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Population regulation in a sub-Arctic wader: insights from variation in breeding density

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Dissertation submitted in partial fulfillment of a
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Abstract

Population numbers result from the combined effect of exogenous (weather, food, predation, anthropogenic impact) and endogenous (behaviour, density) factors on the population, which often act simultaneously resulting in spatial variation in population distribution and density. The effects of these factors can mask each other and operate across different spatiotemporal scales making the study of population regulation challenging. Studies on variation in demography and habitat quality across gradients in breeding density can give important insights into population regulation. The largest lowland basin in Iceland has a unique gradient of wader breeding density, an ideal setting for population regulation studies. Using the variation in Whimbrel, *Numenius phaeopus*, abundance recorded during a long-term monitoring programme and a three-year study in South Iceland, I aimed to better understand the possible mechanisms regulating this population. To do so, I investigated population trends and the relationships between demographic processes, habitat features, and behaviour of this species.

Adult abundance decreased from 2012-2021 possibly due to habitat degradation. Brood abundance did not show a trend (2013-2021) but showed high environmental variability. Adults used a variety of semi-natural habitats, and their annual abundance was not directly explained by the process of ecological succession, potential prey abundance, or potential predator pressure. Adult numbers influenced the frequency of the aerial display behaviour with Whimbrels displaying more often at low densities during pre-incubation, probably for mate attraction. Displaying at all densities occurred during the rest of the breeding season and may serve other functions such as resource defence. Broods avoided areas of anthropogenic origin, and some semi-natural habitats were more important than others during chick-rearing and migration preparation. Food availability is likely a driver of variation in habitat quality and more broods were produced at a higher abundance of potential prey. At a small spatial scale, more broods were produced at higher adult density, yet the probability of raising a brood was estimated to be similar across the adult density gradient. The increasing infrastructure development in South Iceland is threatening wader populations, and understanding how populations are regulated will facilitate management and conservation to minimise human-wildlife conflicts.

Útdráttur

Stofnstærðir dýra velta á samspili ytri þátta (fæðu, afráns, áhrifa manna) og innri þátta (atferlis, stofnþéttleika). Þessir þættir geta verkað á sama tíma og stjórnað dreifingu og þéttleika innan stofna. Áhrif tiltekinna þátta geta verið falin af öðrum þáttum og sýnt breytileika í tíma og rúmi svo veruleg áskorun er að rannsaka stofnstjórnun. Rannsóknir á breytileika í lýðfræði og gæðum búsvæða við mismunandi varpþéttleika geta gefið mikilvægar vísbendingar um stofnstjórnun. Á Suðurlandi má finna mikinn breytileika í þéttleika vaðfugla sem gefur góð tækifæri á að rannsaka stofnstjórnun. Breytileiki í þéttleika spóa (*Numenius phaeopus*) var kannaður með langtímarannsókn og þriggja ára rannsókn með það að markmiðið að varpa ljósi á þætti sem stjórna stofninum. Til að ná því markmiði kannaði ég stofnbreytingar og samband lýðfræðilegra þátta, eiginleika búsvæða og atferlis hjá spóa.

Spóa fækkaði á svæðinu á árunum 2012-2021, mögulega vegna hnignunar búsvæða. Fjöldi systkinahópa, sem taldir voru árlega (2013-2021), sýndi ekki marktækar breytingar en mikinn áramun. Fullorðnir fuglar notuðu fjölbreyttar gerðir af búsvæðum og fjöldi þeirra varð ekki útskýrður með beinum hætti út frá framvindustigi gróðurs, líklegu fæðuframboði innan varpsvæðis eða líklegum afránsþrýstingi innan varpsvæðis. Varpþéttleiki spóa hafði áhrif á tíðni óðalsflugs sem var algengara við lágan varpþéttleika í byrjun varptíma og þjónar líklega hlutverki við pörun. Óðalsflug var stundað á öllum svæðum út varptímann sem bendir til að það þjóni einnig tilgangi við að verja auðlindir. Spóaungar forðuðust búsvæði sem voru undir mestum áhrifum manna og sum búsvæði voru mikilvægari en önnur á ungatíma og fyrir undirbúning fyrir farflug. Fæðuframboð hefur líklega áhrif á gæði búsvæða en fleiri ungar komust á legg þar sem fæðuframboð var meira. Á svæðisbundinn mælikvarða var ungaframleiðsla meiri þar sem varpþéttleiki var hærri en líkur á að pör væru með unga virtust svipaðar við mismunandi varpþéttleika. Aukin landnýting á Suðurlandi skapar hættu fyrir vaðfuglastofna og bættur skilningur á því hvernig stofnum er stjórnað auðveldar vernd stofnanna og minnkar líkur á skörun hagsmuna fugla og manna.

To myself, for those who persevere, and for Science.

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This thesis is a collection of four chapters: three scientific papers and one manuscript .

Chapter I. Maite Cerezo-Araujo, José Augusto Alves, Verónica Méndez, Gunnar Thor Hallgrimsson, Tómas Grétar Gunnarsson. 2024. Annual and spatial variation in adult and brood abundance in a sub-Arctic wader. *In press, Bird Study.*

Chapter II. Maite Cerezo-Araujo, José Augusto Alves, Verónica Méndez, Gunnar Thor Hallgrimsson, Tómas Grétar Gunnarsson. 2024. Seasonal variation in Whimbrel abundance across sub-Arctic habitats of varying succession stage. *Under review, Polar Biology.*

Chapter III. Maite Cerezo-Araujo, Verónica Méndez, Camilo Carneiro, Gunnar Thor Hallgrimsson, José Augusto Alves, Tómas Grétar Gunnarsson. 2024. Do habitat quality and breeding success explain variation in breeding density of a sub-Arctic wader? *Manuscript.*

Chapter IV. Maite Cerezo-Araujo, José Augusto Alves, Gunnar Thor Hallgrimsson, Böðvar Thorisson, Tómas Grétar Gunnarsson, Verónica Méndez,. 2024. Serenade of a Whimbrel: investigating the function of display behaviour in a sub-Arctic wader. *Under review, Journal of Avian Biology.*

The author's contribution is stated following the CRediT definitions (Contribution Roles Taxonomy).

Maite Cerezo-Araujo: Chapters I-IV. Data curation (lead); formal analysis (lead); methodology (lead); writing – original draft preparation (lead); writing – review and editing (equal); conceptualization (equal).

José Augusto Alves: Chapters I-IV. Conceptualization (equal); methodology (supporting); project administration (supporting); supervision (equal); writing – original draft preparation (supporting); writing – review and editing (equal).

Verónica Méndez: Chapters I-IV. Conceptualization (equal); formal analysis (supporting); methodology (supporting); supervision (equal); writing – original draft preparation (supporting); writing – review and editing (equal); validation (lead).

Gunnar Þór Hallgrímsson: Chapters I-IV. Conceptualization (equal); supervision (equal); writing – original draft preparation (supporting); writing – review and editing (equal).

Tómas Grétar Gunnarsson: Chapters I-IV. Conceptualization (lead); formal analysis (supporting); funding acquisition (lead); investigation (lead); methodology (supporting); project administration (lead); supervision (equal); writing – original draft preparation (supporting); writing – review and editing (equal); resources (lead).

Camilo Carneiro: Data curation (supporting); writing – review and editing (equal).

Böðvar Þorisson: Data curation (supporting); writing – review and editing (equal).

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At the time of applying for this PhD, I wrote in the cover letter, 'I know this will be challenging and frustrating at some point (...).' It has indeed been so, but above all, it has been absolutely rewarding.

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1 General introduction

1.1 Population regulation

1.1.1 Populations in time and space

Population regulation occurs when a population persists over time, its size is bounded by upper and lower limits, and tends to increase at low abundance of individuals and decrease at high abundance (Murdoch, 1994; Turchin, 1995; Hixon et al., 2002). Population size cannot grow indefinitely, and its limits are imposed by a combination of both exogenous and endogenous factors which can affect demography. Exogenous factors include food supply, breeding sites, stochastic events, weather patterns, different types of human impacts, disease, and parasites. Endogenous factors are intrinsic to the population itself or population density, and are driven by different demographic rates: births, deaths, emigration, and immigration (Newton, 2003). The synergy between these exogenous and endogenous factors determines the population growth rate (Sibly et al., 2005) and ultimately the lower and upper limits by which the population persists over time. A population's growth rate slows down under resource limitation (Sibly & Hone, 2002) through increased competition, predation, or disease, and stops when the carrying capacity of the environment is reached. When this occurs, the number of new individuals in the population, determined by births and immigration, equals the number of individuals abandoning the population through deaths and emigration (Sutherland, 1996). Multiple mechanisms of population regulation exist and most times, not only one but a combination of them are responsible for fluctuations in the size of populations (Rodenhouse et al., 2003; Nevoux et al., 2011; Santini et al., 2023).

For a species to occur at a given location, a series of environmental and biological properties must be met (Elton, 1927; Hutchinson, 1957). The number of individuals found in a site is determined by the habitat quality, population density, and biological interactions or the species behaviour (Sutherland 1996). The resources and environmental conditions within a habitat i.e. habitat quality, and how they vary across space and over time will determine individual fitness and population survival (Fretwell & Lucas, 1969). Therefore, sites with better resources will generally host higher species density which can happen through several mechanisms. For example, high conspecific density can be maintained through a combination of higher individual fitness and higher return rates or philopatry (Newton, 1989); while for mobile species that can make a choice, site selection may result from the actual knowledge of resource distribution (Fretwell & Lucas, 1969; Piper, 2011), conspecific attraction (Stamps, 1988; Gill, 2019), or other cues individuals might use to select a site.

1.1.2 Populations across habitats and the effect of conspecific density

Habitat quality can be defined as the "ability of the environment to provide conditions appropriate for individual and population persistence. (…) a continuous variable, ranging from low to medium to high, based on resources available for survival, reproduction, and population persistence, respectively" (Hall et al., 1997). These conditions or resources can be both physical features, such as spatial attributes and water chemistry, or biotic ones such as vegetation structure and food availability (Mott et al., 2023). At the same time, access to resources can be limited by disturbances, other ecological constraints such as predation pressure and the species behaviour (Laundré et al., 2010; Bock and Jones 2012; Mott et al., 2023), or temporal abiotic conditions (Olofsson et al., 2013). This spatiotemporal variation in resources occurs naturally but can be created, maintained and amplified by anthropogenic effects (Bock & Jones, 2004). As a consequence, the carrying capacity of habitats can change through changes in quality, and the direction and strength of these changes will partly depend on historical processes that occurred within these habitats (Olofsson et al., 2013; Chang & Turner, 2019). Geographic and temporal changes in suitable resources and habitat quality can have cascading effects on demographic rates (Higgins et al., 2010; McKinnon et al., 2012), species distribution and abundance (Tellería & Pérez-Tris, 2003).

It is often assumed that better quality habitats host a higher density of individuals, Fig. 1. A, as is often the basis for protected areas and natural reserves (Gray et al., 2016; Soriano-Redondo et al., 2023). However, this premise might be misleading as it does not consider the effect of different demographic rates on the population itself (Van Horne 1983; Johnson 2007; Bock and Jones 2012). In fact, different processes can cause a mismatch between population density and habitat quality. Density dependence (DD) affects the population growth rate as the population's density increases following changes in habitat quality or resource abundance, Fig 1. B-D (Nicholson, 1935). The intensity of DD will depend on the number of individuals in the population (Murray, 1982). In some instances, a lack of relationship between a demographic rate and population density can indicate an underlying process affecting only individuals at certain density of conspecifics, or differences based on habitat quality, Fig. 1. B. For example, in an experiment with Prothonotary Warbler, *Protonotaria citrea*, where breeding sites and predation were manipulated, fledgling production was similar across density due to the high invertebrate abundance that partly reduced the negative effect of high conspecific density (Hoover et al., 2020). In a colony of Common Guillemot, *Uria aalge*, on the Isle of May, the probability of fledging young was higher on sites of better quality but was independent of conspecific density (Kokko et al., 2004).

Negative DD results from a decrease in the population growth rate with increasing density of individuals (Sutherland, 1996; Turchin, 1999) and can occur through several processes such as depletion of resources or interference competition, Fig. 1. C and D. For example, in Mono lake in California, the nesting success of Snowy Plovers, *Charadrius alexandrinus*, was reduced at high conspecific density due to increased predation (Page et al., 1983), while in Lake Mývatn and River Laxá in North Iceland, the number of breeding pairs of Barrow's Goldeneye, *Bucephala islandica*, decreased prior to egg laying due to temporal oversaturation of high quality habitats where territory defence was difficult and feeding efficiency was reduced (Einarsson, 1990). DD can also operate at multiple age stages within a population as for Mauritius Kestrel, *Falco punctatus*, in the island of Mauritius. For this population, breeding success decreased as increased numbers forced weak individuals to use lower quality habitats, and juvenile survival was reduced at high population size through interference competition for resources after fledging (Nevoux et al., 2011).

On the other hand, a positive DD can result from an increase in population growth rate with population density that occurs at low conspecific density, Fig. 1. E (Allee, 1931; Kramer et al., 2009; Stephens et al., 1999; Turchin, 1999). This was reported to be the reason behind coloniality in a population of Lesser Kestrels, *Falco naumanni*, breeding in Spain where higher dispersal probability from very small (one to three breeding pairs) to medium (ca. nine breeding pairs) size colonies with reduced nest predation and increased survival was found (Serrano et al., 2005). In a population of cooperative breeders Arabian Babbler, *Turdoides squamiceps*, in the Negev desert, Israel, the *per capita* population growth rate increased with population density through higher fledging success in small groups. But when group size increased too much, negative DD reduced reproductive success and lowered group persistence, decreasing average group size (Keynan & Ridley, 2016).

Finally, in some instances, both positive and negative DD effects can occur simultaneously at the same or different spatial scales, Fig. 1. F (Ashbrook et al., 2010; Kim et al., 2009; Rodenhouse et al., 2003), buffering each other and, in some instances, resulting in an overall positive effect. For example, for the Common Guillemot colony on the Isle of May, chick survival in plots of high conspecific density was higher than at low density due to communal attendance that improved parental provisioning rates, but also suffered from high infanticide rate by conspecifics (Ashbrook et al., 2010). For a colony of Blue-footed Booby, *Sula nebouxii*, in Isla Isabel, México, individuals dispersed from patches of high conspecific density to patches of lower density improving chick fledging. However, individuals from low density patches dispersed to high density patches, likely through conspecific attraction, resulting in fewer fledglings per year (Kim et al., 2009).

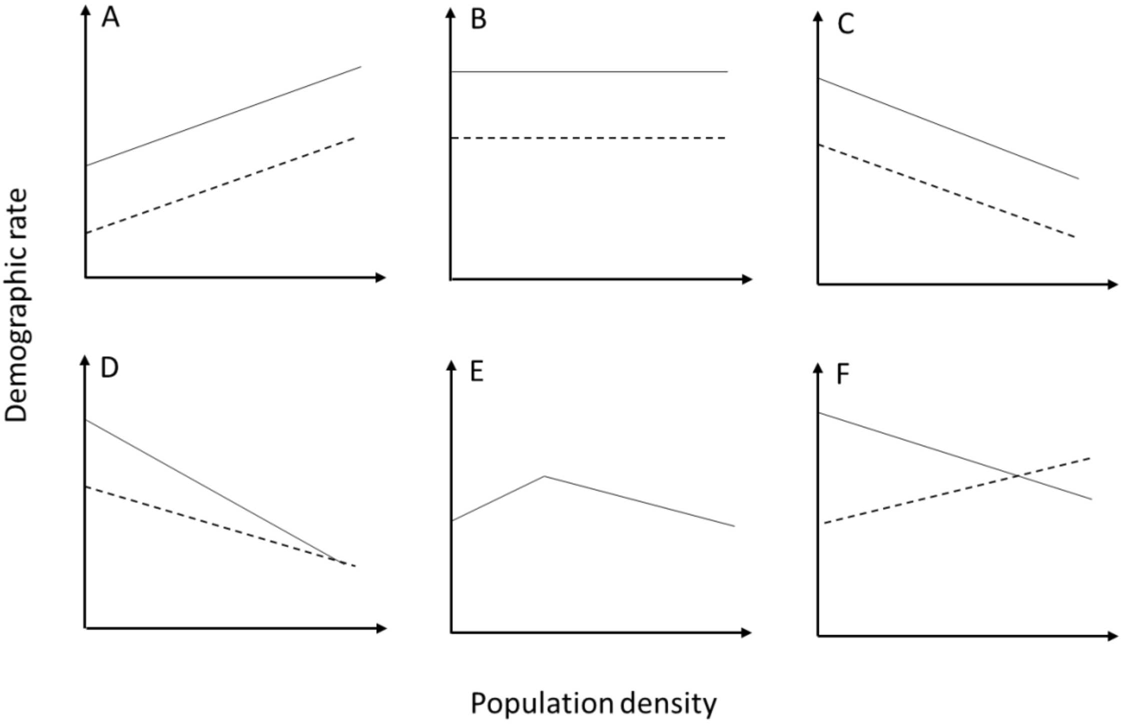


Figure 1. Schematic representation of the relationship between a demographic rate and population density. A. Demographic rate increases with population density in two habitats of different quality (solid line: higher quality and dotted line: lower quality) when resources are not limited across sites. B. Demographic rate depends on the specific use of a site of different quality but is independent of population density. C. Demographic rate depends on the specific use of a site and on population density, as individuals suffer higher competition/predation/parasitism at increased population density. There will be a similar effect of density at all sites D. Demographic rate depends on site quality and population density, but the effect of density depends on the quality of the site: demographic rate declines more rapidly in high quality sites. E. Demographic rate in a single site increases with population density only at low levels of population density (Allee effect). F. Demographic rate depends on site quality and population density with opposite effect. Modified from Nevoux et al., 2011 and Stephens et al., 1999.

1.1.3 Space use can be mediated through behaviour

In a similar fashion to the examples above, behaviour can play an important role in population regulation affecting individual fitness, reproduction, and ultimately population size (Sutherland, 1996). A positive effect may occur at high densities mediated through cooperation, as increased breeding success due to alloparental care in Superb Starlings, *Lamprotornis superbus*, (Guindre-Parker & Rubenstein, 2018), or due to group mobbing of predators in waders like Northern Lapwing, *Vanellus vanellus*, Eurasian Curlew, *Numenius arquata*, and Pied Avocet, *Recurvirostra avosetta* (Berg, 1996; Valkama et al., 1999; Hotker, 2000; Šálek & Šmilauer, 2002). On the other hand, a negative effect may occur due to competitive exclusion through territoriality and hierarchy (Sutherland, 1996; Newton, 2004; Johnson, 2007). In competitive species, the best resources will be used first by better competitors that will restrict the access of resources to subordinates. Meanwhile, subordinates can experience equal benefit from occupying a high quality and highly competitive site as from moving to a lower quality site with fewer competitors (Ideal Despotic Distribution, Fretwell & Lucas, 1969). This occurs for example in some populations of Eurasian Oystercatcher, *Haematopus ostralegus*, Northern Goshawk, *Accipiter gentilis*, and Common Guillemot, with better competitors occupying higher quality territories and weaker competitors using lower quality sites or skipping breeding, with demographic consequences (Ens et al., 1992; Krüger & Lindström, 2001; Kokko et al., 2004). Access to resources can also be reduced due to conspecific attraction. In this case, density of individuals is used as a positive cue to settle on a site (Stamps, 1988; Kim et al., 2009; Cunningham et al., 2016; Gill, 2019; Valente et al., 2021; Swift et al., 2023) but might result on an ecological trap if for example, resource depletion at increased densities prompts negative DD (Battin, 2004). Ecological traps occur when animals misjudge the cue or cues they use to assess the quality of a habitat and settle on it (Battin, 2004) resulting in subsequent declines in population reproduction and/or survival that can potentially lead to extinction. Although these traps can be of natural origin, they also originate from the increasing anthropogenic changes to habitats (Gilroy & Sutherland, 2007). The previous example of Blue-footed Boobies breeding in patches of high density illustrates such an ecological trap. The same was also found in a population of Bobolink *Dolichonyx oryzivorus* in Canada, that were attracted to unsuitable breeding areas where decoys and playbacks simulated high conspecific density resulting in an increased number of floaters (Nocera et al., 2006).

1.1.4 Other complex processes of population regulation

Multiple mechanisms can regulate population simultaneously and their effects can be extended across large spatial and temporal scales. Such is the case with buffer effects in which a larger proportion of a population occupies lower quality sites as the population increases (Sutherland, 1996). For example, at low population density of Grey Plovers, *Pluvialis squatarola,* most individuals could be found in the warmest British estuaries, but as the population increased, a higher number occupied (colder) less suitable estuaries (Moser, 1988). A similar pattern was shown in Icelandic Black-tailed Godwits, *Limosa limosa islandica*, that are occupying poorer quality sites at both their wintering and breeding grounds as the population size has increased (Gill et al., 2001; Gunnarsson et al., 2005a).

The seasonal variation in resources during one season affecting individual fitness in a non-lethal manner which cascades to the next season is known as carry-over effects. These occur in many migratory species, and their effect at the individual level can have consequences at the population level via density independent or DD mechanisms (Norris, 2005; Inger et al., 2010). For example, in the East Canadian High Arctic population of Light-bellied Brent Geese, *Branta bernicla hrota*, individuals that reproduced during the summer, finished the following winter season in poorer condition than non-breeders (Inger et al., 2010). On the other hand, Icelandic Black-tailed Godwits and American Redstarts, *Setophaga ruticilla*, occupying better quality sites during the winter, arrive earlier to the breeding grounds, occupy better quality sites during the summer and have higher breeding success (Gunnarsson et al., 2005a, b; Studds & Marra, 2005; Alves et al., 2012).

For species that occupy different locations depending on the season, DD can occur in more than one time period during the annual cycle. Sequential or seasonal DD occurs when DD reduces the density of individuals during one season resulting in an increase in population numbers in the following season, through for example higher survival or reproduction (Betini et al., 2013; Ratikainen et al., 2008). A study on survival in Red Knot, *Calidris canutus islandica*, found that seasonal compensation masked food limitation in the Dutch Wadden Sea (Rakhimberdiev et al., 2015). During years of severe winter resource limitation, winter and summer survival estimates differed greatly. Once resource limitation stopped, these demographic rates became similar masking the effect of food shortage (Rakhimberdiev et al., 2015). High winter mortality due to DD resource depletion turned into fewer individuals in the spring, and lowered DD pressure during preparation for migration and re-fueling on staging sites (Rakhimberdiev et al., 2015). Moreover, annual survival estimates were similar before and after resource depletion stopped, meaning that the population was able to sustain similar numbers regardless of the effects of food limitation, complicating the detection of DD mechanisms (Rakhimberdiev et al., 2015). Another study in wild Mallards, *Anas platyrhynchos*, also reported sequential DD as a regulatory mechanism in lakes in southern Sweden (Elmberg et al., 2005). In this study, the experimental increase in Mallard density decreased the number of broods but not the number of almost fledged ducklings, probably due to predation or brood movements after hatching (Elmberg et al., 2005). The researchers concluded that two DD mechanisms occurring during the same season balanced each other out, resulting in the lack of a relationship between density and number of old ducklings.

The aforementioned factors are probably the most relevant for bird population regulation, but many more exist such as genetic bottlenecks (Briskie & Mackintosh, 2004), parental effects (Méndez et al., 2021), conditions during early development (Lindström, 1999) and generational shifts (Gill et al., 2019), and further complications can arise when interactions over time and space are considered.

1.2 Challenges of studying population regulation

As mentioned above, multiple mechanisms act simultaneously regulating populations. Their effects may balance each other out (Ashbrook et al., 2010; Kim et al., 2009; Rodenhouse et al., 2003; Kokko et al., 2004) or may be masked by other factors especially if they occur within a restricted period of time, such as stochastic weather events (Freckleton et al., 2006; Herrando-Pérez et al., 2012). Moreover, DD mechanisms can be very subtle, and many studies overlook their effects or fail to detect them when sampling methods of the species density and/or the spatial scale used is not appropriate (Hubbell et al., 1990; Krebs, 1995; Monnier-Corbel et al., 2022). For example, it was first thought that the decline in a population of Silvereye, *Zosterops lateralis*, in Heron Island, Australia, was driven by mortality after cyclones. However, a close examination of different demographic rates revealed that the mechanism behind this trend was DD food limitation affecting juvenile survival (McCallum et al., 2000). Therefore, in order to detect DD, studying different demographic rates and relating them to extrinsic factors, such as food or predation, and intrinsic ones, like behaviour, facilitates the understanding of how species respond to changes in the environment and population numbers (Bretagnolle et al., 2008), and integrating these factors into management planning can be crucial for conservation actions (Sutherland, 1998; Anthony & Blumstein, 2000).

To study population regulation, studies should ideally be carried out over large temporal scales in a relatively constant environment that can capture population changes over time

(Hixon et al., 2002; Sutherland & Norris, 2002; Bretagnolle et al., 2008), or in sites with different habitat quality located along the density range of the species in focus that confers some variability for comparison (Gaston & McArdle, 1994). Time-series studies are in many instances focused on recovering populations or comparing the conditions before and after a disturbance (Sinclair & Pech, 1996; Sutherland & Norris, 2002; Nicoll et al., 2003; Rakhimberdiev et al., 2015). While comparisons between sites or locations are common for assessing the value of protected versus unprotected areas (Devictor et al., 2007; Soriano-Redondo et al., 2023), covering a density range of populations is increasingly difficult as the amount and quality of wildlife habitats decline due to habitat loss and degradation. However, studies in open systems pose some difficulties as measuring population density and other demographic traits is subject to some uncertainty like observer bias, census error or due to the species ecology (Freckleton et al., 2006). When that is the case, underestimation of the strength of DD and other processes may occur. Measuring demographic rates over large temporal scales for highly mobile species can be very challenging if individual identification is not possible and/or if individuals disperse over large areas. Hence, studying highly philopatric, territorial, and long-lived species will partly overcome this difficulty, as the chances of sampling the same individuals over time are higher.

Common demographic rates used in population studies are density and absolute numbers as measures of abundance of individuals; measures of reproductive output such as hatching success, fledging success, number of chicks or broods; as well as survival. Birds are a common group to study population regulation and investigate DD effects. This is especially true for long-lived, territorial and philopatric species that reproduce once a year (Newton 2004; Gunnarsson et al., 2006; McKellar et al., 2014). These species will tend to prioritize survival over reproduction, use the same sites and pair up with the same mate. Their single annual reproductive output can be relatively simple to measure, and their relatively stable year to year numbers suggest the presence of a regulatory mechanism (Sæther et al., 1996).

Finally, since demographic rates can vary throughout the seasons and across spatial scales (Ratikainen et al., 2008), and DD mechanisms can occur at the same time, identifying the proper sampling period is crucial. For many species, measures of population size occur when one season changes to the following one, that is focusing on reproductive output in the breeding season and measuring survival after winter (Fretwell, 1972; Ratikainen et al., 2008). However, population size alone might not provide enough detail on the underlying regulatory process if, for instance, several DD mechanisms are occurring at the same time masking their detection (Elmberg et al., 2005; Ratikainen et al., 2008).

In conclusion, here I highlight the importance of using appropriate timing of sampling, relevant spatial scales, and different demographic variables to study population regulation, since a number of different events can occur at the same scale and time, affecting different demographic rates.

1.3 Model system and the study species: why Iceland and why Whimbrels?

Iceland, with a human population of 396.960 (Statistics Iceland, information retrieved in October 2023) and an area of 103.529 km^2, is one of the countries in the world with the lowest population density of ca. 4 individuals/km^2 (World Population Review, information retrieved in October 2023). This number is reflected in the low human infrastructure and development, especially when compared to other European countries, but more importantly, it is also reflected in large areas of semi-natural landscapes where steep gradients in the density of some common bird species, particularly waders, still exist (Jóhannesdóttir et al., 2019). This provides a unique opportunity to study population regulation in this group, by investigating the relationship between different demographic rates and relating them to components of habitat quality across different breeding densities.

The species studied for this doctoral thesis is the Icelandic Whimbrel, *Numenius phaeopus islandicus* (Whimbrel hereafter). Whimbrels are long-lived waders from the Numeniini tribe, hold a longevity record of 24 years and their annual survival rate has been estimated at 0.71-0.89 (Klima et al., 2013; Méndez et al., 2018a). This monogamous wader migrates from the tropics to the Arctic and sub-Arctic regions using the East Atlantic Flyway (Alves et al., 2016; Gunnarsson and Guðmundsson 2016), and is highly philopatric to both the wintering and breeding grounds (Mallory, 1982; Carneiro et al., 2021). During the winter months, they can be found along the west-African coast, Fig. 2, occupying coastal environments and wetlands where they feed on macroinvertebrates like Fiddler crabs, *Uca tangeri*, and West African bloody cockles, *Senilia senilis* (Zwarts, 1990; Carneiro et al., 2017; Lourenço et al., 2017). Northward migration starts in April and early May, and most individuals stopover in Britain and Ireland before arriving to the breeding grounds in Greenland, Iceland, Shetland, and the Faroe Islands (Carneiro et al., 2019a; IUCN, 2023).

