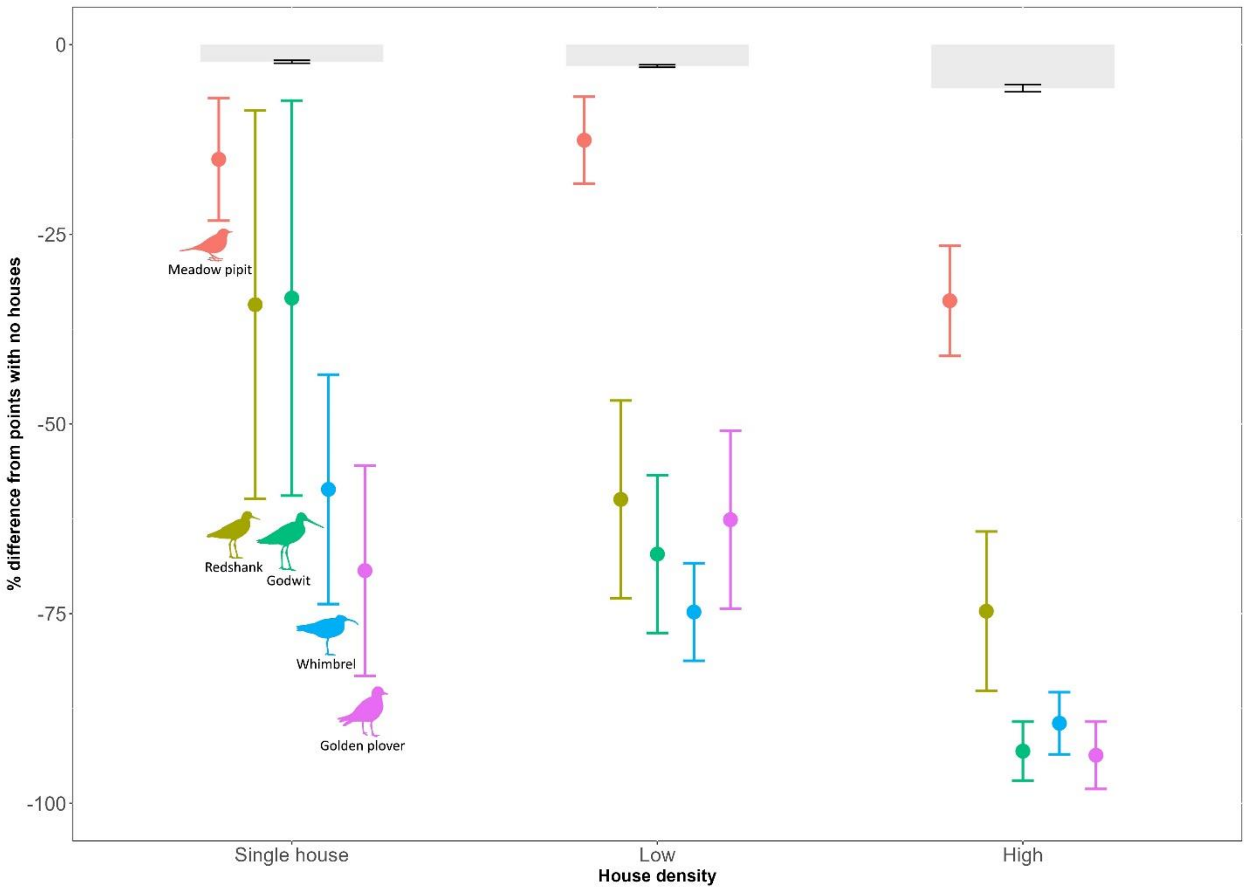

Figure 4: Mean (± SE) percentage difference in bird abundance from areas with no houses for five bird species (colored per species) and the reduction of available breeding habitat (grey bars ; area with housing infrastructure) in areas with differing house densities (Single = 1, Low = 2-5, High = 6-35).

Table 1: Estimates (±SE) from GLMMs of variation in abundance of birds in sites with varying numbers of summer houses and in differing habitat types. Site was included as a random factor in all models. Significance as compared to the reference levels is indicated by asterisks (p<0.05 *; p<0.01 **; p<0.001 ***).