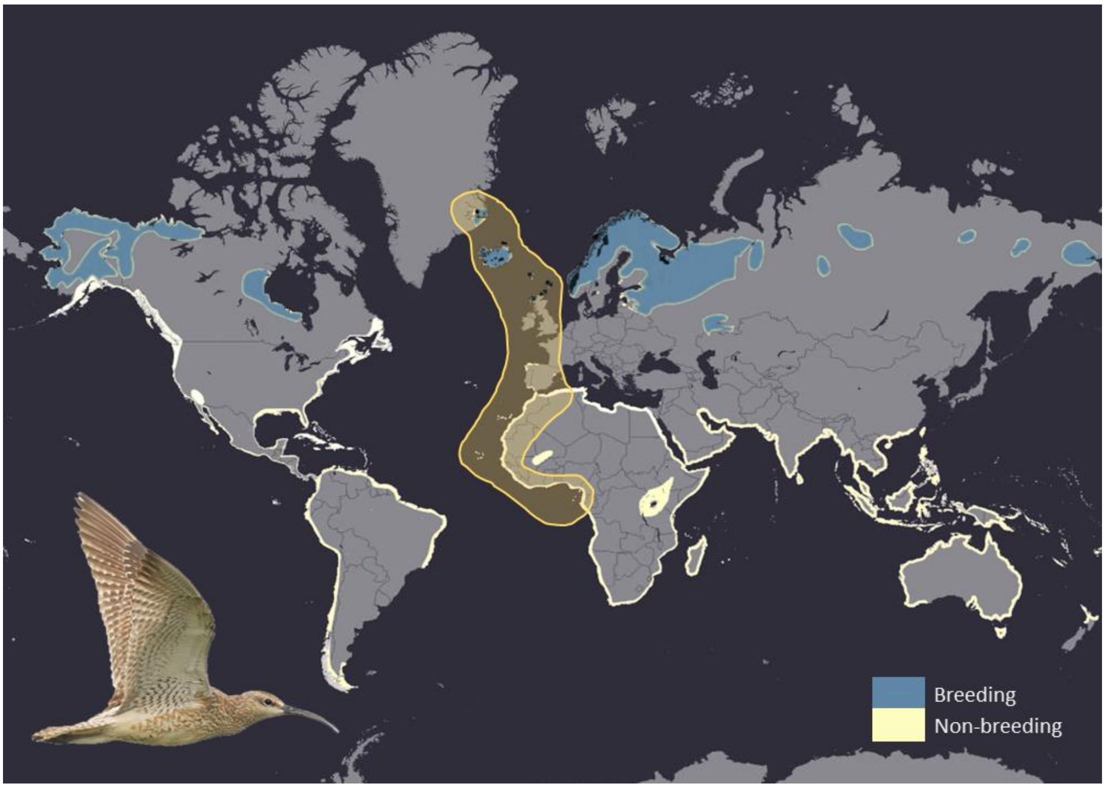


Figure 2. Global distribution of the Whimbrel, Numenius phaeopus. The range of the islandicus subspecies studied is highlighted in orange. Most Icelandic Whimbrel spend the summer months (May to August) breeding in Iceland, but few breed in Faroe Islands, East-Greenland, and Shetland. After the breeding season, the Whimbrel starts the southbound migration to the non-breeding grounds in the West-African coast. Distribution data obtained from IUCN Red List with OpenStreetMap as base layer. Range information obtained from Delany et al., 2009.

In Iceland, where the bulk of the population breeds, Whimbrels can be found in different semi-natural open habitats of low elevation such as river plain or heathland and mostly avoiding areas of taller vegetation structure, dense stands of lupin and forested land, Fig. 3 (Gunnarsson et al., 2006; Jóhannesdóttir et al., 2014; Katrínardóttir et al., 2015; Méndez & Gunnarsson, 2020). There, they breed on a gradient of density ranging from very low, ca. 1-2 pairs/km^2, to very high, ca. 40-45 pairs/km^2, among the highest density recorded worldwide (Gunnarsson, 2000).

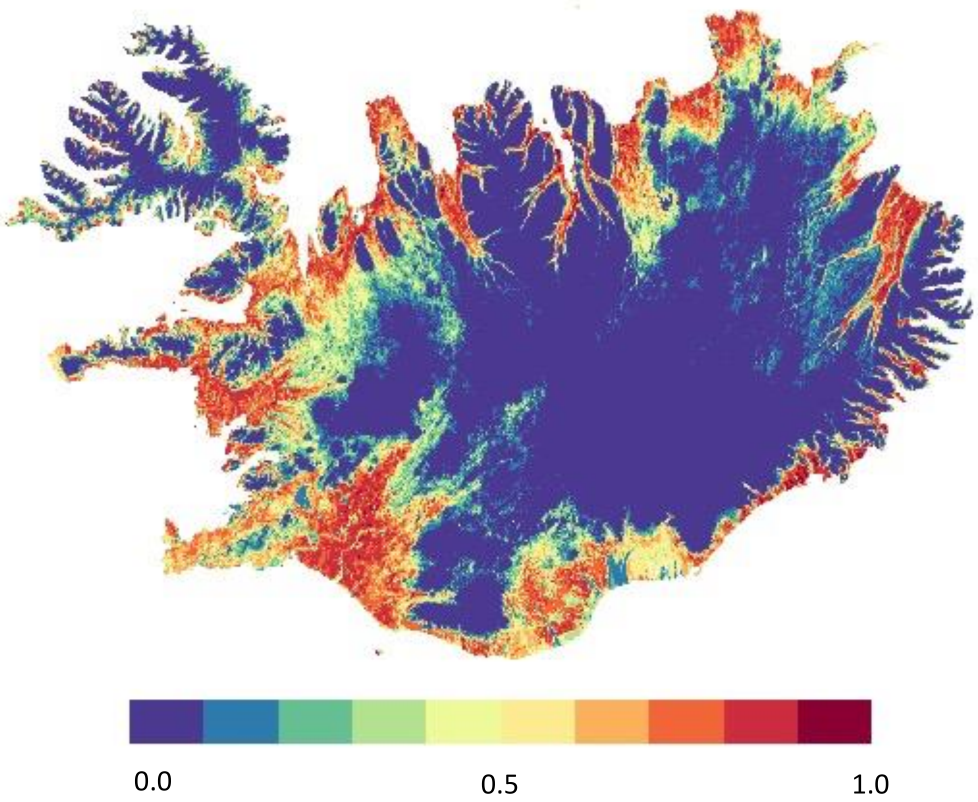


Figure 3. Distribution of Whimbrel in Iceland. The colour gradient shows the probability of Whimbrel occurrence. Unsuitable areas (glaciers, mountains of high elevation) are shown in dark blue and suitable areas are shown in warmer colours (orange and red). Most areas in warm colours are below 200-300 m above sea level. Notice the extension of the southern lowland basin, shown mostly in red, especially important for Whimbrels and other waders during the summer months. Map from Méndez & Gunnarsson, 2020.

The Icelandic breeding season starts soon after birds arrive as they are on a tight schedule to breed (Gunnarsson, 2010; Carneiro et al., 2019b). Adults quickly pair up, frequently with previous mates, and most occupy old territories (Skeel & Mallory, 1996). Whimbrels are highly territorial towards conspecifics (Mallory, 1982), and aggressive chases and aerial displays are usually observed during this period (Skeel, 1978). A clutch of four eggs is laid in a scraped nest cup on the ground (Fig. 4) that adults feistily defend from predators like Arctic Skua, *Stercorarius parasiticus*, and Common Raven, *Corvus corax* (Skeel & Mallory, 1996; Jónsson & Gunnarsson, 2010). Both parents incubate the eggs that hatch 27-28 days after the first egg is laid and tend to the brood (Guðmundson, 1957; Skeel & Mallory, 1996). The chicks are precocial, feed independently soon after hatching, and fledge after ca. 28 days (Grant, 1989). Although limited information on prey preference exists for Whimbrels in Iceland during the breeding season, Guðmundsson (1957) analysed the stomach content of 20 adults and found high amounts of berries and some remains of Coleoptera, Diptera and Lepidoptera.

Figure 4. Example of Whimbrel nests in different vegetation. From left to right: grassland, heathland, and moss heath.

The breeding season finishes around mid-July to the beginning of August, when Whimbrels start fuelling up before the southward migration (Carneiro et al., 2019a). During this final part of the breeding season, the birds become restless and gather in small flocks prior to departure (Guðmundson 1957), after which adult individuals return to their wintering grounds commonly on a non-stop flight, followed shortly after by the fledged chicks (Carneiro et al., 2019a, 2023). By early September, only scattered birds remain in Iceland (Guðmundson, 1957; Gunnarsson, 2006).

The global Whimbrel population is decreasing, but the species is regarded as of Least Concern by the UICN Red list (IUCN, 2023). Within Europe, declining population trends have been reported in Shetland (Massey et al., 2016), Fennoscandia (Lindström et al., 2019), and locally in East Iceland (Lárusdóttir et al., 2019) while stable numbers have been reported locally in the Northeast and West parts of Iceland (Harðardóttir 2019; Kolbeinsson et al., 2020). Threats to the species include loss and degradation of breeding, wintering and stopover habitats, hunting, and poaching (IUCN 2023). Targeted conservation measures towards the species do not currently exist in Iceland or elsewhere, but the species also occurs in some protected areas such as Ramsar sites and IBAs together with other wader species (the Ramsar convention on Wetlands; BirdLife International, 2022).

2 Aims of the thesis

The goal of this doctoral thesis was to investigate the relationships between demographic processes, habitat features and behaviour along the unique gradient of wader breeding density found in Iceland to gain insights into possible mechanisms regulating the Whimbrel population. To do so, I first (**Chapter I**) investigated variation in adult and brood abundance and their relationship using a long-term dataset collected across South Iceland, to identify demographic trends, traffic influence, habitat occurrence and how adult abundance and brood abundance are related over time and at a local spatial scale. The next step (**Chapter II**) consisted of investigating how Whimbrel abundance varied between important habitats at different stages of ecological succession and throughout the breeding season, the possible shifts these habitats might undergo under natural and anthropogenic disturbances, and the implications these changes might have for Whimbrels in the future. This analysis also had the practical application of assessing variation in Whimbrel numbers throughout the season to identify the proper time-window to estimate their breeding density. Following this, I explored if variation in local adult and brood abundance were explained by two proxies of habitat quality and if local breeding success was explained by differences in breeding density across several study sites and for three consecutive years in South Iceland (**Chapter III**). Finally, since behaviour can play an important role in determining local breeding density, I explored the function of the aerial display, an energetically expensive and honest signal traditionally associated with mate attraction and resource defence. I did so by studying this behaviour throughout the breeding season and along the density gradient to cast light on the relationship between display behaviour and local breeding density to infer the function of this behaviour **(Chapter IV)**.

3 Methodology and data collection

3.1 Long-term study (Chapter I)

3.1.1 Study site

This long-term study is part of a large wader monitoring programme in South Iceland that started in 2011 and is currently ongoing. The study is carried out across the largest lowland basin of Iceland in the south of the country, characterized by intermixed patches of semi-natural habitats and agricultural land (Fig. 5. A; Jóhannesdóttir et al., 2018, 2019).

3.1.2 Data collection

Data collection followed the same survey route as in Gunnarsson et al., 2017. Adult Whimbrels were counted during the last 10 days in June, coinciding with late incubation for most species (Gunnarsson et al., 2017; Gunnarsson and Thorisson, 2019; Laidlaw et al., 2020). The counts were performed at 63 fixed points along 198 km of roads and tracks and were separated by 3 km (Fig. 5. B). At each point the car was stopped and the number of adult Whimbrels within 200 m were recorded for five minutes using binoculars to aid detection. Brood surveys started in 2013 during the last 10 days in July, when most nests have hatched (Gunnarsson, 2010). Instead of counting them at pre-determined points, they were recorded opportunistically along the same road transect where the adult fixed points were located (Fig. 5. B). The observer drove along the roads at a maximum speed of ca. 20 km/h with open windows to aid detection. Broods were located by detecting chicks or by observing the feisty parental behaviour as an indicator of the presence of chicks (Grant et al., 2000; Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Gunnarsson et al., 2017). During the chick-rearing period, breeding Whimbrels as many other waders, perform noisy and conspicuous behaviour like alarm calls and circling movements around the intruder, to deter predators and signal their presence (Katrínardóttir et al., 2015). When a brood was located, the bearing was recorded and the distance from the observer to the chicks or the alarming parent(s) was measured with a laser range finder. See section **3.3 Data analysis** and **Chapter I** for a more detailed description of methods.

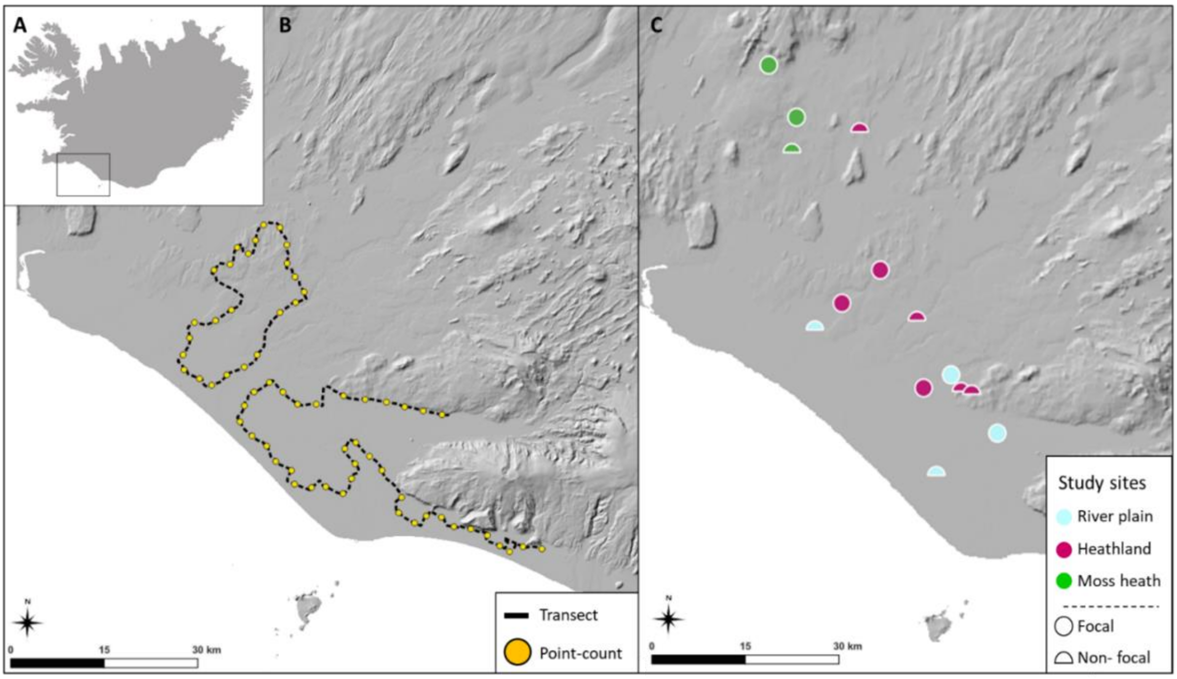


Figure 5. A. Map of Iceland showing the position of the study area. B. Long-term study area (chapter I) showing the road transect in a black discontinuous line, and the position of the 63 points where adults were surveyed as yellow dots. C. Map with the locations of the 14 short-term study sites (chapters II- IV) covering the Whimbrel breeding density gradient in South Iceland. Symbols indicate the type of sampling and methodology in the field: full circles are focal sites where Whimbrel monitoring was continuous (May to end of July) and habitat quality and behaviour was measured (see methods in chapters III and IV), and half circles are non-focal sites where monitoring occurred in the beginning and end of the Whimbrel breeding season (first two/three weeks in May and last two weeks in July). Colours indicate the three habitat categories, on different stages of ecological succession, on which sites were grouped. See Table 1 for information on individual sites. Base layer: Geodesy of Iceland, digital elevation model with CRS ISN93 (Landmælingar Íslands, ÍslandsDEM 1.0).

3.2 Short-term studies (Chapters II - IV)

3.2.1 Study sites

A total of 14 study sites in the lowland basin in South Iceland were sampled based on a gradient of Whimbrel breeding density and habitat type (moss heath, n= 3; heathland, n= 7; and river plain, n= 4; Fig. 5. C.; Fig. 6; Table 1). These habitats are on early and mid-stages of ecological succession due to the synergy of different natural and anthropogenic forces, such as volcanic eruptions, periodic floods or sheep grazing. The moss heath sites, Fig. 6, were located close to the 200 m isopleth and were characterized by a thick layer of moss and lichens, first colonizers after a disturbance, forming a dense mat (Vilmundardóttir et al., 2018). Within the moss mat, intermixed patches of bare ground, heath, and graminoids were also common (Gísladóttir, 2001). River plain sites, Fig. 6, were located along rivers, some of glacial origin, and are, or have been subject to periodic floods keeping the vegetation structure on a mosaic of intermixed patches of sand, gravel, heath, rushes, sedges, and forbs (Nilsson & Dynesius, 1994; Gunnarsson et al., 2006; Björnsson, 2010; Katrínardóttir et al., 2015). Heathland sites, Fig. 6, were on a more advanced succession stage, where disturbance is less frequent than in the other two habitats but where grazing of sheep and horses is also more common (Gísladóttir, 2001). See **Chapter II** for a more detailed explanation of habitats and species.

Moss heath: habitat on early succession due to erosion and volcanic activity. A continuous layer of mosses and lichens cover the ground creating and retaining humidity. Vascular species like small shrubs and forbs establish themselves on patches of bare ground. Located below 200-300 m. Main species: Mosses: *Racomitrium lanuginosum*, *Hylocomium splendens*. Lichens: *Cladonia arbuscula*, *Cetraria islandica*. Patches of shrubs: *Empetrum nigrum*, *Vaccinum uliginosum*, *Salix herbacea*.

River plain: habitat on early succession stage due to river floods interrupting vegetation development. Located in flat lowlands, most often close to the sea. Presence of shrubs, forbs, sedges, and rushes intermixed with sand and gravel on a dry-wet gradient. Main species: *E. nigrum*, *Salix* sp., *Silene acaulis*, *Dryas octopétala,* grasses, rushes (particularly *Juncus arcticus*), and sedges.

Heathland: habitat on mid-stage of succession due to heavy anthropogenic activity, such as grazing pressure, wetland drainage or cut-down of wooded land. Rather dry areas with denser vegetation where the presence of hummocks is common. Main species: mosses, lichens, and shrubs like E. *nigrum*, *V. myrtilus*, *Calluna vulgaris*,and *Salix* sp.

Figure 6. The three habitats at different stages of ecological succession on which the study sites were classified. From early to mid-stages of succession: moss heath, river plain and heathland. Picture credits: Maite Cerezo-Araujo, moss-heath; Tómas Grétar Gunnarsson, river plain; and Sigurður Kristinn Guðjohnsen, heathland.

Table 1. Information of study sites in South Iceland covering a gradient of Whimbrel density. Sampling type indicates differences in the timing of sampling and methodology in the field: both focal and non-focal sites were surveyed once a week at the beginning of May and the two last weeks of July, while only focal sites were surveyed twice a week between that period. Sampling years are 1 = 2019; 2 = 2020 and 2021; and 3 = 2019 – 2021. Mean breeding density per year: mean density was calculated using counts during incubation for the focal sites, and counts during pre-incubation for the non-focal sites (not sampled during incubation). The area of the sites was calculated with an Icelandic map engine (www.já.is/kort), and the elevation was obtained from the Google Earth engine.

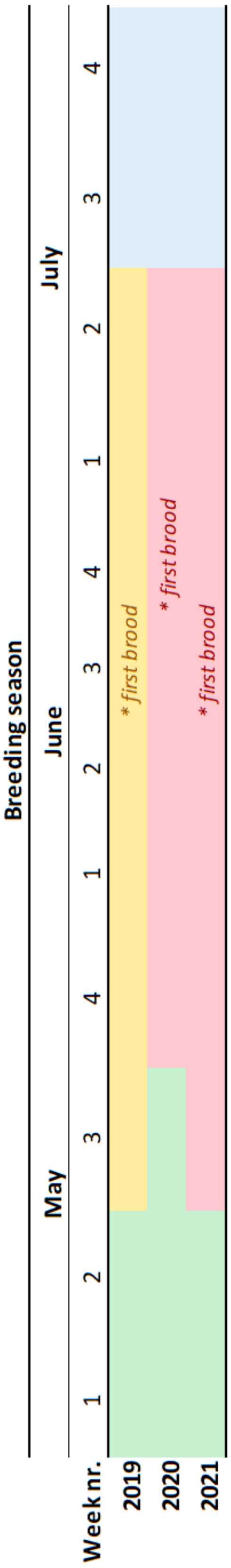
Site	Coordinates	Area (km^2)	Elevation (m)	Sampling type	Habitat	Sampling years	Mean density ±SE (nr./ km^2)
Affall	63.662485, -20.233231	0.42	17.09	Non- focal	River plain	3	39.3±5.7
Apavatn	64.142501, -20.695732	1.09	224.75	Focal	Moss heath	3	7.18±0.6
Björk	64.088619, -20.755372	1.06	109.4	Non- focal	Moss heath	2	2.9±0.5
Drumbabót	63.728296, -20.141549	2.2	41.16	Focal	River plain	3	30.2±2.8
Helluvað	63.858140, -20.340119	2.13	38.8	Focal	Heathland	1	7.20±1.6
Hvolsfjall	63.759633, -20.200748	0.56	95.95	Non- focal	Heathland	1	18.4±2.3
Kotamannafjall	63.757496, -20.158112	0.74	160	Non- focal	Heathland	1	9.4±0
Lyngdalsheiði	64.212177, -20.821905	1.17	127.72	Focal	Moss heath	3	3.42±0.5
Moeiðarhvoll	63.762776, -20.317074	0.34	20.03	Non- focal	Heathland	2	36.5±5.6
Raftholt	63.933924, -20.475244	0.67	116.3	Focal	Heathland	3	20.6±2.1
Rangá	63.784972, -20.213912	0.97	46.23	Focal	River plain	3	35.9±2.0
Sel	63.886275, -20.593547	0.43	19.02	Focal	Heathland	2	33.2±2.7
Skálholtstunga	64.114762, -20.547494	0.95	86.51	Non- focal	Heathland	2	15.3±2.2
Þjorsá	63.853267, -20.660271	1.21	8.14	Non- focal	River plain	3	15.6±2.5

All sites were grouped into two categories based on sampling intensity (Table 1). The timing of sampling and methods varied between sites and was adjusted to the aims of the different chapters. Accordingly, the sites were divided into two groups: focal sites (n= 7) which were studied more intensively, and non-focal sites (n= 7, Fig. 5. C, Table 1). In 2019 a total of 10 sites (focal = 6; non-focal = 4) were sampled from the beginning of May to August. Of these 10 sites, one was replaced in the following year due to infrastructure development in the area and two were replaced due to difficult access (Table 1). In 2020 and 2021, a total of 12 sites were sampled. All sites in the last two years (2020 and 2021), both focal and non-focal, were sampled only during the beginning (until the second/third week of May) and final part (two last weeks in July) of the breeding season, while more intensive effort was set on the focal sites from ca. mid-May to the second week of July (Table 1). All sites were used in **Chapter II,** while only focal sites were used in **Chapters III and IV.**

3.2.2 Data collection

Surveys of adults and broods

Adult and brood counts were performed throughout the breeding season, during the three years of study, and at all sites (focal and non-focal, Fig. 5. C, Fig. 7). Sites were surveyed by driving on gravel tracks with open windows at a maximum speed of 10-20 km/h, and on foot. Every time I visited a site, I counted adult Whimbrels on the ground and flying low over the site. When the tracks were impassable, I walked to cover the whole study area. Counts were done in the mornings and in one direction using binoculars to aid detection. Breeding territories were identified by using parental behaviour, i.e., alarm calls, mobbing behaviour towards the observer, broken-wing display (Brown & Shepherd, 1993; Grant et al., 2000; Gunnarsson et al., 2006; Bolton et al., 2012; Katrínardóttir et al., 2015; Gunnarsson et al., 2017; Baines et al., 2023; Bowgen et al., 2022; Douglas et al., 2023), and nests found during another monitoring programme (Carneiro et al., 2019b; Laidlaw et al., 2020). Brood counts were done following the same methodology as adult counts and since monitoring was continuous (Fig. 7), by re-visiting previously detected territories when hatching date approached to determine nest fate (predated or hatched). I used chick presence and the feisty parental behaviour as indicators of broods (Grant et al., 2000; Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Gunnarsson et al., 2017), but chicks were not systematically recorded to minimize disturbance. Effort on counting broods started in late June, when the first nest hatched (Carneiro et al., 2019b; Laidlaw et al., 2020) and lasted to the end of the breeding season covering the brood-rearing period until fledging (Fig. 7). The data on both adult and brood counts was used for **Chapters II, III and IV**, where more information on methods can be found.



Methodology

	Whimbrel counts	Brood counts*	Invertebrate sampling	Predator pressure	Behaviour
Pre-incubation	Once a week - all sites	*na*	*na*	Once a week - focal sites	Once a week - focal sites
Incubation 2019	Once a week - all sites	Once a week - all sites	Once a week - focal sites	Once a week - focal sites	Once a week - focal sites
Incubation 2020&21	Twice a week - focal sites	Twice a week - focal sites	Once a week - focal sites	Once a week - focal sites	Twice a week - focal sites
Chick rearing	Once a week - all sites	Once a week - all sites	Once a week - focal sites	Once a week - focal sites	Once a week - focal sites
Chapters:	II- IV	II- IV	III	III	IV

Figure 7. Calendar of the Whimbrel breeding season and sampling methodology used in chapters II- IV. Fieldwork was performed daily from May to August. Pre-incubation period is shown in green, incubation period in 2019 is shown in yellow while for 2020 and 2021, with a different methodology, is shown in pink. Chick-rearing or post-incubation is shown in blue. Methods and effort in the field varied during the breeding season (pre-incubation, incubation, and chick-rearing) according to the aims of the chapters.

Habitat quality: invertebrate traps and predator surveys

To determine habitat quality, we used two common surrogates (Johnson, 2007; Mott et al., 2023): invertebrate abundance as potential prey for Whimbrels and predator intrusions as potential predator pressure.

Pitfall traps for invertebrates were placed on the focal sites for the three years of study (Table 1; Fig. 5. C; Fig. 8). We set up a total of six traps per site in two groups of three. The traps were placed in line and separated by 5-10 meters, as topography of the site permitted. For every trap, I used plastic (skyr, a traditional Icelandic cultured dairy product) pots of 9.5 cm in diameter partially filled with a mixture of water, clear antifreeze and soap and buried them into the ground. To avoid rainwater from filling them up, I used a cover placed 5 cm above each trap. The location of the traps did not change over the years. The traps were set up at the end of May and beginning of June coinciding with the initiation of the incubation period and were emptied every seven days until the end of July or beginning of August, covering the chick-rearing period (Fig. 7).

Figure 8. Pitfall traps for invertebrates were set up on the focal sites during the incubation and chick-rearing period. Plastic containers (skyr pots) filled with a mixture of water, clear antifreeze and soap were buried into the ground with the opening at surface level and with a cover 5 cm above them to prevent rainwater from overflooding the traps.

To estimate potential predation pressure, predator intrusions were recorded opportunistically when surveying the sites during the three years of study (Fig. 7). Predators do not normally target adult Whimbrels, but focus on eggs and chicks instead. The most common Whimbrel predators in South Iceland are Common Raven, Arctic Skua, large gulls, *Larus spp.*, Arctic Fox, *Vulpes lagopus*, and American Mink, *Neogale vison* (Jónsson & Gunnarsson, 2010). Every instance an avian predator showing predatory behaviour was observed, the species of predator and the number of individuals and species mobbing it were recorded (Fig. 9). The predatory behaviour considered in this study were signs of searching, irregular flight or hovering of avian predators, while all mammalian predators were considered a potential threat.

The data on habitat quality was used in **Chapter III,** where more details on potential invertebrate prey invertebrate, potential predator pressure and methods are described.

Figure 9. Whimbrel deceiving its size during an Arctic Skua attack in Iceland. Picture by Tómas Gretar Gunnarsson.

Display behaviour surveys

To determine the function(s) of Whimbrel displays and explore whether it changes at different breeding densities and throughout the breeding season, I selected three to five fixed points within the study sites to properly cover their extension. The acoustic surveys were performed in the early mornings when birds show higher activity (6am to 10am) (Davidsdottir, 2010; Jóhannesdóttir et al., 2019). The starting time was mostly constant and was occasionally adjusted to unfavourable weather conditions such as rain, fog, and high winds that could hinder visibility and sound detection. On each point, I performed acoustic surveys for three minutes where I counted the number of displays. Following Skeel (1978), a display was considered every instance a bird was seen manoeuvring in the air by flying up at high speed on an acute angle and slowly gliding down in circles while emitting at least two consecutive low whistle calls followed by a trill call (Fig. 10). In some instances, the aerial manoeuvre was not fully observed but the bird was clearly heard emitting the calls. Other times, only the call was clearly detected above, but the individual could not be located due to light conditions or cloud cover. In both cases, if the song (at least two low whistle calls followed up by a trill call) was clearly heard, I considered the event as a display. See **Chapter IV** for more details.

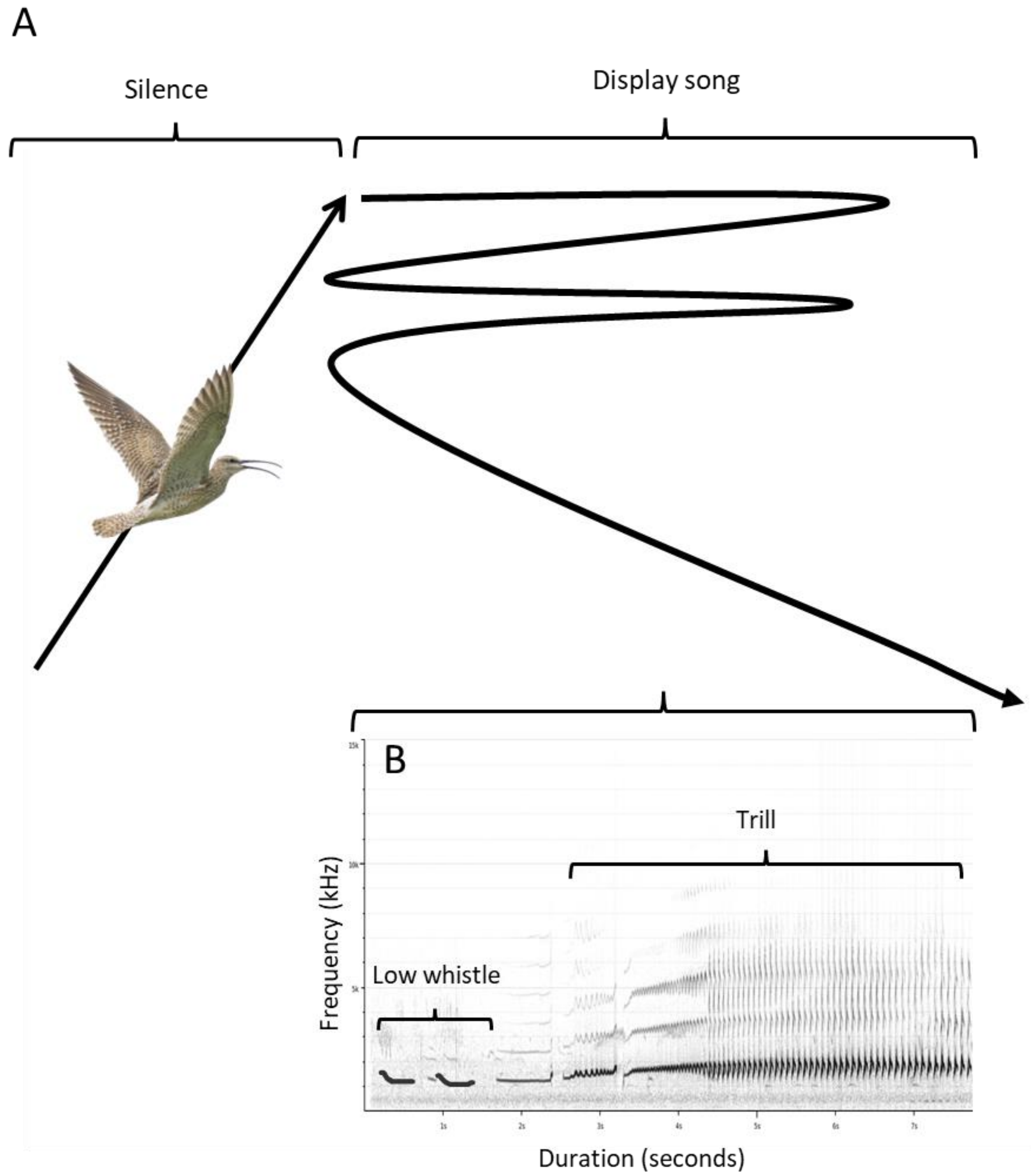


Figure 10. Whimbrel display behaviour. A. Display flight: aerial manoeuvre and display song. The Whimbrel flies up without emitting sound on an acute angle to gain a high altitude of up to 300m, and then slowly glides down emitting the display song. B. Sonogram of the display song: the display song is composed by at least two low whistle calls followed by a trill call. Sources: Low whistle: Benoit Nabholz, XC88214. www.xeno-canto.org/88214. Trill: Patrik Åberg, XC83934. www.xeno-canto.org/83934.

3.3 Data analysis

Statistical analyses and visualization were performed in R v.4.1.1 (R Core Team, 2021) using Generalized Linear Models (GLM) and Generalized Linear Mixed Effect Models (GLMM) with different error distributions based on the structure of the data. I checked model validation and performance and reported the results using a gradual language of evidence (Muff et al., 2021). Maps were done in QGIS v.3.20.3 (QGIS Development Team, 2021). All the computer softwares, packages and extensions used for this thesis were open source.

The main response variables throughout the thesis were Adult and Brood abundance, for which the effect of different explanatory variables was tested, Table 2. Abundance refers to the number of adults or broods recorded per survey unit, that is, for the long-term study, the number of adults observed per point and year, or number of broods along the road transect per year; and for the short-term studies, it refers to number of adults or broods observed per day and site. Abundance was used instead of density throughout the thesis based on several reasons. For the long-term study (**Chapter I**) this decision was based on the sampling methodology, as it occurred on the same fixed point-counts and on the same area along the same road transect over the years, and abundance is therefore comparable. For the short-term studies where several sites were surveyed (**Chapters II and III**), this decision was based on the original structure of the data and the error structure associated with it. Using a modified response variable such as nr./km^2 where numerator and denominator are subject to observer error into the model might lead to spurious results if the relationship between these two factors is not linear with an intercept of zero (Packard & Boardman, 1988; Allison et al., 1995; Jasienski & Bazzaz, 1999). Thus, whenever count data is available, as in this case, it is recommended to explicitly account for the relationship between the variables of interest instead of manually modifying it. When performing regression analysis, this can be done either by including an extra covariate in the model, or by using an offset term that forces the relationship of the response (abundance) and the covariate (area of the site) to be linear with a zero intercept. Here, I decided to use area as a covariate or as an offset term separately in each chapter based on the CI values of the regression coefficient of this variable and on model penalization and performance (Sokal & Rohlf, 1995). If area is used as a covariate, the model calculates the effect sizes of the additive variables using a zero unit change in area as intercept (used in **Chapter II**), while if it is used as an offset (used in **Chapter III**), the model will calculate the effect of area on the response variable itself (thus calculating nr./km^2 or density), skipping its additive effect with the other covariates. These two methods make possible the comparison of abundance across sites of different sizes by calculating changes in abundance relative to an increase in unit area (area as covariate) or by calculating the density (area as offset), while respecting the structure of the count data (non-negative integers). Therefore, since the response variable in the models based on model syntax was strictly speaking abundance only, I refer to it as such throughout the thesis to better describe the statistical methodology used and avoid confusion in this regard.

Other response variables used were Breeding success and Display frequency, Table 2. Breeding success (**Chapter III**) was calculated using the brood:pair ratio in a model with binomial error structure, which computes the probability of raising a brood given the number of pairs (abundance of adults divided by two). Display frequency (**Chapter IV**) was used in a model with negative binomial error structure due to overdispersion of the dataset, and in this case, area of the site was not considered as an offset term given model performance and penalization.

Regarding the explanatory variables (Table 2), the temporal covariates with a large enough sample size were treated as continuous (Year on **Chapter I**; Day and Week on **Chapters II and III**), and otherwise they were treated as categorical (Year in **Chapters II and III** with three levels: 2019, 2020, 2021, and in **Chapter IV** with two levels: 2020 and 2021). Other continuous variables included Habitat Heterogeneity, Traffic volume, Area, Potential prey abundance, Potential predator pressure and Adult density during incubation (not to be mistaken with the response variable Adult abundance), Table 2. Other non-temporal categorical variables were Breeding period with three levels: pre-incubation, incubation, and post-incubation; and Habitat, also with three levels: river plain, heathland and moss heath. A more detailed description of the variables is provided in each chapter. Finally, the random terms used were grouping variables of several levels (Point ID= 93; Site= 6-14; Week= 8; Road ID= 27; Point within Site= 24) that accounted for the non-independence of the data (repeated sampling) in the models.

Hereafter, I use "adult abundance" to refer to the response variable and "adult density or breeding density" to refer to the explanatory variable.

Table 2. Summary of the variables and model structures used in each chapter. See chapters for a more detailed explanation of the statistical analysis and how the different variables were obtained.

Response variable	**Explanatory variables and random terms**	**Model structure**	**Data source**	**Chapter**
Adult abundance	Year, Habitat Heterogeneity, Traffic volume. Random term: Point ID	GLMM, Poisson	Long-term study	Chapter I
	Day, Breeding period, Habitat, Year, Area. Random term: Site	GLMM, Negative binomial	Short-term study	Chapter II
	Potential prey abundance, Potential predation pressure, Year. Random term: Site, Week	GLMM, Negative binomial	Short-term study	Chapter III
Brood abundance	Year, Traffic volume. Random term: Road ID	GLMM, Negative binomial	Short-term study	Chapter I
	Potential prey abundance, Potential predation pressure, Adult density, Week, Year. Random term: Site	GLMM, Negative binomial	Short-term study	Chapter III
Breeding success	Adult density, Year. Random term: Site	GLMM, Binomial	Short-term study	Chapter III
Display frequency	Breeding period, Adult density, Year. Random term: Site, Point	GLMM, Negative binomial	Short-term study	Chapter IV

4 Summary of the chapters and results

4.1 Long-term study

Chapter I. Annual and spatial variation in adult and brood abundance in a sub-Arctic wader.

In this chapter, I first examined the variation in adult abundance over time and across points of different habitat heterogeneity and traffic volume, and the variation in brood abundance (used as proxy of productivity) over time and along the same surveyed transect. I also examined habitat preference of Whimbrel broods within the surveyed transect. Finally, the relationship between adult and brood abundance on a local and temporal scale was explored. The results showed a strong adult annual decline in South Iceland (2012-2021). Moreover, adult abundance was higher within points of a more heterogenous habitat, and mostly similar at different volumes of traffic along the surveyed road. The decline in adult abundance was not followed by an evident decrease in brood abundance (2013-2021) which was similar along the different road transects regardless of traffic volume. None of the habitats where broods occurred were selected over what was available along the surveyed transect, but broods were less likely to be found in anthropogenic habitats such as agricultural and domestic land and mixed forestry plantations. Finally, the positive relationship between adult and brood abundance found spatially did not hold temporally, suggesting that large-scale spatial variation in productivity is largely a product of local adult abundance whereas annual variation in productivity is highly affected by environmental variation.

4.2 Short-term studies

Chapter II. Seasonal variation in Whimbrel abundance across sub-Arctic habitats of varying succession stage.

Here I investigated variation in Whimbrel adult abundance (I) across habitats at different stages of succession and (II) throughout the breeding season within these habitats. The results showed highest and lowest Whimbrel abundance in habitats on early stages of succession. Moreover, Whimbrel abundance varied differently within habitats as the breeding season advanced. During pre-incubation, abundance increased in all habitats and stabilized during incubation. During post-incubation, contrasting trends in abundance were found as it decreased in moss heath but not in river plain nor heathland. These results suggest some habitats are better suited than others for the final part of the breeding season when chick-rearing and pre-migration preparation occur.

Chapter III. Do habitat quality and breeding success explain variation in breeding density of a sub-Arctic wader?

In this chapter I explored the relationships between adult and brood abundance of Whimbrels with potential invertebrate prey abundance and potential predator pressure (two components of habitat quality); and explored whether breeding success (brood:pair ratio) was related to local breeding density. The results showed that variation in adult abundance was not directly related to any of the measures of habitat quality during incubation, but more broods were produced with higher abundance of invertebrate prey measured during chick-rearing and higher adult breeding density. Finally, breeding success was similar along the gradient of Whimbrel breeding densities. These results suggest that variation in adult density across the Icelandic landscape is probably maintained by a combination of higher number of broods produced in areas of higher adult density, where higher abundance of potential prey is also found, coupled with the philopatry of the species. Moreover, given the species habitat preference, the similar breeding success found here might be explained by density dependent mechanisms.

Chapter IV. Serenade of a Whimbrel: understanding the function of display behaviour in a sub-Arctic territorial wader.

Here I explored the function of display behaviour in Icelandic Whimbrels to infer whether this behaviour is used for mate attraction and/or territory defence. The results showed displays were performed throughout the whole breeding season, but display frequency was higher at low density of individuals prior to incubation. These results suggest that the Whimbrel display behaviour has a pluripotent function as it is used to attract mates at low densities during the pre-incubation period, while it might also be used to defend resources at higher density during the whole breeding season.

5 General conclusions and future directions

The goal of this PhD thesis was to shed light on processes regulating the population of Whimbrels breeding on a density gradient in the southern Icelandic lowlands, the largest lowland basin in the country. Within this area, Whimbrels can be found breeding on a gradient of low to high density (ca. 1 – 45 pairs/km^2) in different semi-natural open habitats where some sites present among the highest densities recorded worldwide. Here, I studied temporal and spatial drivers of two important demographic factors, adult and brood abundance, and their relationship. To do this, I used both a long-term dataset collected between 2011 and 2021 along a 198 km road transect, and a short-term dataset that spanned from 2019 to 2021 and covered 14 study sites. The specific aims were (i) to explore population trends and habitat associations using the long-term dataset, and then, explore possible drivers explaining the variation in different demographic parameters using the short-term dataset. More specifically, I investigated (ii) variation in adult abundance within and between habitats in different stages of ecological succession and throughout the breeding season; (iii) whether potential invertebrate prey abundance and potential predation pressure could explain adult and brood abundance, and whether breeding success (brood:pair ratio) was related to local breeding density. Finally, I also explored (iv) the frequency of display behaviour in relation to local breeding density. The results from these four chapters revealed that adult Whimbrel abundance in South Iceland declined in 2012-2021, Fig. 11. A, and abundance was positively associated with habitat heterogeneity, Fig. 11. B. The short-term studies revealed that adult abundance differed between sites at different stages of ecological succession and throughout the breeding season, Fig. 11. C, and adult abundance was not directly correlated with potential prey abundance or potential predation pressure, Fig. 11. D. Brood abundance in South Iceland recorded during the long-term study (2013-2021) did not show significant changes, Fig 11. E, and broods were less likely to be found in anthropogenic habitat types, Fig. 11. F. The short-term studies revealed a positive relationship between brood abundance and potential prey abundance but no relationship with potential predation pressure, Fig. 11. G. Regarding the relationship between adult and brood abundance, the long-term study revealed no correlation across years (2013-2021), but a higher number of broods were located closer to points that had more adults. The same pattern was found during the short-term studies where brood abundance was partly explained by higher adult density during incubation, Fig. 11. H. Breeding success, expressed as the brood:pair ratio, was similar across different local breeding densities, Fig. 11. I. Finally, Whimbrel display behaviour was more frequent at low breeding density during pre-incubation.

The adult declines found here mirror the declines reported on the Eastern population of Whimbrels in Iceland (Lárusdóttir et al., 2019), and the declines of other wader species in Europe (Lindström et al., 2019; Smith et al., 2020). It is thus possible that this decline is driven by habitat loss and degradation in the Southern lowland basin, but other drivers like predation should not be ruled out. Brood abundance did not follow this negative trend probably due to the high environmental variability in the system for which many broods were produced in some years but not in others. However, detecting a trend for only eight years in such a variable time-series is challenging and has high risk of type II error. This result should therefore be interpreted with caution as it is not conclusive yet how much changes in productivity can and have contributed to the observed changes in adult density. Adult abundance was positively associated with higher habitat heterogeneity, a common pattern in other bird species (Berg, 1997; Elliott et al., 2019; Lorenzón et al., 2016) that could be mediated through higher invertebrate prey abundance or lower predation rates in more heterogenous areas (Jonsson et al., 2011). Despite this, broods did not occur more often in any specific habitat type within the surveyed transect, but they were less likely to be found in mixed forestry plantations, agricultural and domestic habitats (i.e.: gardens, fields, arable and agricultural land where perennial and annual crops are grown; Ottósson et al., 2016), strongly related to human presence. This may reflect the increase in human infrastructure during recent years in the southern lowland basin (Jóhannesdóttir et al., 2019) where densities of most waders are lower close to structures such as farms and forests (Pálsdóttir et al., 2022).

Adult Whimbrel abundance was higher in habitats of early and mid-stages of ecological succession, river plain and heathland, characterized by the mosaic vegetation structure. On the other hand, abundance was lowest in moss heath sites, characterized by a homogeneous and thick mat of moss and lichen covering the ground. Changes in abundance throughout the season followed the breeding phenology of the species, as abundance increased during pre-incubation to become stable after, and this was reflected in the species behaviour since frequency of displays varied with density and breeding season. Adult abundance increased during the pre-incubation period while Whimbrels arrived in Iceland and occupied their breeding territories. During this period, the aerial display behaviour was more frequent than during the rest of the season, especially at low conspecific density, suggesting that finding mates in these low-density areas may be challenging. Abundance became stable during incubation once egg laying started. However, the differences in abundance during incubation were not directly explained by the variation of potential prey abundance and potential predation pressure, the two components of habitat quality explored during the same period. At the same time, the frequency of the aerial display behaviour was generally low and similar across the Whimbrel breeding density gradient. During the post-incubation period which spanned from hatching to the end of the season, adult abundance decreased in moss heath but not in river plain and heathland habitats. These different trends could partly be explained by the higher detectability of the species during chick-rearing period, especially in areas of high adult abundance that produced more broods, but also suggest that river plain and heathland might be more valuable than other habitats during the final part of the breeding season when chicks are growing, and adults and fledged chicks are preparing for migration. On the other hand, variation in brood abundance was directly explained by differences in adult density during incubation and abundance of potential invertebrate prey during post-incubation. Hence, more broods were produced at higher adult densities and higher invertebrate abundance. However, breeding success was similar across the different Whimbrel densities. Finally, the aerial display behaviour during the final part of the breeding season, was once again, relatively low and similar across densities.

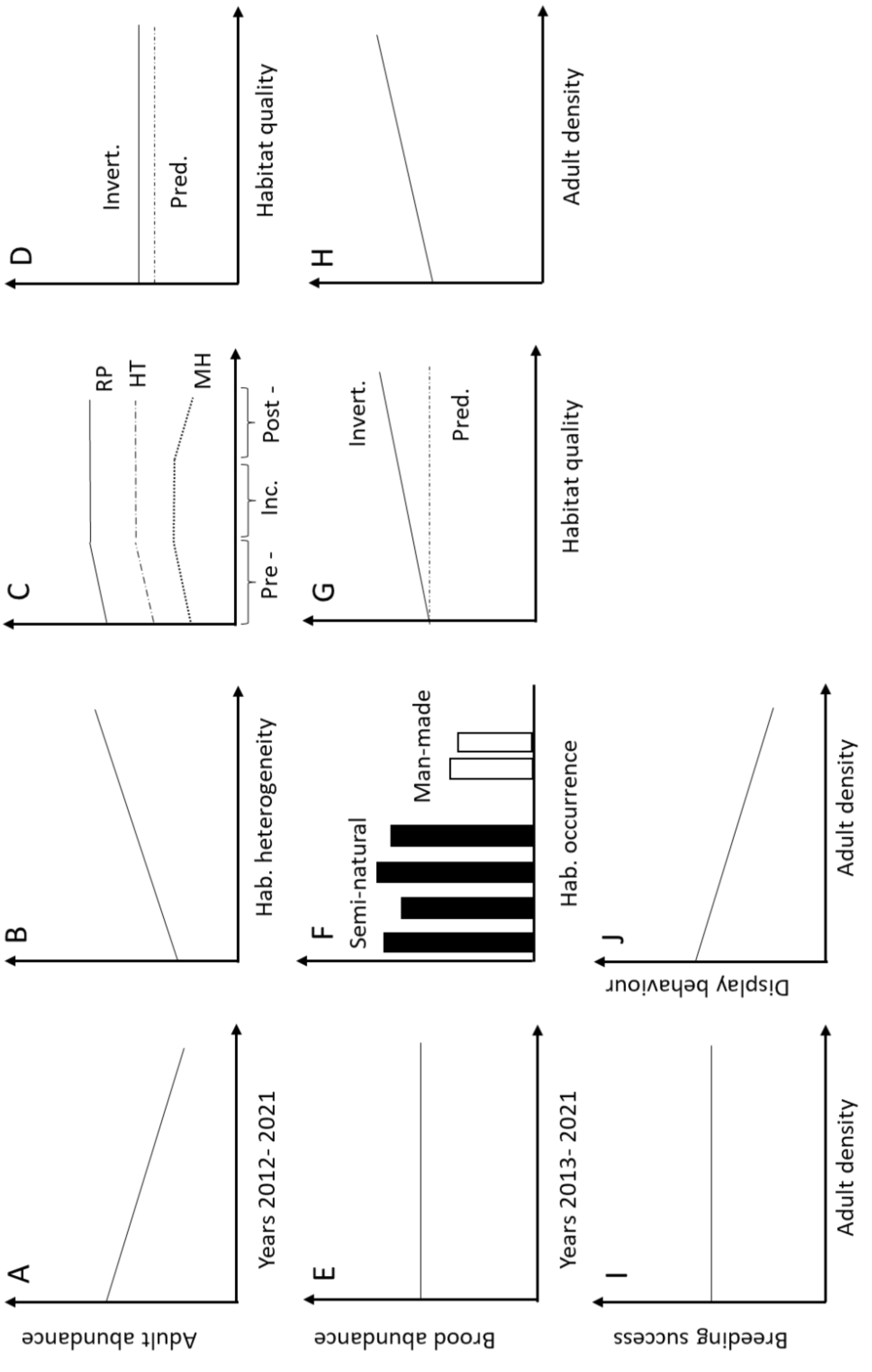


Figure 11. Schematic representation of the results found during this PhD thesis. A. Adult abundance decreased over time during a study performed along a 198 km road transect in south Iceland (Chapter I). B. Adult abundance was higher on points with higher habitat heterogeneity (Chapter I). C. Adult abundance increased during the beginning of the breeding season in three habitats of different ecological succession, to become stable during incubation. During post-incubation, adult abundance decreased in moss-heath habitat (Chapter II). D. Variation in adult abundance recorded at six different sites for

three years was not explained by differences in abundance of potential invertebrate prey or the number of potential predator intrusions (Chapter III). E. Brood abundance recorded along the 198 km road transect did not show a trend over the years of study (Chapter I). F. Broods occurred in a variety of semi-natural habitats but occurred less frequently than expected (given habitat availability) in habitats of anthropogenic origin (man-made; Chapter I). G. Brood abundance recorded at six sites for three years was higher on sites with higher invertebrate abundance but was similar across sites with varying in potential predation pressure (Chapter III). H. Brood abundance was partly explained by higher adult density during incubation (Chapter III). I. Breeding success expressed as the brood:pair ratio recorded for three years was similar across varying adult densities (Chapter III). J. Whimbrel aerial displays were more frequent at low adult density during pre-incubation period (Chapter IV).

The differences in adult and brood abundance between habitats found here may be explained by differences in one or more components of habitat quality like resource availability, combined with the philopatric nature of the species. Variation in local breeding densities can be maintained by the combination of more broods produced in areas of higher potential prey abundance during chick-rearing and subsequent philopatry (Gunnarsson et al., 2005a). Moreover, recent GPS tracking of breeding adults from two river plain sites of high density revealed frequent trips of adults outside of the breeding territories (Fig 12; Alves and Carneiro, *unpublished*), and these movements are likely to be foraging trips. This may further suggest that breeding sites may be selected based on benefits for raising chicks as adults are able to use resources outside of breeding territories. Regarding the aerial display behaviour, the higher frequency of this energetically demanding and honest signal during pre-breeding period and at low density suggests it might function for mate attraction while the displays performed throughout the rest of the season might function for resource defence, likely territories and/or mates. These results indicate that this behaviour is therefore context-dependent and pluripotent (Hebets et al., 2016).

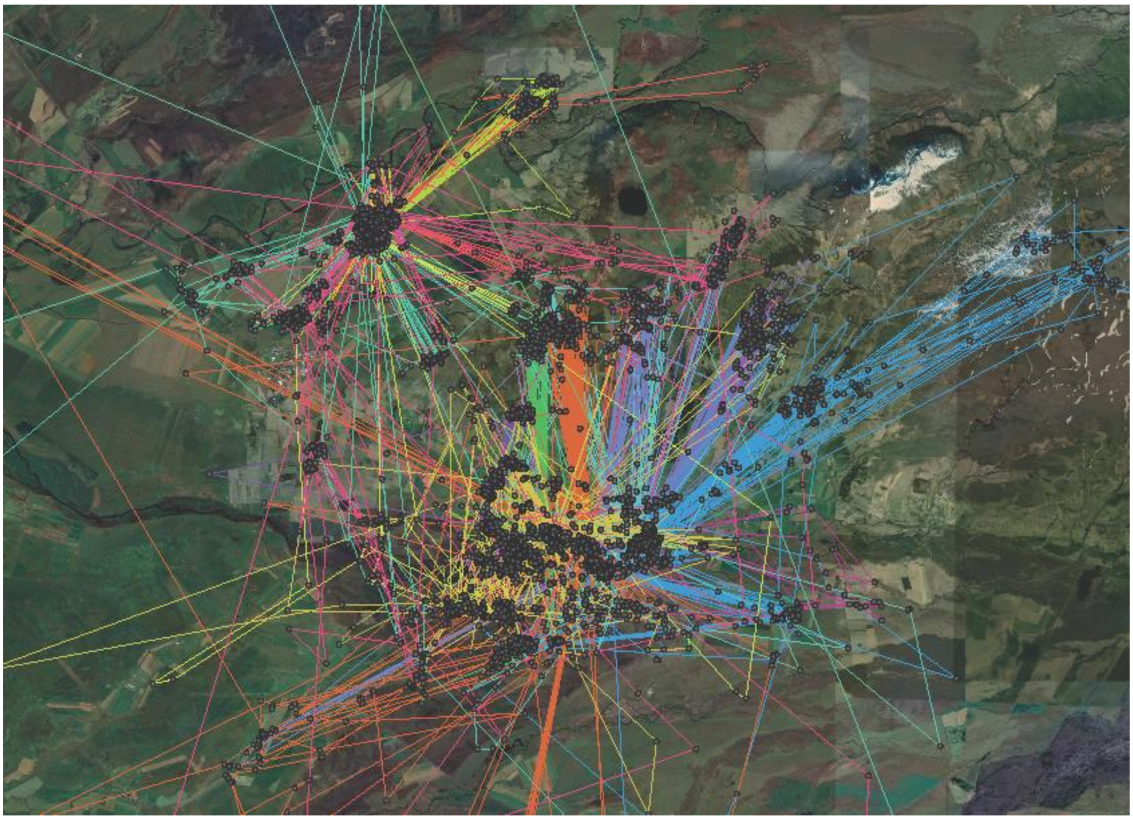


Figure 12. Individual GPS tracking data for 10 Whimbrels breeding on two river plain sites of high density during 2019. Grey circles indicate the location of individuals and coloured lines indicate movement between locations. Each individual is represented by a different colour. The two big central clusters of circles are the two breeding sites where Whimbrels were equipped with GPS transmitters, Rangá upper left, and Drumbabót, centre. Note the individual consistency in the use of areas outside of the breeding grounds. Trips can be up to 8 km in one direction away from the breeding location. Data from José Alves and Camilo Carneiro, unpublished.