A: Full model: Bird abundance (birds/point) ~ no. of houses + habitat +(1|site)										
Variable		**All birds**	**Golden Plover**	**Whimbrel**	**Godwit**	**Redshank**	**Meadow pipit**	**Redwing**	**Snipe**
Houses	(Intercept)[a]	2.21 (±0.05)	-0.93 (±0.26)	-0.03 (± 0.17)	-0.90 (±0.29)	-0.82 (± 0.24)	0.94 (±0.08)	-0.11 (±0.13)	0.71 (±0.10)
	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 (±0.24)***	-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)***	1.20 (±0.12)***	0.14 (±0.11)
Habitat	Grassland	-0.12 (±0.7)	-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)
	Poor heathland	-0.28 (±0.08)**	0.12 (±0.34)	-0.51 (±0.28)	-2.11 (±0.64)**	-1.93 (±0.59)***	-0.21 (±0.12)	-0.23 (±0.15)	-0.05 (±0.14)
	Semi-wetland	0.12 (±0.09)	-0.42 (±0.52)	0.25 (±0.32)	0.56 (±0.31)	0.94 (± 0.34)**	0.07 (±0.16)	-0.52 (±0.22)*	0.27 (±0.16)
Site[b]		0.06 (±0.24)	0.79 (±0.89)	0.31 (±0.56)	1.65 (±1.28)	0.81 (±0.90)	0.06 (±0.25)	0.22 (±0.47)	0.15 (±0.39)
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 (±0.08)	-2.05 (±0.79)*	-1.69 (±0.48)**	-2.14 (±0.64)**	-0.51 (±0.42)	-0.28 (±0.15)	0.66 (±0.14)***	0.02 (±0.14)
Low→high house density		0.04 (±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)
B: Full model: Bird abundance (birds/point) ~ no. of houses + habitat + offset(log(available area)) + (1|site)									
Houses	(Intercept)[a]	-2.59 (±0.05)	-5.81 (±0.29)	-4.85 (± 0.18)	-5.53 (±0.28)	-5.55 (± 0.26)	-3.84 (±0.09)	-4.63 (±0.13)	-4.14 (±0.11)
	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)***	-1.09 (±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[a]	Grassland	-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)
	Poor heathland	-0.26 (±0.08)**	0.36 (±0.37)	-0.52 (±0.30)	-1.95 (±0.64)**	-2.14 (±0.67)**	-0.16 (±0.13)	-0.21 (±0.16)	-0.09 (±0.15)
	Semi-wetland	0.07 (±0.09)	-0.40 (±0.58)	0.35 (±0.34)	0.37 (±0.35)	0.86 (± 0.38)*	0.02 (±0.17)	-0.89 (±0.27)***	0.35 (±0.16)*
Site[c]		0.05 (±0.22)	0.88 (±0.94)	0.33 (±0.57)	1.32 (±1.15)	0.85 (±0.92)	0.05 (±0.22)	0.20 (±0.45)	0.15 (±0.39)
Post hoc analysis									
Single house→low house density		0.01 (±0.08)	0.22 (±0.49)	-0.61 (±0.36)	-0.69 (±0.36)	-0.43 (±0.40)	0.06 (±0.14)	0.25 (±0.15)	-0.01 (±0.13)
Single house→high house density		0.08 (±0.08)	-1.56. (±0.82)	-1.42 (±0.50)*	-1.99 (±0.65)*	-0.51 (±0.51)	-0.23 (±0.16)	0.71 (±0.16)***	0.04 (±0.15)
Low→high house density		0.08 (±0.07)	-1.78 (±0.77)	-0.80 (±0.49)	-1.30 (±0.65)	-0.08 (±0.48)	-0.28 (±0.14)	0.46 (±0.13)**	0.04 (±0.13)

[a]Reference group: Points with no houses; reference habitat: Rich heathland
[b]Random effect: No. of obs: 292; groups: 71
[c]Random effect: No. of obs: 251; groups: 68

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