Finally, the relationship between adult and brood abundance across the 198 km survey transect in South Iceland did not change significantly over time, but this relationship was subject to high risk of type II error. On a small spatial scale, points and sites with higher abundance of adults also had more broods, and this result was reported in both the long and the short-term studies. Bearing in mind the decrease in numbers during the post-breeding period in moss heath, with lowest Whimbrel abundance, but not on heathland and river plain habitats, this result emphasizes again the importance of these two habitats of higher adult density and of probably better quality than moss heath. Breeding success (brood:pair ratio) was similar across the varying Whimbrel adult density recorded during incubation indicating that the probability of raising a brood was similar across the range of densities studied. Despite this, the fact that Whimbrels systematically breed in highest numbers in river plains across Iceland (Gunnarsson 2000; Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Cerezo-Araujo et al., *under review*) is likely to have some fitness advantage. This may suggest that breeding success may be buffered through density dependence at higher adult densities, like the river plain sites studied here. If that is the case, this buffering could partly occur through attraction of predators to these areas (Page et al., 1983) and/or interference competition at high densities (Goss-Custard, 1980; Vahl et al., 2005 Møller et al., 2018) as described in other wader systems. Although potential predation pressure seemed to be similar across different adult densities, this result should be interpreted with caution as our methodology focused on diurnal events and captured mostly avian predators, and nocturnal predation may be important.

The variation in breeding density across the landscape can be maintained by more broods produced in areas of higher breeding density and the philopatry of the species, assuming that other, less known factors such as juvenile and adult survival during winter or across breeding habitats are similar. Similar apparent adult survival rates over time for Whimbrels breeding in Canada and for Whimbrels wintering in Chile have been reported (Andres et al., 2018; Ausems et al., 2023), and mortality along the Western Atlantic Flyway was higher during migration periods than during wintering or breeding (Watts et al., 2019). Following this, it is thus possible that resource limitation in the wintering and breeding grounds might not currently pose such a serious threat as for some other wader species (Rakhimberdiev et al., 2015). For Whimbrels using the East-Atlantic flyway, winter resource limitation in combination with a digestive bottleneck was proposed to condition pre-migration preparation in Mauritania (Zwarts & Dirksen, 1990; Zwarts, 1990), but the use of a new and abundant prey, the West African bloody cockle, might buffer this effect (Carneiro et al., 2017, 2019b). Despite this, it is currently unknown if winter resource limitation could be operating there or elsewhere.

Regarding survival across breeding habitats, two studies in Iceland reported similar return rates in two consecutive years within a river plain site with 42-46 pairs/km^2 and a moss-heat site with 5.7 pairs/km^2 (Gunnarsson 2000); and between river plain and grassland/heathland habitats with densities over 10 pairs/km^2 (Katrínardóttir et al., 2015). In a study in Canada, return rates were highest in hummock-bog habitats with ca. 10 pairs/km^2 when compared to sedge-meadow and heath-tundra habitats with 0.7 – 4.8 pairs/km^2 (Skeel, 1983). It is thus possible that survival across breeding habitats might be higher at high breeding density, as more adult Whimbrels seem to return to these areas of probably better quality, or philopatry to lower density sites is lower. In a related species in Iceland, the Black-tailed Godwit, individuals that occupied higher quality sites during the breeding season also did so in the wintering grounds, arrived earlier to Iceland and had higher reproductive success, highlighting the fitness consequences of site occupancy (Gunnarsson et al., 2005a; b).

Higher abundance of Whimbrels in river plain habitat has been consistently reported in Iceland and in this thesis (Gunnarsson, 2000; Gunnarsson et al., 2006; Katrínardóttir et al., 2015) and can be explained by the factors presented above (more food, more broods, more adults returning), but the mechanisms by which other individuals occupy apparently lower quality sites remains an open question. At very high densities such as in river plains, certain individuals returning to a high density and highly competitive site might be more likely to disperse (source) to sites of lower density and subsequent lower competition (sink) (Fretwell and Lucas 1969; Pulliam 1991). Such a pattern has been suggested for Icelandic Black-tailed Godwits where certain phenotypes are found more often on lower quality sites (Gunnarsson et al., 2012), and other wader systems (Méndez et al., 2018b).

The process of both juvenile and adult dispersal is generally poorly known in waders, including this system, but it can be a key factor regulating local densities. Dispersal in waders is more frequent in females while breeding site fidelity is often male-biased (Jackson, 1994; Tomkovich & Soloviev, 1994; Stenzel et al., 2007; Gunnarsson et al., 2012; Cimiotti et al., 2023; Sandercock & Gratto-Trevor, 2023), and some studies suggested that high breeding success and site-familiarity were the reasons behind low dispersal for some populations (Jackson, 1994; Klima & Johnson, 2005). Since Whimbrels are on a tight schedule to initiate breeding (Gunnarsson et al., 2010; Carneiro et al., 2019b), adult dispersal should be a rather fast process. However, given the high philopatry and the low inter-annual dispersal rates for adult Whimbrels reported in other studies in sub-Arctic Canada (Skeel 1983; Ausems et al., 2023) dispersal might be more common at the juvenile stage. If such is the case, juveniles could potentially spend more time prospecting for potential sites before settling. If a site becomes saturated and some individuals are forced to move, dispersal might be facilitated by using conspecifics as a cue to assess the suitability of potential sites (Cunningham et al., 2016; Gill, 2019; Swift et al., 2023), on the basis that successful breeders are more likely to return to a site (Jackson, 1994; van Leeuwen & Jamieson, 2018), and density in some natal-philopatric species can be related to breeding success (Swift et al., 2023).

The use of conspecific cues has been previously described for waders (Cunningham et al., 2016; Swift et al., 2023) although it might also pose a risk. High breeding densities might have negative consequences on nest survival and breeding output through attraction of predators (Page et al., 1983; Møller et al., 2018; Ellis et al., 2020; Freeman et al., 2023), as it may apply to Whimbrels in favoured habitats which do not appear to have higher breeding success than Whimbrels breeding at lower densities. At the same time, individuals breeding at higher densities could benefit through collective predator defence as has been reported in several studies of other wader species (Berg, 1996; Soloviev & Tomkovich, 1998; Valkama et al., 1999; Hotker, 2000; Šálek & Šmilauer, 2002; Macdonald & Bolton, 2008; Wilde et al., 2022). In this case, both points might be true, and despite breeding success in high density sites potentially being buffered, nesting close to conspecifics probably facilitates defence against intruding predators, especially of avian species like Raven and Skua.

The knowledge gained from this thesis, added to the previous studies of Whimbrels in Iceland, hints that breeding success may be density dependent given the similar probability of raising a brood across adult breeding densities. Such a scenario could operate either through some mechanisms reducing breeding success at high densities such as attraction of predators, or through interference competition and resource depletion at high quality sites forcing individuals to occupy lower quality areas. This thesis reflects a common scenario in studies of wild populations, in which density dependence is often a complex process challenging to detect and might be masked by feedback processes (Freckleton et al., 2006; Herrando-Pérez et al., 2012; Catlin et al., 2019).

Final remarks and future perspective for Whimbrels in Iceland

Understanding population regulation of a species presents many challenges. Regulation can occur through different mechanisms, at different stages of the life cycle and at different locations, and habitats especially if the species in focus occupies several geographically distant areas (Rodenhouse et al., 2003; Kim et al., 2009; Rakhimberdiev et al., 2015). Alongside the regulatory processes occurring at a specific space and time, their interplay at different scales should also be considered. For instance, different mechanisms can act on a demographic rate, with a different effect depending on the age of the individual, which will have consequences on individual fitness in the next season or location (Gunnarsson et al., 2005a; b; Ratikainen et al., 2008). Thus, detecting when and where regulatory mechanisms operate is key (Morrison et al., 2016). Habitat loss, food-web changes and trophic mismatches have been recognized as important factors driving wader populations (Meltofte et al., 2007; Sutherland et al., 2012), and some studies have been able to detect the effects that changes in these factors can have in populations over time and space (Aharon-Rotman et al., 2015; Rakhimberdiev et al., 2015; Van Gils et al., 2016; Machín et al., 2019). Under the current climate crisis, these regulatory mechanisms and their interactions are changing with consequences for the demography of species (Post et al., 2009). Some will be able to respond and benefit from these changes, but those showing less plasticity will suffer the most.

Warming temperatures and more intense weather events are predicted to affect Arctic and sub-Arctic regions similarly, but increased precipitation and snowfall will be especially harsh in the sub-Arctic (Popova, 2004; Saha et al., 2006; Serreze et al., 2007; IPCC, 2014; Post et al., 2019). For species breeding in sub-Arctic areas with a slightly longer summer season than in the Arctic, this can result in, for example, changes in the duration of the breeding season, and trophic mismatches. These changes have the potential to affect productivity and resource availability for migratory birds unable to track environmental changes and respond to them. For Whimbrels in particular, it is difficult to assess the consequences of these changes, although some studies have given some insights (Ballantyne & Nol, 2011; Carneiro et al., 2019b). In Iceland, although food-web changes might not be as problematic as in mainland countries where predators are expanding their range, habitat loss in lowland areas is a pressing reality (Jóhannesdóttir et al., 2018; Pálsdóttir et al., 2022) and will likely be the most problematic factor for survival of Whimbrels and other waders in near future. Current national plans involve agricultural expansion in the lowlands, infrastructure development, and introduction of woody species for economic purposes (Jóhannesdóttir et al., 2017; Pálsdóttir et al., 2022). Although under an increased human population these plans seem inevitable, effective planning to avoid human-wildlife conflicts and protect native species should be a priority. Considering the population trends of Icelandic Whimbrels in particular and Icelandic waders in general, these results could be incorporated in landscape planning and conservation decisions, as this will be imperative for the global future of Whimbrels.

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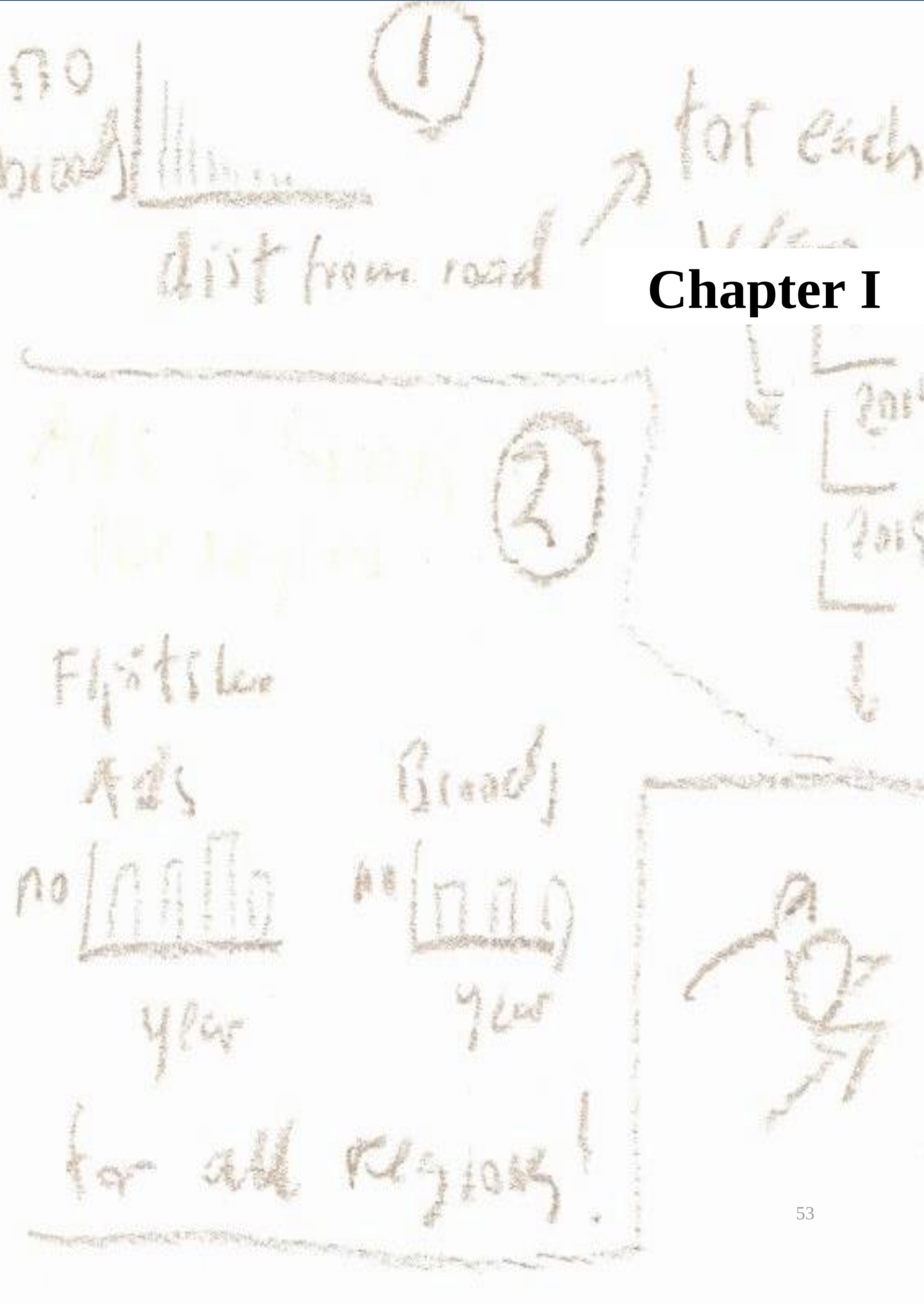
Chapter I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Chapter I. Annual and spatial variation in adult and brood abundance in a sub-Arctic wader

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Summary

Capsule: Adult Whimbrel (*Numenius phaeopus*) numbers declined steeply across Iceland's largest lowland basin during 2012-2021 but brood abundance during 2013-2021 did not. Sites with more adults generally held more broods.

Aims: Many Arctic breeding wader species are experiencing population declines and gaining a better understanding of how habitats and demography interplay in driving the dynamics of wader populations is imperative. We investigated temporal and spatial variation in adult and brood abundance (a proxy for productivity), and habitat associations of adults and broods in a sub-Arctic wader to assess whether sites holding more adults were also more productive.

Methods: Temporal and spatial variation in the abundance of Whimbrels were analysed using generalized linear models in an 11-year dataset of adult counts and a 9-year dataset of brood counts, collected in a road-based survey across Iceland's largest lowland region.

Results: We found a strong adult population decline but no trend in brood abundance which showed high annual variation. Both adults and broods occurred in a range of semi-natural habitats, and broods occurred less frequently in cultivated, built-up and forested habitats than expected by chance. More broods were associated with survey points with higher adult abundance suggesting the same sites both hold more adults and are more productive.

Conclusions: Spatial variation in brood abundance is largely a proximate product of local adult abundance whereas its temporal variation seems strongly affected by annual environmental conditions. Incorporating such results into landscape planning and prioritising habitats for conservation where adults are more abundant should also favour more productive sites in this population.

Keywords

Shorebird; Icelandic Whimbrel; Broods; Density; Habitat occurrence; Productivity

Introduction

Biodiversity has seen a rapid decline since 1970 (WWF, 2022) and two of its key drivers are climate change and anthropogenic habitat conversion (Leclère et al., 2020). These factors often work simultaneously leading to declining populations, higher species extinction risk, and changes to ecosystem functioning (Newbold et al., 2015). Arctic and sub-Arctic regions are especially sensitive to these threats and are currently experiencing climate change at an intensity of twofold the global average (Collins et al., 2014), threatening many migratory species by reducing the quantity and quality of the remaining breeding habitats (Hof et al., 2017). Prioritizing habitats and sites for conservation is therefore more urgent than ever in these regions under the current environmental crisis.

It is often assumed that sites and habitats hosting more adult individuals of a given species are of higher quality and thus these sites are generally designated for protection (Van Horne 1983; Méndez et al., 2018a). Despite this being a common practice, sometimes the number of individuals (e.g., breeding adults) may be a misleading indicator of site importance or habitat quality, as abundance may not always be positively correlated with demographic parameters (Battin 2004; Johnson 2007; Bock and Jones 2012). A mismatch between abundance and demography can occur through several processes such as density dependence (Van Horne, 1983; Rodenhouse et al., 2003), legacy effects (Cuddington, 2011) or when sites function as ecological traps (Gilroy & Sutherland, 2007).

In bird populations a positive relationship between adult abundance and productivity is often found due to preference for certain habitats whose characteristics such as food or territories, maximize individual fitness (Johnson, 2007). However, this relationship is less common in degraded and fragmented landscapes or under strong anthropogenic influence where birds might fail to correctly recognize optimum habitats (Bock & Jones, 2012). Understanding habitat preference and its relationship with demography is therefore key to inform management decisions (Kneib et al., 2011), as it can unravel the role of specific habitats and their features on species abundance and productivity and ultimately on population regulation. Successful prioritization of sites for conservation should thus be based on the study of different demographic parameters and ideally, across the range of abundance occurring within populations over multiple habitats. This could be highly relevant as the relationship between abundance and demographic parameters may vary across the gradient of abundance and habitats of different quality (Bock & Jones, 2012). Furthermore, large temporal variation in abundance and demography is often found in populations (Blomqvist et al., 2002; Beale et al., 2006; Meltofte et al., 2019), hence the robust inference needed to prioritize habitats and sites for conservation should ideally rely on studies which span enough time to provide meaningful information about the demography of the focal species.

Wader species dominate the Arctic terrestrial bird guild, comprising 47% of the breeding bird species (Smith et al., 2020) and are key indicators of changes in those ecosystems (Zöckler et al., 2012). Population declines have been reported for half of the Arctic breeding waders (International Wader Study Group 2003; Meltofte et al., 2007; Rosenberg et al., 2019) due to several threats such as climate change, increased human disturbance, habitat loss and degradation (Pearce-Higgins et al., 2017, Murray et al., 2017, Møller et al., 2018). Within waders, the Numeniini tribe is especially threatened, and half of the species are of conservation concern (Pearce-Higgins et al., 2017). Particularly, the large bodied, long distance migrants, and habitat specialists that have slow generation time, are currently facing negative population trends and are exposed to higher extinction risk (Pearce-Higgins et al., 2017). Several species of this tribe breed in remote Arctic and sub-Arctic regions, which are logistically challenging to survey (Zöckler et al., 2003; Lindström et al., 2015). Due to this, most studies at high latitudes are either focused on migration or localized in time and space and cover limited areas (Lindström et al., 2015). This highlights the need for longer-term studies of demography in such breeding areas, ideally covering a gradient of abundances and different habitats. Such studies can address knowledge gaps in understanding the relationships between abundance and demography at conservation-relevant scales for waders. Although programmes monitoring variation in abundance and important demographic rates across a large scale exist for many avian groups (MAPS Programmemes at The Institute of Birds Populations; Pan European Common Bird Monitoring Scheme, PECBMS; UK Breeding Bird Survey), most of them do not focus specifically on waders.

Iceland, a sub-Arctic island, is one of the most important wader breeding grounds in Europe (Jóhannesdóttir et al., 2014). It hosts internationally important populations of several species, among them, a large part of the world population of Whimbrels (*Numenius phaeopus*), with the Icelandic population (*islandicus* subspecies) estimated at 400,000-500,000 individuals and representing ca. 40% of the global population of this subspecies (Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Skarphéðinsson et al., 2016). Whimbrels are long-lived, highly territorial and philopatric birds (Klima et al., 2013; Mallory, 1982; Skeel, 1983). A stable population trend was reported for the *islandicus* subspecies a decade ago based on limited data (Delany et al., 2009), but negative trends have been reported in more recent studies in Fennoscandia (Lindström et al., 2019). This long-distance migrant winters on the west African coast and spends the summer months mainly in the Icelandic lowlands (Alves et al., 2016, Carneiro et al., 2019). There, it breeds on a gradient of abundance across a fine-scale mosaic of different semi-natural open habitats (Gunnarsson et al., 2006), like heathlands, river plains and moss fields, with river plains generally supporting the highest densities (Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Cerezo-Araujo et al., *under review*). Despite some broad habitat types being identified as important, the intricate habitat structure present in the lowlands suggests that Whimbrels might respond to ground-cover characteristics at a smaller patch scale and to the surrounding habitat composition, as habitat heterogeneity can be a strong driver of biodiversity variation (Benton et al., 2003; Durant et al., 2008; Jóhannesdóttir et al., 2019). In the Icelandic lowlands, large wader populations have co-existed with low-intensity agriculture, suitable grazing regimes, relatively small human population and little infrastructure (Jóhannesdóttir et al., 2018, 2019). However, land-use patterns have rapidly changed during the last three decades. Increasing human population, agricultural expansion, a rising number of settlements and accompanying infrastructure, such as roads and power lines, and habitat transformation, like wetland drainage and afforestation, have occurred with unforeseen changes to Icelandic wader populations (Jóhannesdóttir et al., 2014; Gunnarsson 2020; Pálsdóttir et al., 2022a; Pálsdóttir et al., 2022b).

The unusual conditions found in Iceland, where Whimbrels occur on a gradient of breeding abundance (Gunnarsson et al., 2006), coupled with the fact that this species belongs to a group with declining populations across all flyways (Smith et al., 2020), provides an urgent opportunity to study the links between abundance and demography in this population. The aims of this study were to (i) quantify recent trends in adult abundance and brood abundance (an index of productivity), (ii) identify links between habitats and abundance of adults and broods and (iii) explore the relationship between adult abundance and brood abundance to assess whether sites holding more adults are also likely to be more productive. We did so by analyzing 11 and 9 years of data on adult abundance and brood abundance respectively, in the southern lowlands of Iceland, the single most important area for breeding Whimbrels in this country and a global stronghold for the species (Gunnarsson et al., 2006; Katrínardóttir et al., 2015).

Material and methods

Study area

The study was carried out in lowland South Iceland, the largest lowland basin in the country (Fig. 1). The region is characterized by a fine-grained mosaic of semi-natural habitats, such as damp and saturated wetlands, grasslands, heathlands, sparsely vegetated land and agricultural land of which over 90% are hayfields (Jóhannesdóttir et al., 2018, 2019).

Annual surveys of breeding adults

The annual variation in adult abundance was assessed at 63 fixed points (adult points hereafter) with unique ID (point ID) on a 198 km transect along tracks and roads in the eastern half of the southern lowlands (Fig. 1). The survey was road-based to cover as large an area as possible during the same part of the breeding season. Surveying was paused when cars passed to ensure detectability, and traffic volume was generally light (Table S1) compared to international standards (Pálsdóttir 2022). The surveys took place during the last 10 days of June 2011–2021 coinciding with late incubation of Whimbrels (Gunnarsson 2010), and spanned on average 4.0 days ± 1.12 SD (mean date: 24 June). Point counts were made along the road transect at every 3 km (Fig. 1). At each point the car was stopped, the observer exited the car, and all birds within 200 m of the observer were counted from the verge of the road or track for five minutes, and the distance from the observer to the birds was measured using a laser range finder. Fieldwork was conducted in dry conditions and at windspeeds below 7 m/s, and the same observer counted birds in all the years.

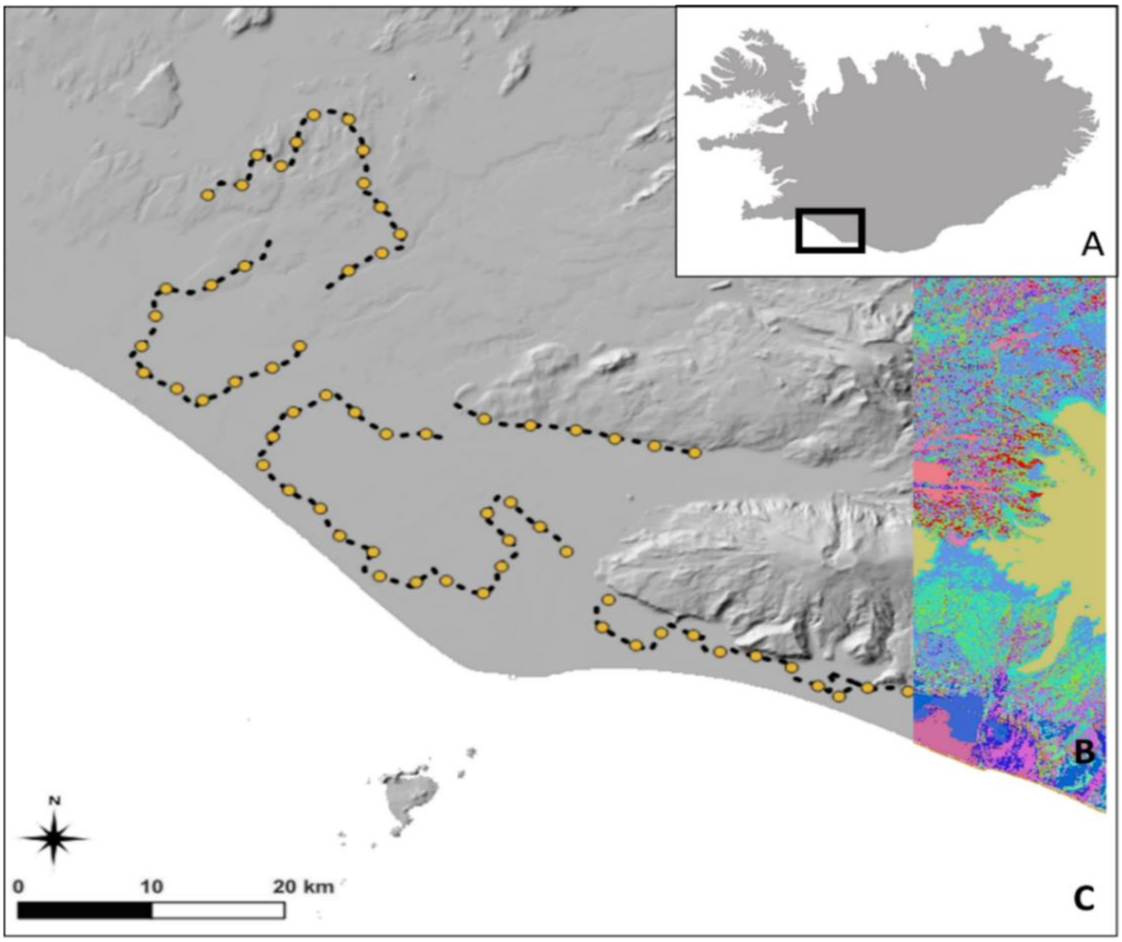


Figure 1. Map of Iceland showing the position of the study area (A), example of the fine grain mosaic of habitats (Icelandic Institute of Natural History, Ottósson et al., 2016) (B), and the study area (C). The annual survey of adult abundance (2012-2021) was carried out on 63 fixed points (yellow dots) along the road transect (dashed line) in the lowland plains of South Iceland in late June. Broods were recorded all along this transect line annually between 2013-2021 in late July (see methods for details).

Annual surveys of broods

Annual number of broods (brood abundance) along the road transect was used as a proxy for variation in annual productivity. Small and cryptic wader chicks can be especially challenging to detect when they hide or lay still as a response to disturbances or parental behaviour (Jarret et al., 2023). Therefore, brood abundance offers a conservative yet robust and less time-consuming alternative to other methods (e.g., brood fate of individual pairs). Previous studies of several large waders, including Whimbrels, used strongly alarming adults as a robust indicator of the presence of one or more chicks, hence each strongly alarming pair or individual was considered to indicate the presence of a brood (Brown & Shepherd, 1993; Grant et al., 2000; Gunnarsson et al., 2005; Bolton et al., 2012; Katrínardóttir et al., 2015; Gunnarsson et al., 2017; Baines et al., 2022; Bowgen et al., 2022; Douglas et al., 2023). Whimbrels, as many other large waders breeding in open habitats, are feisty during the chick-rearing period (Larsen et al., 1996) and perform noisy and conspicuous alarm behaviour near their chicks. Moreover, they often perch on fenceposts and other elevated positions, or run around the intruder, indicating the presence of young (Gunnarsson et al., 2005). Alarming and protective behaviour of adults can be assumed to be costly, both in terms of energy spent and risk, and is hence very unlikely to be undertaken without chick presence in most cases. The surveys occurred on the same road transect where adults were surveyed during the last 10 days of July, when most eggs have hatched (mean survey date: 23 July, mean survey duration: 2.3 days ± 0.66 SD) from 2013 to 2021. Instead of stopping at pre-determined intervals and exiting the car as in the adult survey, all broods located along the transect were recorded from the vehicle. This survey method is likely to provide a minimum estimate of the broods actually present, but as this was done consistently and in the same manner in all years, it still confers a robust estimate.

The car was driven at a maximum speed of 25 km/h, usually slower, with open windows to aid the detection of alarm calls. In every instance an alert or alarming Whimbrel was detected, the car was stopped. As in Gunnarsson et al., 2017, we estimated the position of the broods using the GPS coordinates of the car on the road, the bearing, and the perpendicular distance from the car to the broods with a laser rangefinder. When chicks were not detected, we measured the distance from the car to the midpoint between an alarming pair or the distance to a single alarming adult. Alarming Whimbrels are easily detected in the open landscapes and all families were located within 200 m from the road. The total number of broods recorded along the transect (visually detected or assumed given adult behavior) was used as an estimate of annual productivity.

Data analysis

Data analysis and visualization was performed in R v.4.1.1 (R Core Team 2021). All models were validated by inspecting QQ plots, residuals, dispersion and fitted values (package DHARMa v.0.4.6, Hartig and Lohse 2022). Model results were reported using a gradual language of evidence as proposed by Muff et al., 2021. Accordingly, p-values below 0.001 indicated very strong evidence of the effect of the explanatory variable(s) on the response variable, while p-values above 0.05 were interpreted as having little evidence supporting a relationship.

Variation in adult abundance over time and in relation to habitat heterogeneity

To investigate the variation in adult abundance (Number of Adults) over time and across a gradient of habitat heterogeneity, we used generalized linear mixed effect models with Poisson error distribution and logit-link function (GLMM, R package *lmer4* v1.1-33, Bates et al., 2017). Year (2012 to 2021) and Habitat heterogeneity per point were included in the model as continuous explanatory variables. Traffic volume in log scale, was included in the model as it can affect the abundance of some waders close to roads (Pálsdóttir 2022). Year 2011 was excluded due to a volcanic eruption in May which temporarily affected breeding wader populations in the region causing unusually low breeding success and detectability (Katrínardóttir et al., 2015; Gunnarsson et al., 2017). To calculate habitat heterogeneity, we first extracted information on the proportions of each habitat type covering the 200 m buffer where adults were counted for each point (R package *terra* v1.7-29, Hijmans et al., 2021; Fig. S1; Table S2). This information was extracted from the most up-to-date land cover database available for the country (Icelandic Institute of Natural History, Ottósson et al., 2016), which uses a classification of terrestrial habitat types based on the EUNIS system (Ottósson et al., 2016). We then calculated Habitat heterogeneity for each adult point using the Shannon-Wiener index (R package *vegan* v2.6-4; Dixon, 2003; Fig. S1). Traffic volume was obtained from the Icelandic Road and Coastal Administration (IRCA; information retrieved in 2022) from which data was available as the mean number of cars/day for the summer months June to September combined. Point ID was included as random term to account for non-independence among counts on the same points. Finally, to further explore the relationship between Habitat heterogeneity and habitat type, we performed Pearson correlation tests on those habitats which cover the highest proportion (4%) of the buffer (Fig. S2).

Variation in brood abundance over time and habitat occurrence by broods

In order to investigate variation in brood abundance over time, we modelled Number of Broods (as a proxy for productivity) as a function of Year (2013-2021) and Traffic volume on the road sections where broods were recorded, both as continuous variables, using a GLMM with Poisson error distribution and a logit-link function. Road section was included in the model as random factor.

To investigate which habitats along the transect broods were most likely to occur in (habitat occurrence) we compared the habitat where broods were located (i.e., habitat used) with the habitat profile available along the road transect. To calculate the habitat profile, we first created 1000 random points along the transect and within 200 m from the roads and tracks, the maximum distance within which broods were detected during the annual survey. Then, we extracted habitat information from the Icelandic Institute of Natural History relative to these positions (Ottósson et al., 2016). After this, we compared the habitat used with the habitat available using Manly's selection ratios for design I (population level, Manly et al., 2002) which tests the random use of habitats with an overall test statistic (log-likelihood χ^2), and then compares the mean proportion of each habitat type where broods occurred to habitat availability at random points along the transect (R package adehabitatHS v0.3.17, Calenge, 2011). Due to the small-scale mosaic of the focal landscapes, we selected points at random to capture the habitat availability reasonably well without excessive sampling.

Relationship between brood abundance and adult abundance

To test whether brood abundance was related to adult abundance at the landscape scale across years we used a GLM (R package *stats,* R Core Team 2021) with Poisson error distribution and logit-link function, where Number of Broods per year was included as a response variable and Number of Adults per year and Year (continuous) were included as the explanatory variables.

To examine whether brood abundance was related to adult abundance at a local scale (i.e., per point), we combined both datasets by calculating the nearest adult point for each brood observation. To merge these two datasets, we associated each brood observation with the nearest adult survey point, to explore whether the number of adults counted at each point is related to the number of broods found closer to that point than to other points. As the association between the two datasets depends both on spatial congruence which decreases as broods further away from the adult point are included, and on sample size which increases when more broods further away from the adult point are included, we explored the effect of including broods at different distances from adult points. We first included only broods within the range of an adult point (200 m) but given the small sample size of broods per point (most points had either 0 or one brood for the different years, and only eight points had two broods), we expanded the inclusion distance between adult points and brood locations to include broods within 300 m, 500 m, 1000 m, 1500 m (the midway distance between two consecutive points), and 2000 m (which included all broods as six broods at the ends of transects were > 1500 m away) from an adult point (Table S3). We then compared the model fits and as the model at 2000 m explained most of the variation in the data and had the best model fit (Fig. S3), we included all the broods observed based on this result, independently of the distance to an adult point. In this finer spatial analysis, we used a GLMM with Poisson error distribution (R package *lmer4* v.1.1-33, Bates et al., 2017) and logit-link function with Number of Broods per point as response variable. Number of Adults per point and Year (continuous, 2013-2021) were included as explanatory variables, and Point ID as a random term.

Results

Variation in adult abundance over time and in relation to habitat heterogeneity

The mean number of adult Whimbrels recorded per year was 76.3 ± 5.82 SE for the period 2012 – 2021. The highest number of adults recorded in a year was 110 individuals in 2013, and the lowest, 54 individuals, was recorded in 2018 (Fig. 2). The Shannon-Wiener values (indicating habitat heterogeneity) for the adult points ranged from 0.18 to 2.21. A total of 38 different habitats were present within the surveyed adult points (Fig. S1). The mean number of different habitats within a point was 10.01 (± 0.5 SE) and ranged from 2 – 17 (Fig. S1). None of the adult points were covered by a unique habitat type, but Agricultural and domestic habitat dominated the total cover when all points were combined (L14.2, 38.7%), followed by Boreo-subalpine *Agrostis* grasslands (L9.6, 18.3%) and Oroboreal willow scrub (L10.10, 6.4%, Fig. S2). We found very strong evidence for a decrease in adult abundance during the time period of the study (Fig. 2; Table 1A), and for higher adult abundance on points with more heterogenous habitat (Fig 3.A, Table 1A). Further exploration of the association between habitat characteristics revealed a negative relationship between habitat heterogeneity and proportion of Agricultural and domestic habitat (L14.2) cover per point ($r= -0.63$, $p< 0.001$; Fig. S2), and a positive relationship between habitat heterogeneity and Oroboreal willow scrub (L10.10, $r= 0.31$, $p< 0.001$; Fig. S2), Boreo-subalpine *Agrostis* grasslands (L9.6, $r = 0.09$, $p = 0.01$; Fig. S2) and Icelandic *Festuca* grasslands (L9.5, $r= 0.16$, $p< 0.001$; Fig. S2). Finally, traffic volume ranged from 15 – 4402 cars/day during the summer months, and only seven points were located along roads with high traffic (> 2900 cars/day, Table S1). We found little evidence for an effect of traffic volume on adult abundance per point, although a tendency for a negative relationship could be observed in the model output (Table 1A).

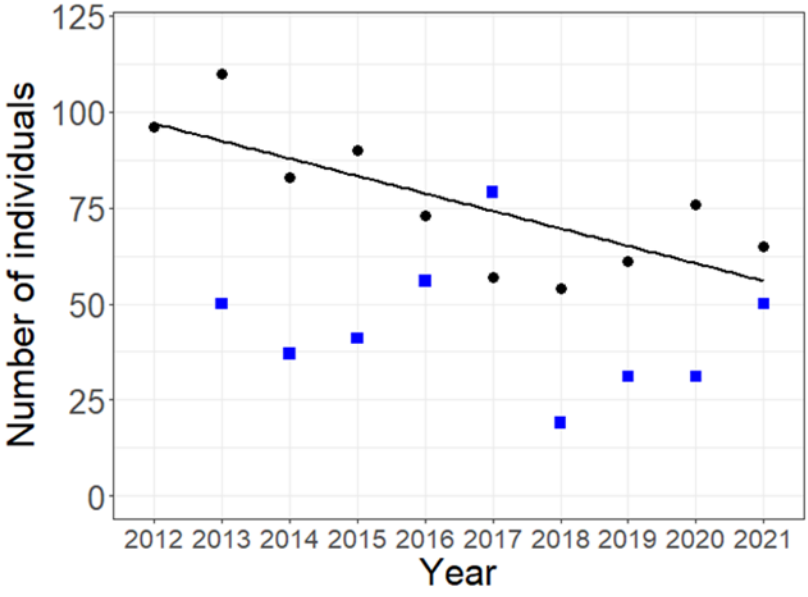


Figure 2. Annual variation in adult abundance and brood abundance (productivity). Black dots and black solid line: total number of adults 2012- 2021 on 63 survey points. Blue squares: total number of broods 2013 – 2021 along a 198 km road transect. Statistical results are shown in Table 2.

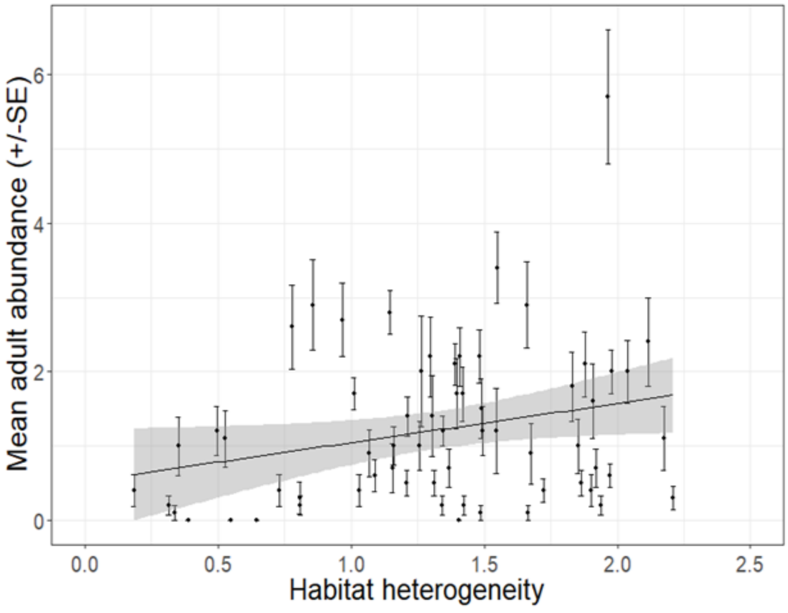


Figure 3. Effect of habitat heterogeneity expressed as the Shannon-Wiener index on mean abundance of adults/year (±SE) on each surveyed point. The straight line represents the regression line and the shaded area the standard error associated to it.

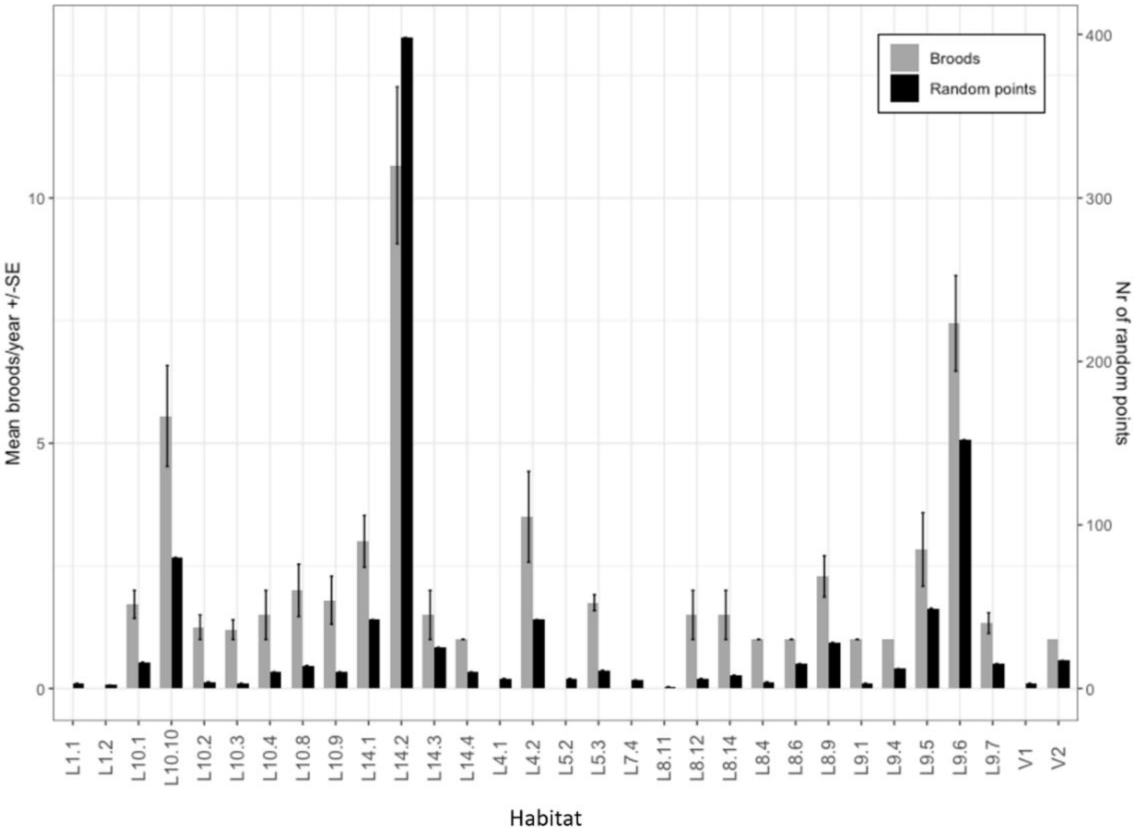
Table 1. Results from two generalized linear mixed effect models (GLMM): A. Effect of Year, Traffic volume in log scale, and Habitat heterogeneity (Shannon-Wiener index) on abundance of adults recorded during the annual surveys 2012 to 2021. B. Effect of Year and Traffic volume in log scale on brood abundance (productivity) recorded from 2013 to 2021. Significant results are shown in bold.

Fixed effects:	**A. Adult abundance (2012-2021)**				**B. Brood abundance (2013-2021)**			
	Estimate	**SE**	**Z**	**p**	**Estimate**	**SE**	**Z**	**p**
(Intercept)	0.132	0.523	0.252	0.801	31.283	40.677	0.769	0.442
Year	-0.057	0.013	-4.436	**< 0.001**	-0.015	0.020	-0.741	0.459
Traffic volume (log)	-0.151	0.079	-1.914	0.056	-0.064	0.070	-0.910	0.363
Habitat heterogeneity	0.578	0.248	2.333	**0.020**	*na*	*na*	*na*	*na*
Random effects:	**Variance**	**SE**	**Groups**			**Variance**	**SE**	**Groups**
Point ID	0.819	0.905	63		Road section	0.1551	0.3938	27
Number of observations: 630					Number of observations: 152			

Variation in brood abundance over time and habitat occurrence of broods

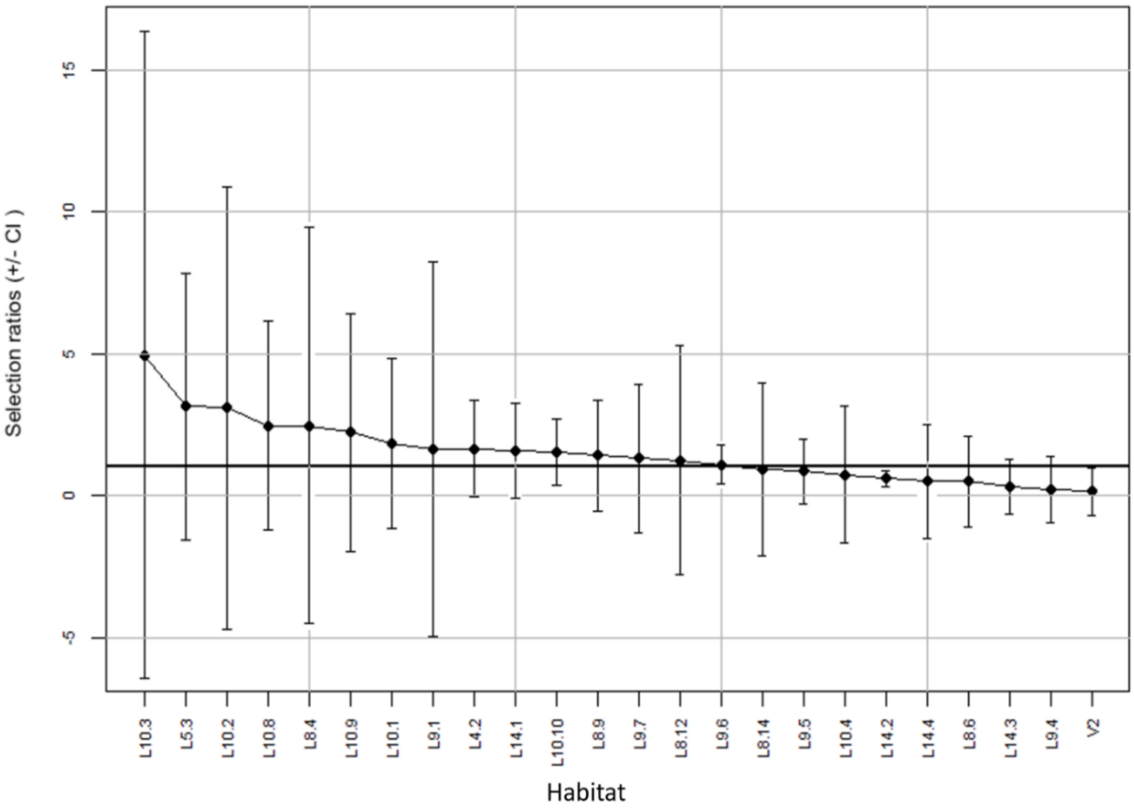
A total of 394 broods were detected during the study period, and at least one chick was observed in 47% of cases. Mean number of broods per year for the period 2013-2021 was 43 ±6.57 SE but brood numbers showed high annual variation (Fig. 2). Number of broods detected was lowest in 2018, with only 19 broods, and highest in 2017, with 79, and only 22 broods were recorded along road sections of high traffic volume (> 2900 cars/day, Table S1). Contrary to adult abundance, we did not find evidence for a trend in brood abundance over time nor at different volumes of traffic (Fig. 2; Table 1B).

Most broods were located in the same habitats where most random points occurred (Fig. 4). These were Oroboreal willow scrub, Agricultural and domestic habitats, and Boreo-subalpine *Agrostis* grasslands (L10.10, L14.2 and L9.6 respectively; Fig. 4; Fig. S2). The analysis of Selection ratios showed that broods occurred (Selection ratio > 1; Fig. 5; Table S4) in fifteen different habitats but did not occur significantly more often in any specific one (Fig. 5; Table S4). Eight habitats were used less often given their availability (Selection ratio < 1; Fig. 5; Table S4) and from these, broods occurred significantly less in Agricultural and domestic habitat, Mixed forestry plantations, and Running waters (L14.2, L14.3 and V2 respectively; Fig. 5; Table S4).



L1.1	Glacial moraines I	L5.3	Moss and lichen fjell fields
L1.2	Glacial moraines II	L7.4	Northern fixed grey dunes
L10.1	Icelandic *Racomitrium* grass heaths	L8.11	Common cotton-grass fens
L10.10	Oroboreal willow scrub	L8.12	Icelandic black sedge-brown moss fens
L10.2	Arctic *Dryas* heaths	L8.14	Icelandic *Carex lyngbyei* fens
L10.3	Icelandic *Carex bigelowii* heaths	L8.4	*Juncus arcticus* meadows
L10.4	Icelandic *Empetrum Thymus* grasslands	L8.6	Boreal black sedge-brown moss fens
L10.8	North Atlantic *Vaccinium-Empetrum-Racomitrium* heaths	L8.9	Icelandic black sedge-brown moss fens
L10.9	Icelandic *Salix lanata, S. phylicifolia* scrub	L9.1	Icelandic *Carex bigelowii* grasslands
L14.1	Constructed, industrial and other artificial habitats	L9.4	Boreal tufted hairgrass meadows
L14.2	Cultivated agricultural, horticultural and domestic habitats	L9.5	Icelandic *Festuca* grasslands
L14.3	Mixed forestry plantations	L9.6	Boreo-subalpine *Agrostis* grasslands
L4.1	Unvegetated or sparsely vegetated shores	L9.7	Northern boreal *Festuca* grasslands
L4.2	Icelandic braided river plains	V1	Standing waters
L5.2	Icelandic *Racomitrium ericoides* heaths	V2	Running waters

Figure 4. Comparison between brood occurrence in different habitats and the proportion of habitats available along the survey transect. Mean number of broods per year (±SE, grey), and total number of random points per habitat (black). Habitat names are shown below.



L10.3	Icelandic *Carex bigelowii* heaths	L9.7	Northern boreal *Festuca* grasslands
L5.3	Moss and lichen fjell fields	L8.12	Icelandic black sedge-brown moss fens
L10.2	Arctic *Dryas* heaths	L9.6	Boreo-subalpine *Agrostis* grasslands
L10.8	North Atlantic *Vaccinium-Empetrum-Racomitrium* heaths	L8.14	Icelandic *Carex lyngbyei* fens
L8.4	*Juncus arcticus* meadows	L9.5	Icelandic *Festuca* grasslands
L10.9	Icelandic *Salix lanata, S. phylicifolia* scrub	L10.4	Icelandic *Empetrum Thymus* grasslands
L10.1	Icelandic *Racomitrium* grass heaths	L14.2	Cultivated agricultural, horticultural and domestic habitats
L9.1	Icelandic *Carex bigelowii* grasslands	L14.4	Land reclamation forb fields
L4.2	Icelandic braided river plains	L8.6	Boreal black sedge-brown moss fens
L14.1	Constructed, industrial and other artificial habitats	L14.3	Mixed forestry plantations
L10.10	Oroboreal willow scrub	L9.4	Boreal tufted hairgrass meadows
L8.9	Icelandic black sedge-brown moss fens	V2	Running waters

Figure 5. Manly Selectivity measure comparing habitat used by broods and habitat available (random points). In those habitats with Selection ratios >1 (solid black line), broods occurred more frequently than expected given the availability, while in those habitats with Selection ratios < 1, broods occurred less frequently. Habitat names are shown below and statistical analysis is shown in Table S4.

Relationship between brood abundance and adult abundance

Mean distance between broods and the nearest adult point was on average 705.7 m (SE= 22.11 m, range: 14.77 m - 1994.5 m). We found no evidence to suggest that annual brood abundance in late July was related to the total number of adults recorded a month earlier at a landscape scale, and both the highest and lowest brood abundance were recorded during years of lowest adult abundance (Fig. 2; Fig. 6. A; Table 2. A). However, we found evidence indicating that brood abundance tended to be higher closer to points where adult abundance was also higher (Table 2.B; Fig. 6. B). Again, we did not find evidence supporting a temporal trend in the Number of broods per year nor in the Number of broods per point (Table 2.A and B).

Table 2. Results from GLMM's exploring A) the variation in annual brood abundance in relation to annual adult abundance over the whole study area and across years (broods per year), and B) spatial variation in brood abundance in relation to spatial variation in adult abundance per point and year (broods per survey point). Adult points with no broods associated were excluded. Significant results are shown in bold.

Fixed effect:	**A. Broods per year**			
	Estimate	**SE**	**Z**	**p**
(Intercept)	103.476	135.664	0.763	0.446
Total nr. of adults/year	-0.004	0.010	-0.435	0.663
Year	-0.049	0.067	-0.735	0.462

Number of observations: 11

	B. Broods per survey point (Point ID)			
	Estimate	**SE**	**Z**	**p**
(Intercept)	31.227	39.995	0.781	0.435
Nr. adults/Point ID	0.119	0.036	3.324	**< 0.001**
Year	-0.016	0.020	-0.799	0.424
Random effects:	**Variance**	**Std Deviation**		
Point ID, 63 groups	0.522	0.722		

Number of observations: 567

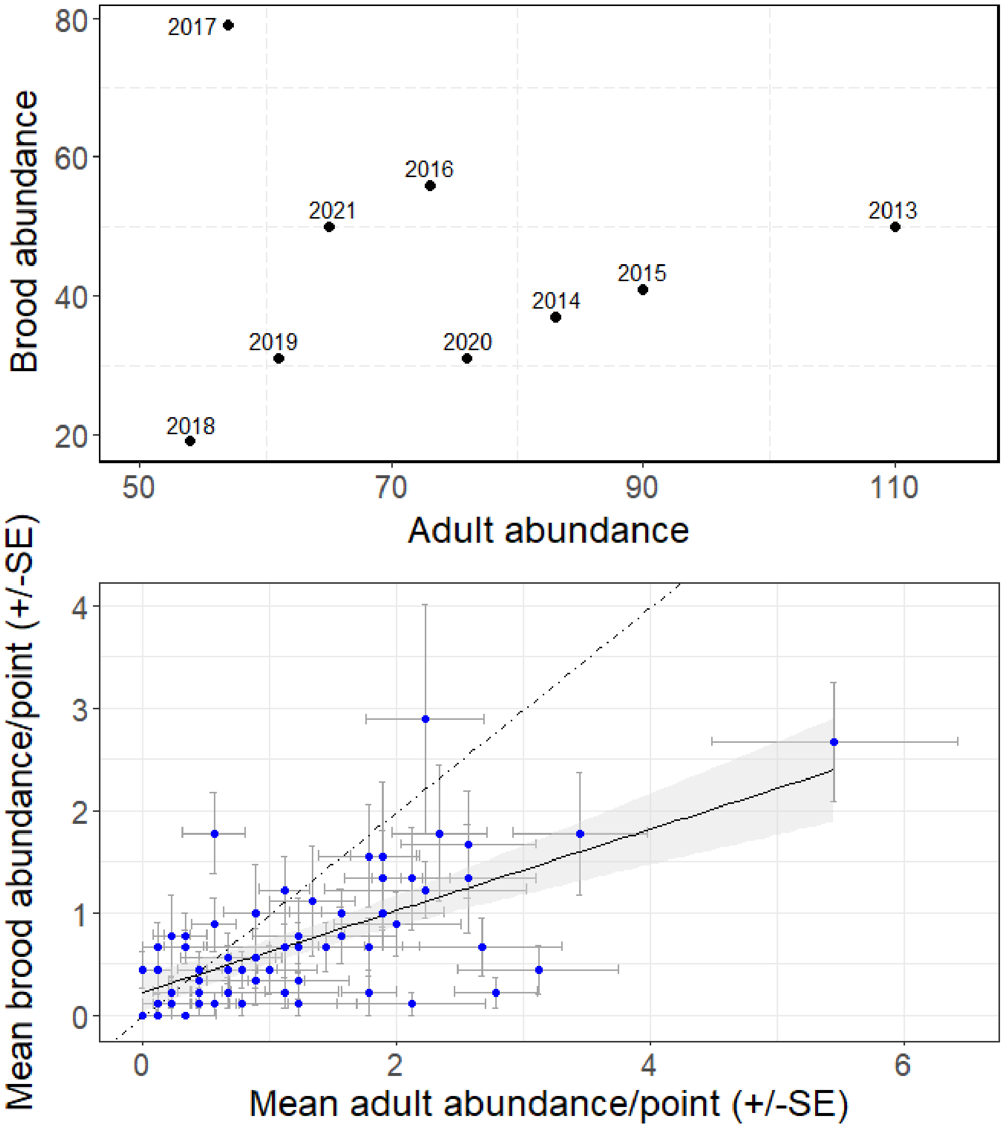


Figure 6. Variation in brood abundance at different adult abundance (model results in Table 2). A) Annual variation in brood abundance (total number of broods) in late July in relation to the total number of adults recorded one month earlier over the years 2013-2021 over the whole study area. B) Relationship between adult annual abundance (mean number of adults on a given point across years) and annual brood abundance (mean number of broods per adult point across years). Solid line represents the predicted relationship, the dashed line represents the 1:1 relationship, and the shaded area indicates the standard error associated to it.

Discussion

Our results showed a strong decrease in adult abundance on the road-based transect during 2012-2021 but no trend in brood abundance for the period 2013-2021. Abundance of both adults and broods was not related to traffic volume, probably due to the low number of cars/day and the similar effect this might have along the surveyed road. Despite this, the results regarding adult abundance and traffic volume should be interpreted cautiously and additional years might show a negative pattern as reported in other studies (Pálsdóttir 2022). Higher abundance of adults was recorded on points of higher habitat heterogeneity. Despite no clear occurrence in specific habitats, broods were less likely to be found in anthropogenic habitats such as Agricultural and domestic and Mixed forestry plantations. We did not find a relationship between annual adult abundance and annual brood abundance (productivity), but a positive relationship was detected locally (i.e., per point), as higher number of broods were associated with points which had higher adult abundance. This strongly suggests that targeting sites with higher adult Whimbrel abundance for conservation would on average, also be the sites where higher number of broods are produced, as long as the direction of this relationship does not change.

Variation in adult abundance

Within Iceland, counts on sites in the Northeast and West of the country indicated stable populations for the periods 2010-2020 and 2005-2020, respectively (Harðardóttir 2019; Kolbeinsson et al., 2020). Meanwhile, a negative trend was reported in the East from 2009-2019 (Lárusdóttir et al., 2019) coinciding with our results from the South. These variable population trends within the country highlight the need of an updated survey to assess the status of the Icelandic population. The drivers of the steep population decline observed here are unclear and cannot be explained by the data currently available, and although some birds might have been missed during the point counts, our consistent methodology still makes this a robust result. However the extent and quality of the habitats in the Icelandic lowlands, where highest breeding densities of waders are found, are vulnerable to infrastructure development, changes in agriculture and increasing afforestation (Jóhannesdóttir et al., 2018, 2019; Pálsdóttir 2022; Pálsdóttir et al., 2022a). The effects of such habitat changes on wader populations in this region of Iceland may have started to manifest in the declining trends reported here.

Whimbrel abundance was higher at points of higher habitat heterogeneity. The effect of habitat heterogeneity on species abundance is species-specific (Elliott et al., 2019) but a positive relationship between these two variables has been found for several bird species, including waders (Berg, 1997; Elliott et al., 2019; Lorenzón et al., 2016). This pattern could be mediated by higher abundance of prey species (Jonsson et al., 2011) and/or lower nest predation rates in areas of higher habitat heterogeneity (Benton et al., 2003). Moreover, the higher likelihood of one or more specially important habitats, or keystone habitats (Davidar et al., 2001), to be present within points of higher habitat heterogeneity could partly be the reason for our results. However, given the weak strength of the positive relationships between different habitat types and habitat heterogeneity found here, we cannot conclude if this is indeed the case in our system. The higher proportion of Agricultural and domestic habitat (L14.2) within the adult buffers and its negative relationship with habitat heterogeneity, reflects its prevalence in the landscape as occurs in most European countries, and the lower likelihood of finding Whimbrels within in those habitats. Despite our findings suggesting that a mosaic of habitats rather than a single one explain the variation in adult abundance, further research exploring the relationship between the quality of these habitats and important demographic rates such as breeding success is still needed to assess their relative importance.

Variation in brood abundance and occurrence

Brood abundance showed high annual variation but no significant trend during the study period. Annual variation in wader productivity is frequently very high and many young are produced in occasional years when environmental conditions are favourable (Beale et al., 2006; Gunnarsson et al., 2017; Watts et al., 2019; Frauendorf et al., 2022). Similarly, high annual variation in Whimbrel brood abundance observed in this study suggests that productivity is greatly influenced by environmental variability such as annual variation in weather which in turn, can influence productivity over large areas through processes like nest predation, thermoregulation or food supply (Gunnarsson et al., 2017; Alves et al., 2019; Laidlaw et al., 2020; Ganter and Boyd 2000). Environmental variability is predicted to increase under climate change (Saha et al., 2006) which can in turn initiate cascading effects affecting annual productivity. The scope, direction and extent of these effects are not fully understood, but some studies have reported consequences for wader productivity (Julliard et al., 2004; Kwon et al., 2018;). For example, winter warming and changes in snow cover events can drive annual productivity through changes in phenology, availability, quality, and abundance of critical resources for reproduction and chick survival, such as nesting sites or food. Hence, temperature shifts can potentially drive trophic mismatches by delaying timing of breeding and jeopardizing annual productivity (McKinnon et al., 2012; Machín et al., 2019; Alves et al., 2019). In addition, variation in wader productivity can be subject to changes in predator pressure, especially when availability of their main prey is scarce, as occurs in Fennoscandia during low lemming years (Blomqvist et al., 2002; Machín et al., 2019). In Iceland, where cyclic rodents are absent, the main predators of wader eggs and chicks are generalist species such as Arctic fox (*Vulpex lagopus*), American mink (*Neogale vison*), Common raven (*Corvus corax*), Arctic skua (*Stercolarius parasiticus*), and large gulls (*Larus spp.*) (Jónsson & Gunnarsson, 2010). Although most of these predators are long-lived and their populations most likely do not fluctuate much between consecutive years, local predation pressure might vary depending on the breeding synchrony and abundance of other co-occurring prey species (Lamarre et al., 2017) but this alone may not be strong enough to produce the annual variation in brood abundance found at the landscape scale studied here. Weather dependent factors are more likely drivers of the substantial annual variation in productivity recorded in our system, and have been confirmed for related species in our study area (Beale et al., 2006; Gunnarsson et al., 2017; Alves et al., 2019; Machín et al., 2019).

It is important to note that detection of trends in short time series with large year-to-year variation like the brood abundance data presented here is an ubiquitous challenge (Brook & Bradshaw, 2006; White, 2019). Our measure of productivity using the number of broods detected on a standard route is an efficient and quick indicator that can be used as a proxy for productivity although brood size is a more common measure of breeding success, particularly in taxa where it is easier to count chicks than it is for waders (Page et al., 1983; Bolton et al., 2012; Saalfeld et al., 2021; Douglas et al., 2023). Annual counts of broods are foremost an indicator of the proportion of successful pairs in the population at the time of the survey and ignore annual variation in brood size. The results regarding the productivity trend should, therefore, be interpreted with caution and will benefit from additional data which will build up in years to come. It is also worth noting that our car-based approach to brood counts, which necessarily trades off efficiency and accuracy should be considered a minimum estimate as some broods along the transect may be missed by this method. The consistent approach should nevertheless give a reliable estimate of annual variation.

Heathlands have been identified as important habitats for Whimbrels in other studies (Grant 1989; Jóhannesdóttir et al., 2014), as they provide good visibility of potential threats, and the abundant small shrubs like bilberries (*Empetrum nigrum*) and blueberries (*Vaccinum myrtilus*) are likely an important food resource for adults and chicks (Lappo et al., 2012). Although pairs with broods did not occur in any particular type of heathland more often than expected given their availability (habitat code L10), seven different heathland types were used (Fig 5). Two habitats were clearly used less than expected by their availability: forestry plantations and agriculture. Avoidance of taller vegetation for nesting Whimbrels and lower densities around forest have been previously reported (Stroud et al., 1990; Hancock et al., 2009; Ballantyne and Nol 2011; Wilson et al., 2013; Pálsdóttir et al., 2022a), and avoidance of agricultural land has also been reported in the past (Gunnarsson et al., 2006). The fact that the latter habitat had high brood abundance but brood occurrence there was lower than expected based on its relative availability, indicates the large extent of this habitat type along the transect which runs largely through agricultural areas (Jóhannesdóttir et al., 2017).

Relationship between brood abundance and adult abundance

No relationship was found between annual brood abundance and adult abundance at the landscape scale. Adult Whimbrels are both site faithful and long-lived (Mallory 1982; Skeel 1983; Méndez et al., 2018b) and the actual size of the breeding population is unlikely to fluctuate much between consecutive years. Therefore, although a single annual survey is well suited to detect long term changes in the adult population, it may not be an accurate estimate of the actual size of the breeding population in a given year. In addition, the strong year-to-year variation in brood abundance may mask the detection of a relationship between the number of adults and the number of broods, but if a decrease in adult abundance persists over time, it should eventually be reflected in a negative productivity trend at the landscape scale, as fewer adults will produce fewer broods. This was not observed in our results, perhaps due to the high environmental variation driving brood abundance and the duration of the survey, but additional data in the following years may be used to assess this. Altogether, the sampling methodology used here for the adult population, coupled with the high variation in annual productivity, make this relationship subject to high risk of type II error. Adult abundance and productivity were, however, positively related spatially with brood abundance tending to increase across the range of adult abundance (Fig. 6 B), indicating that more chicks are on average produced on sites where adult abundance is higher. This strongly suggests that sites with higher adult abundance should be prioritized for conservation and that spatial variation in productivity is largely a proximate product of adult abundance, whereas environmental conditions seem to drive much of the annual variation in brood abundance. One topic yet to be addressed is the appropriate scale of suitable sites for Whimbrels and other waders and this remains open for future research. Given than Whimbrel and other wader densities in Iceland are lowest close to human infrastructures and forest edges (Pálsdóttir 2022, Pálsdóttir et al., 2022a), land-sparing practices, coupled with appropriate grazing regimes, are likely to be appropriate for waders which require large open spaces (Green et al., 2005; Feniuk et al., 2019).

Conclusion

Around the globe, many populations of waders have declined due to habitat loss, degradation and fragmentation of habitats driven by climate change and anthropogenic land-use changes. For some species, the negative population trends have been devastating as in the case of the Eurasian Curlew (*Numenius arquata*), the Spoon-billed Sandpiper (*Calidris pygmaea*) or in the more extreme cases, the extinction of the Eskimo Curlew (*Numenius borealis*) (IUCN 2022). Icelandic Whimbrels and other open-landscape specialists, which still have strong populations, are likely to head in the same direction under the increased pressure on their breeding habitats and if space for them is not secured in landscape planning (Zöckler and Lysenko 2000; Wauchope et al., 2017). Given our findings and the land-use development plans predicted for Iceland in the near future (Ministry for the Environment and Natural Resources, 2018), integrating wader conservation into land management plans, where important breeding habitats are secured and maintained with suitable grazing regimes, should be a priority. Prioritizing sites of high adult abundance and high productivity for wader conservation is also imperative in Iceland and elsewhere, and such conservation strategies should consider habitat preferences, demographic rates and their relationship at the relevant scales.

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Appendices

Table S1. Traffic information. Frequency of adult point-counts and broods observed along the road-based transect at different traffic ranges (cars/day). Data on traffic corresponds to the summer months June to September from 2011 to 2021 (The Icelandic Road and Coast Administration, IRCA). Data for 2021 was not available and we used data from 2020 instead. The traffic category was determined according to Holm and Laursen 2011.

Adult points	Brood observations	Traffic range	Traffic category
32	207	0-100	Low
11	64	100-200	
9	74	200-300	
0	25	300-400	
0	2	800-900	
0	0	900-1000	
4	0	1100-1200	
0	9	1300-2200	High
4	0	2200-2300	
0	2	2300-2400	
1	0	2500-2600	
2	0	2800-2900	
0	11	>2900	

Table S2. Habitat types from the Icelandic Institute of Natural History and EUNIS on which these are based on (Ottósson et al., 2016).

Iceland Institute of Natural History		English name (EUNIS – habitat name and code)
Habitat code	Icelandic name	

L1.1	Eyðimelavist	H5.3 Glacial moraines with very sparse or no vegetation
L1.2	Grasmelavist	H5.3 Glacial moraines with very sparse or no vegetation
L1.3	Mosamelavist	E4.21 Oroboreal *Carex bigelowii-Racomitrium* moss-heaths
L1.4	Víðimelavist	H5.2 Glacial moraines with very sparse or no vegetation
L1.5	Sanda- og vikravist	H6.25 Volcanic ash and lapilli fields
L1.6	Landmelhólavist	H5.241 Icelandic inland dunes
L2.1	Moldavist	New type, suggestion. H5.7 Icelandic exposed andic soils
L3.1	Urðarskriðuvist	New type, suggestion. H2.13 Icelandic talus slopes
L3.2	Grasvíðiskriðuvist	New type, suggestion. H2.12 Icelandic *Salix herbacea* screes
L3.3	Ljónslappaskriðuvist	New type, suggestion. H2.11 Icelandic *Alchemilla* screes
L4.1	Eyravist	C3.6 Unvegetated or sparsely vegetated shores
L4.2	Auravist	New type, suggestion. H5.351 Icelandic braided river plains
L5.1	Hélumosavist	E4.115 Boreal moss snowbed communities
L5.2	Melagambravist	New type, suggestion. E4.26 Icelandic *Racomitrium ericoides* heaths
L5.3	Hraungambravist	E4.25 Moss and lichen fjell fields
L6.1	Eyðihraunavist	H6.241 Barren Icelandic lava fields
L6.2	Fléttuhraunavist	New type, suggestion. E4.241 Icelandic lava field lichen heaths
L6.3	Mosahraunavist	E4.242 Icelandic lava field moss heaths
L6.4	Lynghraunavist	New type, suggestion. E4.243 Icelandic lava field shrub heaths
L7.1	Sandstrandarvist	B1.234 Icelandic sand beach perennial communities
L7.2	Malarstrandarvist	B2.3 Upper shingle beaches with open vegetation
L7.3	Strandmelhólavist	B1.311 Atlantic embryonic dunes
L7.4	Grashólavist	B1.41 Northern fixed grey dunes
L7.5	Sjávarfitjungsvist	A2.542 Atlantic lower shore communities
L7.6	Gulstararfitjavist	New type, suggestion. A2.531G1 Icelandic *Carex lyngbyei* salt meadows
L7.7	Sjávarkletta- og eyjavist	B3.31 Atlantic sea-cliff communities
L8.1	Dýjavist	D2.2C12 *Philonotis-Saxifraga stellaris* springs
L8.2	Rekjuvist	D4.1J Icelandic stiff sedge fens

L8.3	Sandmýravist	D4.261 Cottonsedge marsh-fens
L8.4	Hrossanálarvist	E3.416 *Juncus arcticus* meadows
L8.5	Runnamýravist á hálendi	D4.162 Boreal black sedge-brown moss fens
L8.6	Runnamýravist á láglendi	D4.162 Boreal black sedge-brown moss fens
L8.7	Rimamýravist	D3.2 Aapa mires
L8.8	Rústamýravist	D3.1 Palsa mires
L8.9	Starungsmýravist	D4.163 Icelandic black sedge-brown moss fens
L8.10	Hengistararflóavist	New type, suggestion. D2.2933 Icelandic *Carex rariflora* alpine fens
L8.11	Brokflóavist	D2.26 Common cotton-grass fens
L8.12	Starungsflóavist	D4.163 Icelandic black sedge-brown moss fens
L8.13	Tjarnastararflóavist	D2.332 Basicline bottle sedge quaking mires
L8.14	Gulstararflóavist	D5.21B Icelandic *Carex lyngbye*i fens
L9.1	Stinnastararvist	New type, suggestion. E4.3C Icelandic *Carex bigelowii* grasslands
L9.2	Finnungsvist	E1.711 Insular *Nardus-Galium* grasslands
L9.3	Bugðupuntsvist	E1.73 Wavy hair-grass grasslands
L9.4	Snarrótarvist	E3.4132 Boreal tufted hairgrass meadows
L9.5	Grasengjavist	E1.7224 Icelandic *Festuca* grasslands
L9.6	Língresis- og vingulsvist	E1.7221 Boreo-subalpine *Agrostis* grasslands
L9.7	Blómgresisvist	E1.7223 Northern boreal *Festuca* grasslands
L10.1	Mosamóavist	New type, suggestion. E4.28 Icelandic *Racomitrium* grass heaths
L10.2	Flagmóavist	F2.294 Arctic Dryas heaths
L10.3	Starmóavist	New type, suggestion. E4.29 Icelandic *Carex bigelowii* heaths
L10.4	Grasmóavist	New type, suggestion. E1.2617 Icelandic *Empetrum Thymus* grasslands
L10.5	Fléttumóavist	New type, suggestion. E4.27 Icelandic lichen *Racomitrium* heaths
L10.6	Fjalldrapamóavist	F2.255 North Atlantic boreo-alpine heaths
L10.7	Lyngmóavist á hálendi	F2.112 Oroboreal moss-dwarf willow snowbed communities
L10.8	Lyngmóavist á láglendi	F4.211 North Atlantic *Vaccinium-Empetrum-Racomitrium* heaths
L10.9	Víðimóavist	New type, suggestion. F2.113 Icelandic *Salix lanata*/*S. phylicifolia* scrub

L10.10	Víðikjarrvist	F2.322 Oroboreal willow scrub
L11.1	Kjarrskógavist	G1.91711 Boreo-Atlantic crowberry-bog bilberry birch woods
L11.2	Lyngskógavist	G1.91713 Icelandic bog billberry-hairgrass birch woods
L11.3	Blómskógavist	G1.91714 Icelandic cranesbill birch woods
L12.1	Mýrahveravist	New type, suggestion. C2.1431 Geothermal wetlands
L12.2	Móahveravist	New type, suggestion. H6.152 Geothermal heathlands
L12.3	Fjallahveravist	New type, suggestion. C2.1432 Geothermal alpine habitats
L12.4	Hveraleirsvist	New type, suggestion. H6.151 Icelandic solfatars/Geothermal bare grounds
L13.1	Jöklar og urðarjöklar	H4.2, H4.3 Glaciers, rock glaciers and unvegetated ice-dominated moraines
L14.1	Þéttbýli og annað manngert land	J Constructed, industrial and other artificial habitats
L14.2	Tún og akurlendi	I Cultivated agricultural, horticultural and domestic habitats
L14.3	Skógrækt	G4.F Mixed forestry plantations
L14.4	Alaskalúpína	E5.15 Land reclamation forb fields
L14.5	Uppgræðslur	New type, suggestion. E5.16 Land reclamation grass fields
L14.6	Skógarkerfill og fleiri áþekkar tegundir	E5.12 Weed communities of recently abandoned urban and suburban constructions
V1	Vötn	Standing waters
V2	Ár	Running waters
F	Fjöruvistir	Littoral shores
FX1.1	Sjávarlón	Saline coastal lagoons

Table S3. Results from GLMMs exploring the variation in brood abundance using broods at different distances from an adult point, in relation to adult abundance per point. Significant results are shown in bold.

Number of broods

A. All distances	**Estimate**	**SE**	**Z**	**p**	**Random effects: Point ID** (n =63)	
(Intercept)	31.227	39.995	0.781	0.435	**Variance**	**S. Dev.**
Nr. adults/point	0.119	0.036	3.324	**< 0.001**	0.522	0.722
Year	-0.016	0.020	-0.799	0.424		
B. Within 200 m						
(Intercept)	-33.661	103.742	-0.324	0.746	0.612	0.782
Nr. adults/point	0.269	0.076	3.562	**< 0.001**		
Year	0.015	0.051	0.297	0.767		
C. Within 300 m						
(Intercept)	63.931	82.159	0.778	0.436	0.705	0.840
Nr. adults/point	0.213	0.063	3.364	**< 0.001**		
Year	-0.033	0.041	-0.807	0.420		
D: Within 500 m						
(Intercept)	20.631	62.089	0.332	0.740	0.485	0.696
Nr. adults/point	0.224	0.051	4.416	**< 0.001**		
Year	-0.011	0.031	-0.361	0.718		
E. Within 1000 m						
(Intercept)	21.050	48.328	0.436	0.663	0.542	0.736
Nr. adults/point	0.147	0.042	3.461	**< 0.001**		
Year	-0.011	0.024	-0.460	0.646		
F. Within 1500 m						

(Intercept)	28.967	40.263	0.719	0.472	0.510	0.714
Nr. adults/point	0.129	0.036	3.539	**< 0.001**		
Year	-0.015	0.020	-0.739	0.460		

Number of observations: 567

Table S4. Statistical results from Manley Selectivity measure. Habitats that were significantly used more or less often given their availability are marked in bold.

Habitat code	Description (EUNIS)	Selection ratio	upper CI	lower CI	p	
L10.3	Icelandic *Carex bigelowii* heaths	5.076	15.077	-4.925	0.318	Used more often (Selection ratio >1)
L5.3	Moss and lichen fjell fields	3.230	7.353	-0.893	0.185	
L10.2	Arctic *Dryas* heaths	3.173	10.029	-3.683	0.438	
L10.8	North Atlantic *Vaccinium-Empetrum-Racomitrium* heaths	2.538	5.778	-0.702	0.245	
L8.4	*Juncus arcticus* meadows	2.538	8.678	-3.602	0.539	
L10.9	Icelandic *Salix lanata/S. phylicifolia* scrub	2.284	5.945	-1.376	0.390	
L10.1	Icelandic *Racomitrium* grass heaths	1.904	4.535	-0.728	0.400	
L4.2	Icelandic braided river plains	1.692	3.191	0.193	0.258	
L9.1	Icelandic *Carex bigelowii* grasslands	1.692	7.496	-4.112	0.770	
L14.1	Constructed. industrial and other artificial habitats	1.632	3.105	0.158	0.294	
L10.10	Oroboreal willow scrub	1.586	2.606	0.567	0.159	
L8.9	Icelandic black sedge-brown moss fens	1.450	3.177	-0.277	0.523	
L9.7	Northern boreal *Festuca* grasslands	1.354	3.657	-0.950	0.707	
L8.12	Icelandic black sedge-brown moss fens	1.269	4.819	-2.280	0.853	

L9.6	Boreo-subalpine *Agrostis* grasslands	1.119	1.724	0.513	0.631	
L8.14	Icelandic *Carex lyngbyei* fens	0.952	3.614	-1.710	0.965	Used less often (Selection ratio <1)
L9.5	Icelandic *Festuca* grasslands	0.881	1.896	-0.135	0.773	
L10.4	Icelandic *Empetrum Thymus* grasslands	0.761	2.891	-1.368	0.784	
L14.2	**Regularly or recently cultivated agricultural, horticultural and domestic habitats**	**0.612**	**0.876**	**0.348**	**0.000**	
L14.4	Land reclamation forb fields	0.508	2.249	-1.234	0.488	
L8.6	Boreal black sedge-brown moss fens	0.508	1.927	-0.912	0.396	
L14.3	**Mixed forestry plantations**	**0.305**	**1.156**	**-0.547**	**0.045**	
L9.4	Boreal tufted hairgrass meadows	0.212	1.239	-0.816	0.060	
V2	**Running waters**	**0.149**	**0.874**	**-0.576**	**0.004**	

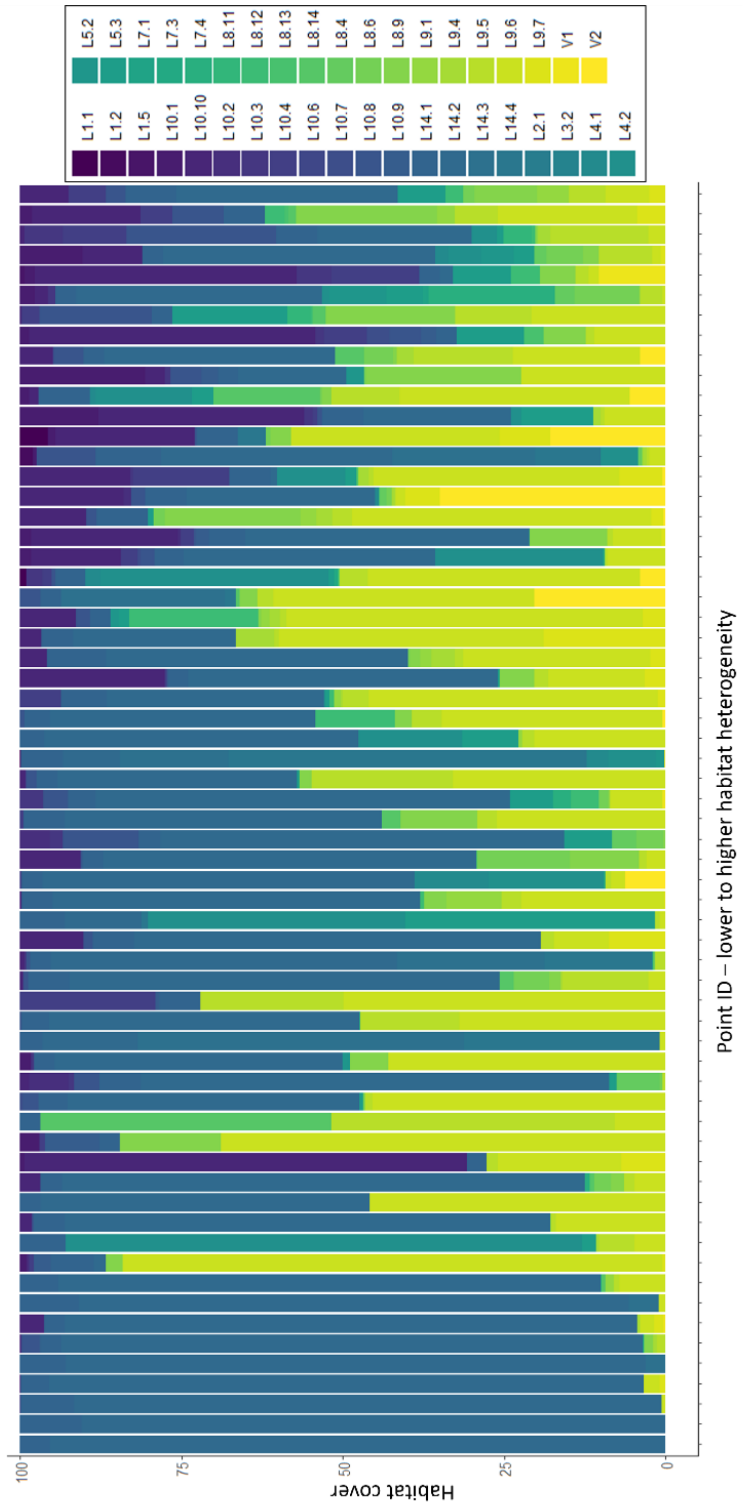


Figure S1. Proportion (%) of different habitats covering the buffers around the 63 adult points (point ID) ordered by low to high habitat heterogeneity.

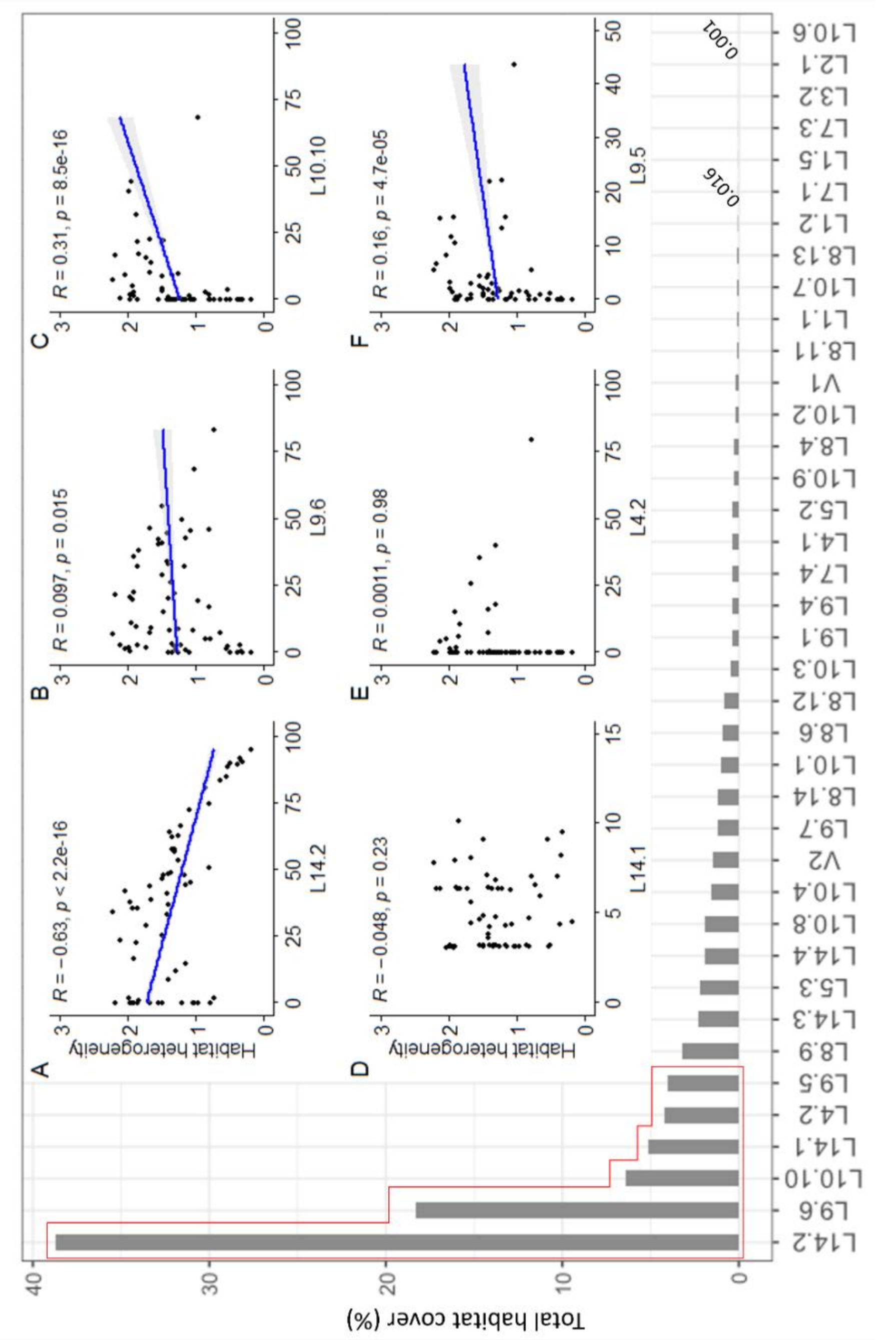


Figure S2. Total cover of different habitats and their relationship with habitat heterogeneity. The total cover corresponds to the number of pixels belonging to certain habitat compared to the combined number of pixels for all the 63 points (e.g., 40% of all the pixels combined from the 63 points, were covered by habitat L14.2). Red box shows cover of habitats whose relationship with habitat heterogeneity was further explored (A-F).

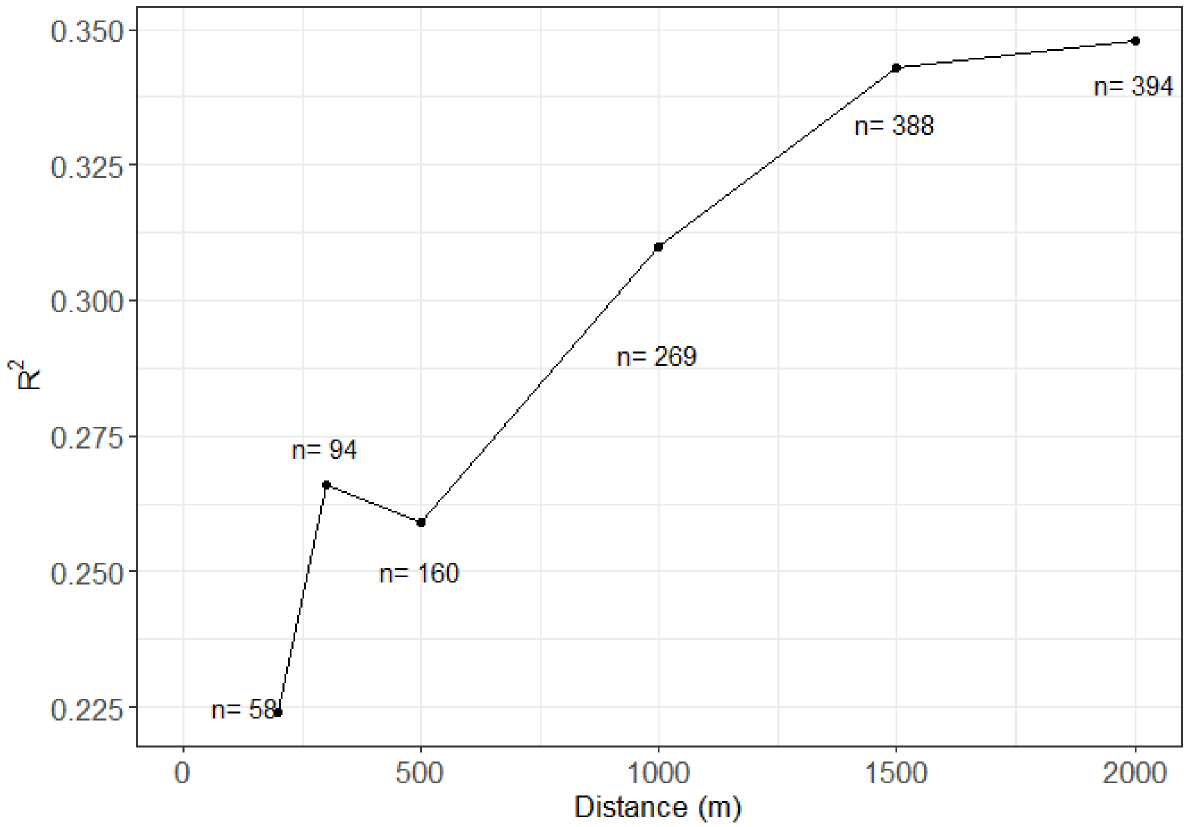
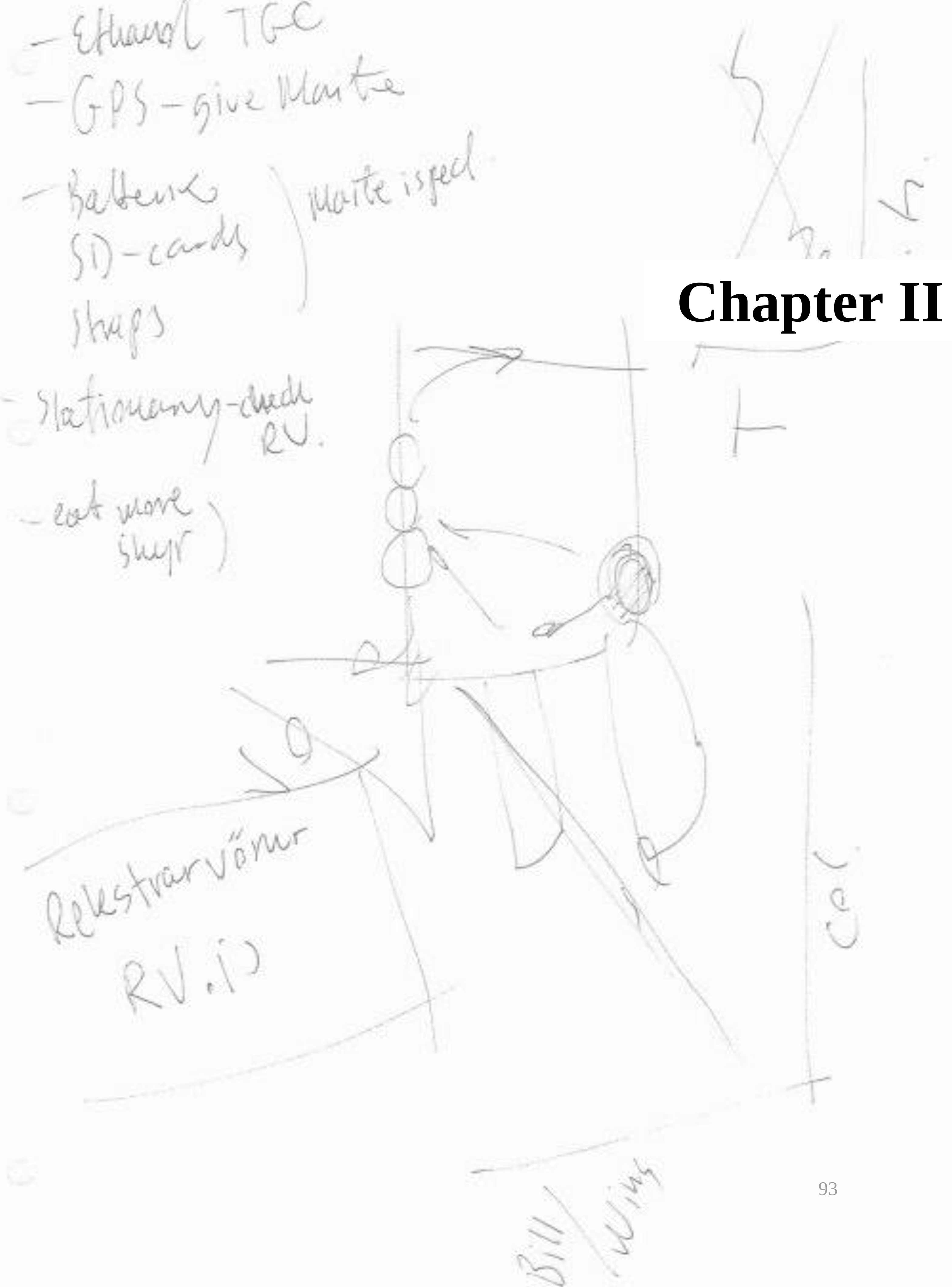


Figure S3. Model fit for the different GLMM´s exploring the relationship between adult and brood abundance per point and year. Models with broods within 200 m, 300 m, 500 m, 1 km, 1.5 km and all broods independently of the distance are shown. Number of broods included in the different datasets (n) are shown on the graph.

Chapter II


- Ethanol TGC
- GPS - give Martie
- Batteries
SD-cards
straps
Martie isped
- Stationary - check RV.
- eat more skyr
Rekstrarvörur
RV.is
Bill/Wing

Chapter II. Seasonal variation in Whimbrel abundance across sub-Arctic habitats of varying succession stage

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Summary

The increase in temperature in Arctic regions is driving significant changes in hydrology and nutrient availability, with consequences at all ecosystem levels ranging from habitats to populations. The direction and strength of these changes is influenced by the succession process and past events in specific habitats. Disruption of the succession processes by natural or anthropogenic causes has the potential to alter ecosystem functioning and habitat composition, influencing population dynamics of species. Iceland is a global stronghold for breeding populations of several waders such as the Whimbrel *Numenius phaeopus*, which breeds on a gradient of abundance in habitats at early to mid-succession stages. The species provides a suitable system to investigate variation in abundance across habitats at different stages of ecological succession and assess how future succession may affect the population through changes in habitat availability. We counted Whimbrels for three years at 14 sites in three habitats at early to mid-succession stages. Highest and lowest abundance was found in habitats of early succession throughout the breeding season. During pre-incubation, an increase in abundance was reported in all habitats, which stabilized during incubation. During post-incubation, abundance decreased in moss heath and remained stable in heathland and river plain. Our findings show consistent differences in overall abundance and progression of numbers through the breeding season between habitats at different succession stages. This has important implications for conservation strategies for the Whimbrel population and for habitat management.

Keywords

Shorebirds; waders; count data; *Numenius phaeopus*; ecological succession.

Introduction

Arctic and sub-Arctic ecosystems are characterized by low species diversity (Taylor et al., 2020), partly driven by a slow rate of vegetation growth, due to extreme environmental conditions such as low temperatures and snow cover, nutrient poor environments, and short growing seasons (Jones & Henry, 2003). Under the current climatic crisis however, ecosystems are changing and Arctic and sub-Arctic regions are experiencing alterations in weather patterns, hydrology and nutrient availability (Taylor et al., 2020), ultimately affecting species composition, abundance and phenology (Gill et al., 2014; Alves et al., 2019; Davidson et al., 2020). During the last decades, several studies have revealed ecosystem shifts (Post et al., 2019) which vary between Arctic and sub-Arctic regions due to spatiotemporal differences in local abiotic conditions (Olofsson et al., 2013; Post et al., 2019). For example, warmer temperatures are facilitating shrub expansion (Post et al., 2009), permafrost and glacial melting in some areas (Grémillet et al., 2015), and increased fire risk in others (Box et al., 2019). These shifts have the potential to modify biotic and abiotic habitat features such as vegetation biomass or hydrology, changing the natural process of ecological succession and reshaping terrestrial and coastal ecosystems (Chang & Turner, 2019). The new habitat conditions will determine resource availability such as food or territories for species in these regions, as well as their seasonal variation, which can have substantial demographic effects (Higgins et al., 2010; McKinnon et al., 2012), and ultimately modify species composition, abundance, and ecosystem dynamics.

Studies focused on ecological succession offer a conceptual framework to understand the complex interactions between species and their environment accounting for historical processes and provide an insight into how resource availability influences the distribution and abundance of species. As ongoing habitat changes in the Arctic and sub-Arctic are predicted to have major impacts on its biota (Wauchope et al., 2017), considering the effects of past and future events on the direction and extent of processes regulating populations is important. Therefore, the study of population dynamics across habitats at different successional stages could be used to better inform species conservation and management by integrating past knowledge and future predictions of environmental change. Forecasting the succession trajectory of a habitat will provide insight into the response of an ecosystem to natural and/or anthropogenic changes, and how the community composition and species abundance may change.

Iceland, a large sub-Arctic island, is currently facing ecological shifts due to climate change and anthropogenic effects. For example, some of the most iconic glaciers in the country have lost 11% of their ice mass since 1995 (Björnsson & Pálsson, 2008), potentially affecting glacier river discharge and flooding regimes that maintain early succession habitats in the lowlands (Björnsson & Pálsson, 2008). Conversely, a positive trend in NDVI (Normalized Differenced Vegetation Index) values from 1980-2000 revealed an increase in vegetation cover (Raynolds et al., 2015). This increase in plant biomass can potentially alter biogeochemical cycles such as carbon and nitrogen fluxes and biodiversity (Koltz et al., 2022), causing changes in the ecological succession of habitats (Chang & Turner, 2019). Iceland is not only influenced by the current climatic changes affecting sub-Arctic regions but also by extensive soil erosion due to abiotic factors and sheep grazing (Gísladóttir, 2001; Barrio et al., 2018), and an active volcanic system traversing the country along an NE/SW axis (Arnalds, 2008). The synergistic interactions among these factors create a very dynamic system, shaping the different ecosystems within the country. In Iceland, early colonization stages of primary succession differ greatly following an altitudinal gradient, volcanic activity and erosion, determining subsequent habitat types. For example, early colonizers, such as bryophytes and lichens, can be found covering lava fields after volcanic eruptions (Vilmundardóttir et al., 2018). In these areas, they create stable habitats at early stages of succession where the establishment of other species is inhibited due to the production of allelopathic compounds (Bjarnason, 1991, moss heath, Table 1, Fig 1. A). Nevertheless, these homogeneous moss fields are highly sensitive to physical disturbances like grazing and trampling that can expose patches of bare ground and are aggravated by erosion from wind and water (Gísladóttir, 2001). Once the erosive process starts, it can quickly become a prevailing force in the landscape modifying species composition and abundance of the affected areas (Barrio et al., 2018). Under certain conditions, these patches will be colonized by vascular plants such as grasses and small shrubs like black crowberry *Empetrum nigrum*, bilberries *Vaccinium* spp. and heather *Calluna vulgaris*. Over time, the expansion of vascular plants will slowly transition into a vascular-plant dominated habitat like heathland (Table 1; Fig 1. B; Vilmundardóttir et al., 2018). Icelandic heathlands, on a more advanced stage of succession than moss heath, are dominated by dwarf shrubs often intermixed with mosses and some herbaceous plants and are rather dry and hummocky (Gísladóttir et al., 2014; Jóhannesdóttir et al., 2014). This habitat also originates from intensive sheep grazing in woodlands, in the first centuries after settlers established themselves in Iceland (Gísladóttir, 2001).

Table 1. Sampling regimen across the three years and the 14 sites surveyed in this study. Mean laying and hatching dates were obtained from a Whimbrel monitoring programme in the same area (see Methods). Hatching dates were estimated as 28 days after the first egg is laid.

Year	**2019**	**2020**	**2021**
Start date	15th May	1st May	2nd May
End date	2nd August	30th July	30th July
Sites sampled (replaced)	10(2)	12	12
River plain sites	4	4	4
Heathland sites	4	5	5
Moss heath sites	2	3	3
Mean laying date	30th May (±1.18 days)	1st June (±0.98 days)	4th June (±0.65 days)
Mean hatching date	27th June (±1.18 days)	29th June (±0.98 days)	2nd July (±0.65 days)
Sampling effort			
Once a week	All sites	1st May - 4th June; 12 sites 20th -30th July; 12 sites	1st - 24th May; 12 sites 19th -30th July; 12 sites
Twice a week	None	5th June - 19th July; 6 sites	25th May - 18th July; 6 sites
Mean duration per site	146 min (±9.6 min)	140 min (±8.7min)	144 min (±8.1 min)
Mean starting time	12:31 (±17 min)	07:59 (±5 min)	07:59 (±5 min)

Figure 1. Examples of habitat types explored in the study. A. moss heath, B. heathland and C. River plain.

Another example of dynamic succession shaping important habitats at lower altitude is found on riverine flood plains, often located relatively close to the sea (river plain, Table 1; Fig 1. C). These fluvial areas are characterized by rivers, often of glacial origin, flowing through them (Gunnarsson et al., 2006a; Katrínardóttir et al., 2015), transporting nutrients, and enhancing local productivity on the depositional zones (Thorp & Delong, 1994). Periodic floods in spring, a consequence of snow melt, and jökulhlaup flash floods, influence vegetation development and shape a heterogenous landscape of intermixed patches of vegetation, sand and gravel (Nilsson et al., 1994; Björnsson 2010). Even though floods are a natural cyclic process shaping this ecosystem, abnormalities in water discharge from glacial origin, longer melting season and ultimately glacier extinction (Björnsson & Pálsson, 2008), jeopardize the persistence of these flood plains (Florsheim et al., 2008). An increase in river flow might lead to higher rates of erosion, modifying sand banks and inhibiting plant growth, while a decrease might promote colonization and establishment of riparian vegetation like rushes and sedges along the barren sand banks, promoting changes in the succession (Florsheim et al., 2008).

River plains are especially important during the breeding season for ground nesting birds, as they contain some of the highest breeding densities of some waders in Iceland (Gunnarsson et al., 2006a). Such high breeding densities on riverplains and other vegetated lowland habitats make Iceland responsible for a large part of the world population of some wader species like Whimbrel (*Numenius phaeopus*), Eurasian Golden Plover (*Pluvialis apricaria*), Dunlin (*Calidris alpina*), Common Ringed Plover (*Charadrius hiaticula*), Common Redshank (*Tringa totanus*) and Black-tailed Godwit (*Limosa limosa*) (Delany et al., 2009). Waders are open landscape specialists and half of the Arctic breeding species are currently declining (Lindström et al., 2019; Zöckler & Lysenko, 2000). Within this group, the large bodied, long-distance migrants are especially compromised for being habitat specialists with slow generation time (Pearce-Higgins et al., 2017). Hence, changes in the habitat or habitats they occupy in the breeding season can directly affect their reproductive output, and they can therefore be considered indicators of ecosystem change (Zöckler, 2012; Saalfeld et al., 2013; Taylor et al., 2020).

The Icelandic Whimbrel (*N. phaeopus islandicus*) population has recently shown signs of regional decline in South Iceland, their most important breeding area (Cerezo-Araujo et al., *under review*). The species mostly winters on the West African coasts and spends the summer in Iceland (Alves et al., 2016; Carneiro et al., 2019a), where the bulk of the population breeds below 200-300 m a.s.l.. In these lowlands, Whimbrels can be found breeding on a gradient of abundance in different habitats on early to mid-stages of succession, but avoiding more advanced stages, i.e. habitats with taller vegetation (Gunnarsson et al., 2006a; Jóhannesdóttir et al., 2014; Katrínardóttir et al., 2015). These long-lived birds (current longevity record is 24 years, Klima et al., 2013; annual survival estimate: 0.71-0.89, Méndez et al., 2018) are both territorial and philopatric (Mallory 1982; Carneiro et al., 2021), and therefore changes in the quality and availability of their habitat, either through natural processes of ecological succession or alterations of succession patterns, are likely to affect their reproduction and thus population dynamics.

Here we used the Icelandic Whimbrel to explore links between habitat succession and potential population consequences. The Whimbrel is an ideal model species due to its common occurrence across habitats at different succession stages and at different breeding abundance. Our goals were to I) estimate variation in breeding Whimbrel abundance across habitats at different successional stages; II) assess seasonal variation in breeding Whimbrel abundance within habitats and III) view our findings in the light of likely scenarios of predicted habitat change to assess the effect of those changes for the Whimbrel population. The answers to these questions can be used to better understand the complex drivers of population abundance while accounting for historical ecosystem processes.

Material and methods

Site selection

The study area was located in the lowland plains of South Iceland. A total of 14 different sites covering three habitats at different stages of succession (see below) were sampled intensively from May to the end of July/ beginning of August 2019-2021 (Fig. 2; Table 1). Ten sites were sampled in 2019 and 12 sites were sampled the following years. In 2020, two sites sampled during the first year were replaced due to infrastructure development and difficult access, and two new sites were added (Table 1). All sites were surveyed once a week throughout the entire season in 2019. All sites were surveyed once a week during May (but sampling was extended until the 4th of June in 2021 due to bad weather limiting the date of the final survey), and from mid-July to the 2nd of August 2019 and 30th of July 2020 and 2021 (see Table 1). During the in-between period, six sites were surveyed twice a week to get better estimates of Whimbrel abundance. The area of each study site was calculated using a measuring tool from an Icelandic online map engine (www.ja.is/kort). Most surveys (ca. 90%) were carried out by the same observer.

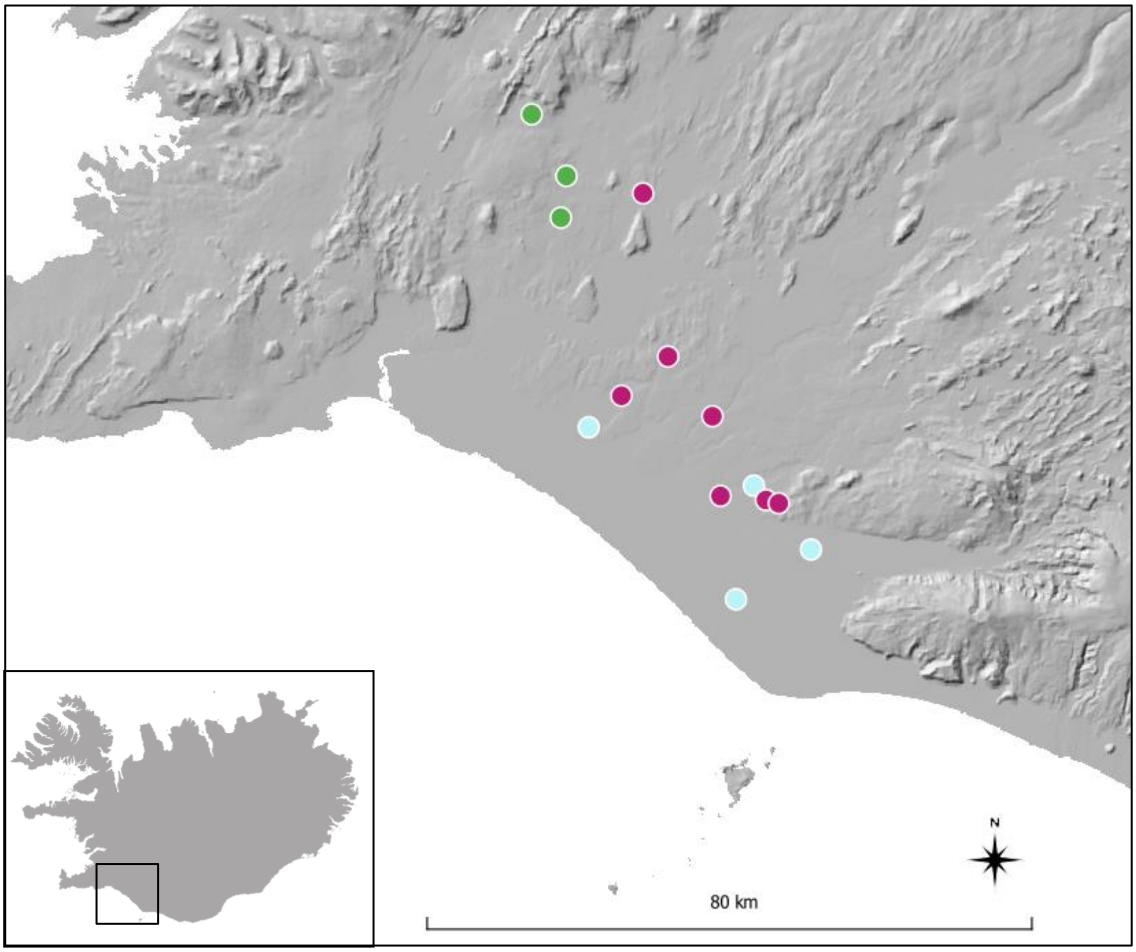

Figure 2. Map of Iceland and the locations of the study sites in the southern lowlands: moss heath in green, river plain in light blue, heathland in purple.

Sites were classified according to their dominating habitat type following the three categories described in Table 2: *Moss heath* habitats (two sites sampled in 2019 and three sites sampled in 2020 and 2021; Fig. 1.A), on early stages of succession (Gísladóttir, 2001), are dominated by a continuous thick layer of moss and lichens intermixed with patches of bare ground and small shrubs (Ottósson et al., 2016). *River plain* (four sites sampled all years, Fig. 1.C) are open areas along rivers and are subject to seasonal and irregular floods keeping them at early stages of succession (Katrínardóttir et al., 2015). The vegetation patches of this mosaic landscape include different intermixed species of mosses, lichens and vascular plants (see Table 2; Gunnarsson et al., 2006a). *Heathland* (four sites sampled in 2019 and five sites in 2020 and 2021, Fig. 1.B) are on a more advanced stage of succession than the previous two habitats, and most sites are or were used for livestock grazing. Here, the sensitive moss layer has been degraded due to trampling and grazing, resulting in open patches suitable for colonization and establishment of small shrubs and forbs (see Table 2; Gísladóttir, 2001; Cutler et al., 2008).

Table 2. Habitat characteristics of three main Icelandic habitat types at different succession stages considered in this study. All habitats are under anthropogenic influence from grazing. See also figure 1 for examples.

Habitat	**Succession stage**	**Characteristics**	**Dominating species**
Moss heath	Early succession	Continuous thick mat of mosses and lichens that increase moisture retention, creating conditions of high humidity (Cutler at al. 2008). Patches of bare ground resulting from erosive processes allow vascular species to establish creating "islands" of small shrubs and forbs.	Mosses: *Racomitrium lanuginosum, Hylocomium splendens*. Lichens: *Cladonia arbuscula, Cetraria islandica.* Patches of shrubs*: Empetrum nigrum, Vaccinum uliginosum, Salix herbácea.*
River plain	Early succession	Located in flat lowlands, most often close to the sea. Irregular or seasonal floods interrupt vegetation development. Presence of shrubs, forbs, sedges, and rushes intermixed with sand and gravel on a dry-wet gradient.	Shrubs: *Empetrum nigrum, Salix sp.*, *Silene acaulis, Dryas octopetala.* Others: grasses, rushes (particularly *Juncus arcticus*), and sedges.
Heathland	Advanced succession	Areas often under significant grazing pressure and sometimes drainage, often on previously wooded land. Rather dry areas, where the presence of hummocks is common together with shrubs, forbs, and grasses. Usually denser vegetation cover than in the two others habitats.	Mosses and lichens. Grasses: *Festuca vivipara, F. rubra.* Shrubs: *E. nigrum, V. myrtilus, Calluna vulgaris, Salix sp.*

Field surveys

On each visit, we performed ground surveys and counted all Whimbrels within the study site following the same methodology. Sampling duration and survey direction were kept constant but starting time varied between years and was adjusted to weather conditions when necessary (see Table 1). Surveys were avoided under harsh weather to ensure similar detectability and minimize disturbance to breeding birds (i.e., rain exceeding 1 mm/h, wind exceeding 7 m/s or fog). Counts were performed by driving slowly (ca. 10 km/h) along tracks when possible, and on foot to cover sections of the study areas further away from tracks. The limits of the study sites were predefined, and the surveys were planned according to the extent of the tracks. In sites with no tracks or with poor visibility due to topography, ground surveys were done on foot following predefined routes to get within clear visibility of the entire study site. Counts were performed by sight and using binoculars (8x42) to help detection. Double counting was avoided by surveying in one direction across the site, and by carefully observing the position of individual Whimbrels and Whimbrel pairs around the observer.

Data analysis

Data visualization and analysis were done in R v.4.1.1 (R Core Team, 2021). In order to investigate seasonal variation in Whimbrel abundance across and within habitats for the three years of study, we used generalized linear mixed effect models, GLMM (R package lme4, Bates et al., 2017) with logit link function and negative binomial error distribution to account for overdispersion. All counts were included in the analysis, except two at the end of the season that doubled and quintupled the number of birds from the previous survey and very likely included flocking behaviour prior to departure. Day, Habitat and their interaction were included as explanatory variables. Day was a continuous numerical variable and spanned from the first to the last day of the field season, and Habitat was a categorical variable with three levels: heathland, moss heath and river plain. Year and Area (in log scale) were included as fixed covariates to account for annual and spatial variation. Site was included as a random term to account for non-independence among site surveys. We considered including Starting time as a fixed covariate but since it did not have any effect explaining variation of Whimbrel abundance, it was not included in the final model. Prior to analysis and to allow comparison of the days between years relative to the breeding phenology of Whimbrels instead of using calendar days, we re-scaled the variable Day relative to the distribution of laying dates of each year (Fig. S1). As such, the start of the incubation period had the same Day number for the three years of study. To do this, we first determined the incubation period using laying dates obtained from an annual wader breeding monitoring programme in South Iceland (Alves et al., 2019; Carneiro et al., 2019b; Laidlaw et al., 2020) and assumed that the second and third quartiles (i.e., 50% of the data) of the annual distribution of laying dates represented the main incubation period, whereas the first and fourth quartiles represented early and late breeding attempts (including re-nests) respectively (Fig. S1). We then re-scaled the variable Day for each year so the starting date of the incubation period (i.e., second quartiles: 23rd May 2019; 26th May 2020; and 29th May 2021) would have the same Day number (Day= 28).

To further investigate variation in abundance throughout the breeding season, we split the dataset into pre-incubation, incubation, and post-incubation. We defined pre-incubation as the period from the first field survey each year to the day before incubation starts (Day = 27). Incubation started from the first date of the second quartile (Day = 28) and spanned 29 days (time for an egg to develop and hatch) after the last date of the third quartile for each year (Fig. S1). Post-incubation lasted from the end of incubation (Day = 75, 69, 68 for 2019, 2020 and 2021, respectively) to the last field survey (Table 1). We then performed a GLMM with negative binomial error distribution and logit link function for each period of the breeding season. We retained the model structure from the previous analysis with Day, Habitat and their interaction as explanatory variables, Year and $\log_e$(Area) as fixed covariates and Site as a random term.

Finally, we performed a pairwise comparison using estimated marginal means or least-squared means for the whole breeding season and for each period to test for differences in abundance between habitats (R package *emmeans*, Lenth et al., 2023).

Model validation was performed by inspecting residuals, QQplots, dispersion and fitted values (R package DHARMa, Hartig & Lohse, 2022). Model results were reported using a gradual language of evidence as suggested by Muff et al., (2021), for which p-values below 0.001 indicate a-very-strong evidence of the effect of the explanatory variable(s) on the response variable, and p-values close and above 0.05 were interpreted as having weak or no evidence respectively supporting the relationship.

Results

When the entire breeding season was considered, we found very strong evidence for differences in abundance across habitats (Table 3A, Fig. 3), with lowest abundance estimated in moss heath and highest in river plain (Table 4). We also found strong evidence for differences in the rate of change in abundance across habitat types, with abundance increasing faster in river plain than in heathland, but almost not changing in moss heath (Table 3A, Fig. 4).

During the pre-incubation period, we found similar results to when the entire breeding season was considered. Whimbrel abundance was highest in river plain and lowest in moss heath sites (Table 4), and the rate of change in abundance differed across habitats (Table 3B, Fig. 5). Both abundance in heathland and river plain increased over time, with a faster rate in river plain than in heathland (Table 3B; Fig. 5). However, the rate of change in abundance during this period did not differ between heathland and moss heath (Table 3B; Fig. 5).

Whimbrel abundance during incubation differed across habitats being highest in river plain and lowest in moss heath (Table 3C & 4). However, we did not find evidence for temporal changes in abundance in any of the habitats, suggesting abundance was largely stable during incubation (Fig. 5; Table 3C).

As in the previous periods, we found strong evidence for highest abundance in river plain and lowest in moss heath during post-incubation (Table 3D & 4). In this latter part of the breeding season, we found that the rate of change in abundance was different in moss heath when compared to heathland, but not between river plain and heathland (Table 3D). During this period, abundance decreased in moss heath (Table 3D; Fig. 5 in green) but did not change in the other two habitats (Table 3D, Fig. 5).

Finally, Whimbrel abundance during incubation differed between years (Table 3C; Fig. 3) where we found strong evidence supporting higher abundance in 2020 and 2021 than in 2019. We also found evidence for higher abundance with increased area of the site when considering the entire season and the first two periods (Table 3A, B, C).

Table 3. Results of a GLMM investigating temporal (Day) and spatial (habitats) variation in Whimbrel abundance for the entire breeding season (A) and for each breeding period: pre-incubation (B), incubation (C), and post-incubation (D). The reference levels are Habitat = Heathland, Year = 2019. Information on random terms and number of observations are shown in E.

	A. Entire season				**B. Pre-incubation**			
Predictors	Estimate	Standar error	z value	p value	Estimate	Standar error	z value	p value
Intercept	2.359	0.149	15.799	**< 0.001**	1.884	0.313	6.011	**< 0.001**
Day	0.005	0.001	3.712	**< 0.001**	0.032	0.011	2.969	**0.003**
Habitat								
Moss heath	-1.039	0.243	-4.268	**< 0.001**	-1.277	0.342	-3.733	**< 0.001**
River plain	0.250	0.208	1.203	0.229	-0.094	0.237	-0.394	0.693
Area (log)	0.463	0.151	3.063	**0.002**	0.210	0.103	2.037	**0.042**
Year								
2020	0.197	0.068	2.902	**0.004**	0.192	0.253	0.760	0.447
2021	0.175	0.069	2.538	**0.011**	0.084	0.256	0.330	0.742
Day : Habitat								
Day : Moss heath	-0.005	0.003	-1.845	0.065	0.007	0.019	0.387	0.699
Day : River plain	0.011	0.002	5.933	**< 0.001**	0.036	0.014	2.607	**0.009**

	C. Incubation				**D. Post-incubation**			
Predictors	Estimate	Standar error	z value	p value	Estimate	Standar error	z value	p value
Intercept	2.561	0.125	20.458	**< 0.001**	2.360	0.312	7.568	**< 0.0001**
Day	0.005	0.003	1.435	0.151	0.012	0.010	1.243	0.308
Habitat								
Moss heath	-1.165	0.214	-5.438	**< 0.001**	-0.423	0.485	-0.872	0.383
River plain	0.596	0.165	3.622	**< 0.001**	1.434	0.432	3.319	**< 0.001**
Area (log)	0.464	0.110	4.225	**< 0.001**	0.425	0.298	1.428	0.153
Year				**< 0.001**				
2020	0.272	0.067	4.089	**< 0.001**	0.092	0.116	0.798	0.425
2021	0.451	0.069	6.531	**< 0.001**	0.024	0.121	0.198	0.843
Day : Habitat								
Day : Moss heath	-0.003	0.007	-0.372	0.710	-0.050	0.016	-3.110	**0.002**
Day : River plain	0.007	0.004	1.678	0.093	-0.005	0.013	-0.359	0.720

E. Random effects	**Entire season**	**Pre-incubation**	**Incubation**	**Post-incubation**
Variable name	Site	Site	Site	Site
Groups	14	13	14	14
Nr. observations	446	133	184	129
Variance	0.068	$7.33\ e^{-16}$	0.025	0.280
Standard dev.	0.260	$2.71\ e^{-8}$	0.159	0.529

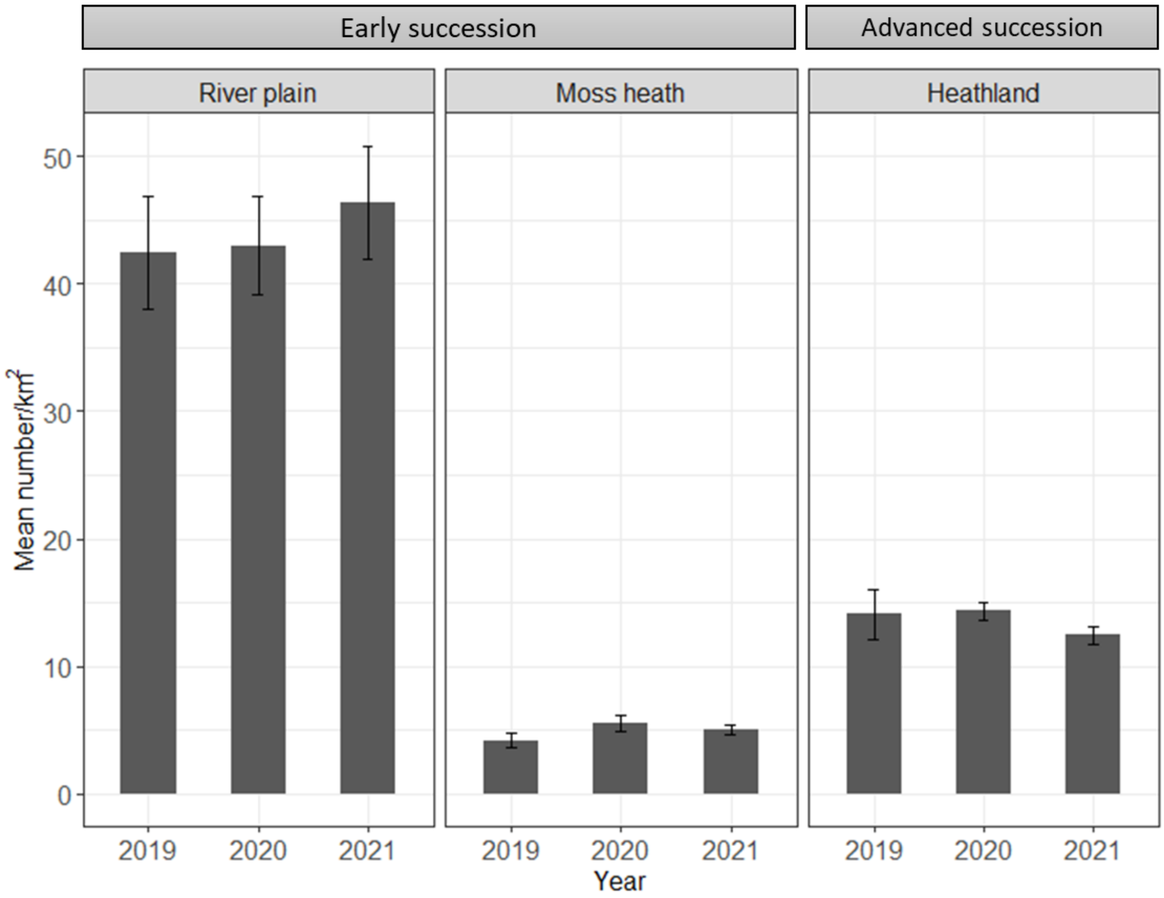

Figure 3. Annual variation in Whimbrel abundance across three habitats at different succession stages for the whole breeding season. Means (±SE) of counts from Whimbrel arrival in spring to the post-breeding season are shown.

Table 4. Pairwise comparisons using estimated marginal or least-squared means testing whether Whimbrel abundance differed between habitats for the entire breeding season and its three periods.

	Entire season			**Pre-incubation**		
Habitat comparison	Estimate	SE	p.value	Estimate	SE	p.value
Heathland-Moss heath	1.264	0.21	**< 0.0001**	1.17	0.157	**< 0.0001**
Heathland - River Plain	-0.776	0.185	**0.0001**	-0.425	0.122	**0.001**
Moss heath - River plain	-2.041	0.212	**< 0.0001**	-1.595	0.137	**< 0.0001**
	Incubation			**Post-incubation**		
Habitat comparison	Estimate	SE	p.value	Estimate	SE	p.value
Heathland-Moss heath	1.219	0.162	**< 0.0001**	1.16	0.421	**0.016**
Heathland - River Plain	-0.754	0.133	**< 0.0001**	-1.37	0.372	**0.001**
Moss heath - River plain	-1.973	0.156	**< 0.0001**	-2.53	0.425	**< 0.0001**

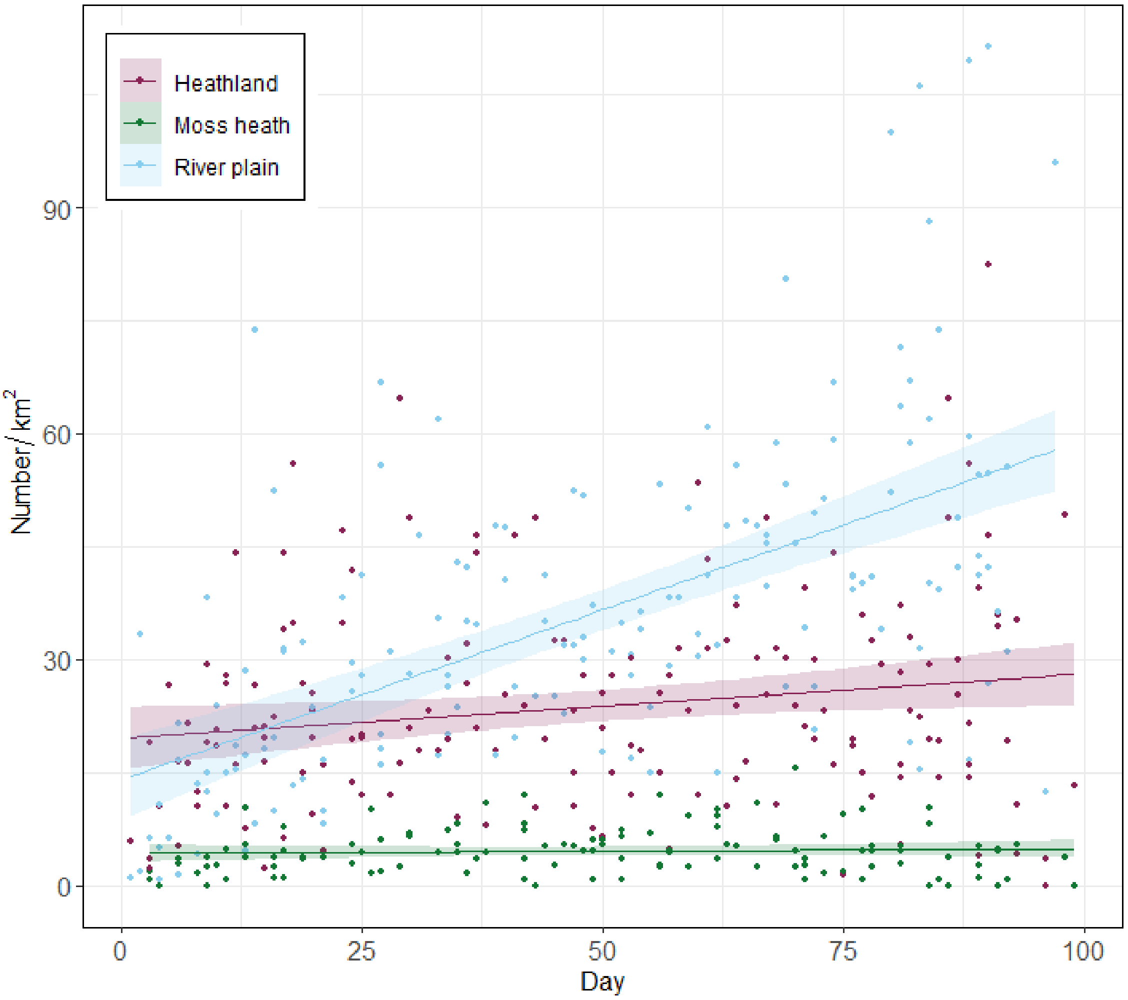

Figure 4. Variation in Whimbrel abundance counted per day (birds/km^2) during the whole breeding season (May to end of July) in river plain, heathland and moss heath habitats. Pre-incubation started on the first sampling day (day 1) and ended on day 27. Incubation started on day 28 for all years and ended on day 74 in 2019, day 68 in 2020 and day 67 in 2021, Fig. S1. Post-incubation lasted from the end of incubation (day = 75, 69, 68 for 2019, 2020 and 2021, respectively) to the last field survey.

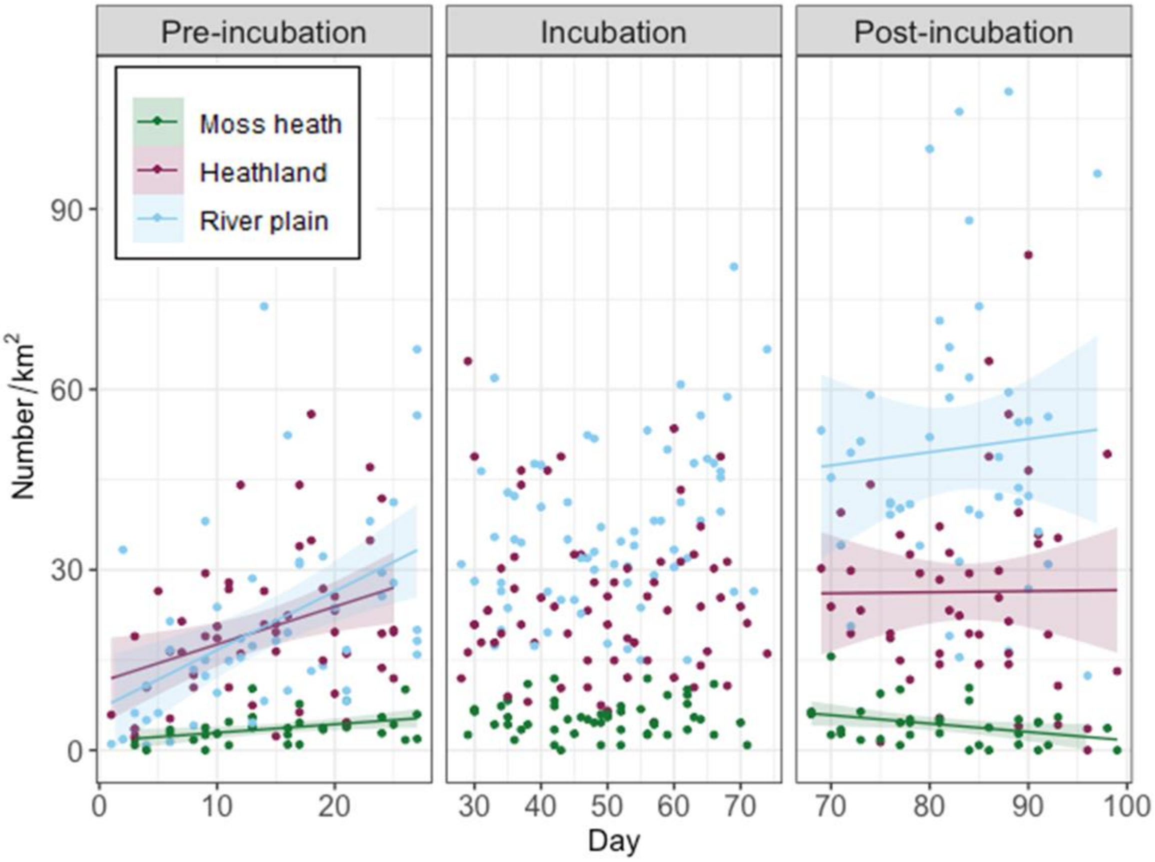

Figure 5. Seasonal variation in Whimbrel abundance (birds/km^2), per day across different habitats during the breeding season. The breeding season was split into pre-incubation, incubation and post-incubation based on mean laying and hatching dates (Table 2).

Discussion

Arctic and sub-Arctic regions are experiencing climate change at an intensity of twofold the global average (Collins et al., 2014). These changes affect ecosystem functioning at all levels, from abiotic traits such as nutrient cycling and hydrology, to biotic ones such as species composition and abundance. As a result, the ecological succession within ecosystems can be disrupted. Iceland has the highest rate of soil erosion and desertification in Europe (Arnalds, 2008), which together with climate change and anthropogenic effects, modifies the natural succession patterns, for example, by altering periodic floods that keep river plain habitats at early stages of succession, or by promoting erosion in stable moss fields which open patches of bare ground suitable for colonization and establishment of vascular plants. Such changes in the succession can modify the habitat composition according to the different historical processes that occurred within them, and ultimately affect population dynamics. In this study, we investigated seasonal differences in Whimbrel breeding abundance across habitats at different succession stages in South Iceland. We found that highest and lowest Whimbrel abundance occurred in habitats at early stages of succession, and that abundance throughout the breeding season varied between habitats. Considering likely trajectories of changes to these habitats, these results have important implications for Whimbrel population persistence.

Variation in abundance amongst habitats

Differences in overall Whimbrel abundance between habitats were consistent for the whole breeding season and its three separate periods. As in previous studies, Whimbrel abundance was highest in river plain habitats (Gunnarsson et al., 2006a; Katrínardóttir et al., 2015), whereas abundance in moss heath was lowest, suggesting this habitat might be of lower quality. Abundance in heathland, the habitat at a more advanced stage of succession, lay in between the other two. Differences in Whimbrel abundance across these three habitats at different succession stages may be driven by local differences in resource availability, predation pressure and/or landscape structure and maintained by the philopatry and longevity of Whimbrels (Johnson, 2007; Brandolin & Blendinger, 2016; Méndez et al., 2018; Gill, 2019). Other studies reported higher abundance of invertebrates, likely prey for Whimbrels, on a river plain than in heathland (Gunnarsson 2000), and lowest invertebrate abundance in moss heath when comparing the same three habitats (Cerezo-Araujo et al., *in prep*). Aggregation of individuals in areas with better resources could result from higher recruitment and/or survival rates within these sites, coupled with the high philopatry of the species for which the same areas will be used year after year.

Variation in abundance throughout the breeding season

General progression of the breeding season suggests that Whimbrel abundance should increase in all habitats when birds arrive from their wintering grounds (pre-incubation period), become stable when territories are established, the first eggs are laid and incubation starts (incubation period), and to decrease towards the end of the breeding season as birds desert territories and migrate to the wintering grounds (post-incubation period). However, this was not as straightforward in our study as the rate of change at which abundance varied differed across habitats.

These differences were first noticeable when we considered the entire breeding season, where we found an increase in abundance in river plain and heathland, but stable abundance in moss heath. These increasing trends in habitats where Whimbrel abundance was higher and the lack of trend in moss heath with lowest abundance, corroborated the idea that river plain and heathland probably offer more favourable conditions for Whimbrels than moss heath. To look further into the importance of these habitats throughout the season, we split the breeding season into three separate periods.

During pre-incubation, an overall increase in abundance was found in all habitats, but the increase was faster in river plain than in the other two habitats (Table 3). The greater rate of change in river plain sites may be explained by the higher Whimbrel abundance and more individuals arriving in this habitat of (probably) better quality. Considering that many waders are philopatric to the natal sites (Redmond and Jenni 1982; Kruk et al., 1997), and evidence for natal philopatry in Whimbrels exists (Skeel 1983), if better quality sites have higher breeding success that could result in a higher number of first breeders returning to their natal site. Alternatively, it could also be explained by differences in arrival schedules between habitats. Although earlier arrival in better quality habitats has been described for other migrant waders like the Icelandic Black-tailed Godwit (Gunnarsson et al., 2006), this may not be the case for our study species. Whimbrels migrate longer distances, arrive later than most of the other Icelandic waders and their arrival period is shorter. Thus, they are time-constrained by the long migration and the short Icelandic summer and their tight individual schedules may be similar across different breeding habitats (Gunnarsson 2010; Carneiro et al., 2019b).

Whimbrel abundance remained stable in all habitats during incubation indicating the advantage of censusing Whimbrels during this period of the breeding season to get reliable estimates of abundance. Similar findings were reported by Meltofte (2001) when studying breeding waders in Zackenberg, Greenland. Differences in nesting success and renesting attempts between habitats might exist, but our data suggest that few Whimbrels left the breeding sites during the incubation period, even after early nest failure.

During the final part of the breeding season, we found a decrease in abundance in moss heath but no changes in heathland or in river plain, which remained quite stable. These results suggest that some habitats might be more suitable than others during the latter part of the breeding season due to either differences in resources for adults and/or breeding success. Hence, a decrease in Whimbrel abundance in moss heath could indicate that this habitat (I) has generally lower breeding success, (II) is less suitable for raising chicks or (III) that it is not suitable for fuelling prior to migration flight and Whimbrels move somewhere else for this purpose. The overall higher abundance in river plain and heathland and no changes in abundance during the post-incubation period suggest that these two habitats may have higher breeding success or offer better resources for either chick-rearing or migration preparation. One study on Icelandic Whimbrels reported low hatching success in moss heath but similar chick survival from hatching to fledging across river plain and heathland (Gunnarsson, 2000), and others reported similar likelihood of adults having broods across different habitats (Katrínardóttir et al., 2015; Cerezo-Araujo et al., *in prep*). Therefore, differences in abundance in the post-incubation period may stem from a combination of differences in overall numbers of Whimbrels using different habitats, variation in breeding success or local resources for migration fuelling.

Finally, differences in detectability might help explain some of the variation in changes in Whimbrel abundance throughout the season. At the start of the breeding season, activities like pair bonding and territory establishment make birds more detectable (Meltofte, 2001), especially in areas of higher abundance. During incubation, these activities normally decrease and adult birds become more cryptic (Meltofte, 2001). During chick-rearing, the feisty behaviour typical of several species of waders (Gunnarsson et al., 2017), increases their detectability, and under certain types of disturbance, like the presence of a predator or a human observer, small groups of adults gather emitting alarm calls (Meltofte, 2001). This would be especially true in habitats with higher Whimbrel abundance and potentially higher productivity.

Variation in abundance in relation to succession

Transition from one habitat to another can be expected over time through ecological succession which can be exacerbated by human impacts. Consequently, changes in the abundance and community composition of species will follow and site importance for breeding Whimbrels could change. Accordingly, a transition from moss heath to heathland, of probably better quality, could result in an increase in Whimbrel abundance. Despite this, not all sites might be suitable for hosting the species since other characteristics such as altitude likely play a role in the species habitat suitability (Jóhannesdóttir et al., 2018).

Although heathland has been identified as an important habitat for breeding Whimbrels, the transition from river plain will probably be reflected in a decrease in local Whimbrel abundance. Finally, the climax of the ecological succession in the Icelandic lowlands is the native birch forest (Kristinsson 1975). The transition from any of the open habitats studied here towards the climax would implicate taller vegetation structure. This will jeopardize the presence of species dependent on open landscapes like Whimbrels. Avoidance of taller vegetation such as shrubby habitats (Ballantyne and Nol 2011) and woodlands (Gunnarsson et al., 2006a) has previously been reported for Whimbrels and it is unlikely that they will be able to adapt to a dense shrub-dominated landscape.

Barrio et al., (2018) developed state-and-transition models describing changes to Icelandic habitats through a combination of natural and anthropogenic factors which cast light on the likely progression of the habitats examined here and the consequences for Whimbrels. All the habitats where Whimbrels consistently breed are open and with short vegetation (Jóhannesdóttir et al., 2014). Both riverplain and moss heath occur relatively early in the succession process but on different topographies and originate from different processes. Heathland, however, is further along the succession gradient with more diversity and vegetation cover. These three habitats are affected by characteristic processes that impact the direction of the succession process (Fig. 6). Besides the aforementioned changes in hydrology, erosion and stochastic events, anthropogenic impact such as grazing and agriculture have widespread impact (Fig. 6). Changes in habitats through expansion of infrastructure like houses, roads and power lines also compromise the persistence of these habitats and hence the breeding populations of Whimbrels and other open-landscape, ground-nesting waders (Pálsdóttir et al., 2022). In addition, the increasing use of non-native species for ecosystem restoration, economic development and recreation pose a risk for open habitat specialists like waders, first in terms of changes in the ecological succession and community composition, and second, in terms of invasions. This was the case with the introduction of Nootka lupin (*Lupinus nootkatensis*) to alleviate soil degradation in Iceland (Benediktsson, 2015), which spreads readily, creating habitats of taller vegetation used by a different bird community than found in comparable open habitats, not colonized by lupins (Davidsdottir et al., 2016). Recent plans aiming to increase carbon sequestration in the Icelandic lowlands with large-scale afforestation of open habitats (Pálsdóttir et al., 2022) could have similar consequences. Replacement of heathland and other open habitats by forest will most likely be followed by changes in the bird community composition for which a shift from open-landscape specialist, to shrubland and forest birds with a preference for taller vegetation is likely to occur. Considering that ca 40% of the world population of Whimbrels breed in Iceland, where they show high preference for river plains and heathland (Gunnarsson et al., 2006a; Katrínardóttir et al., 2015), their transition towards other habitats, either from natural or anthropogenic origin, is likely to have important implications for the population.

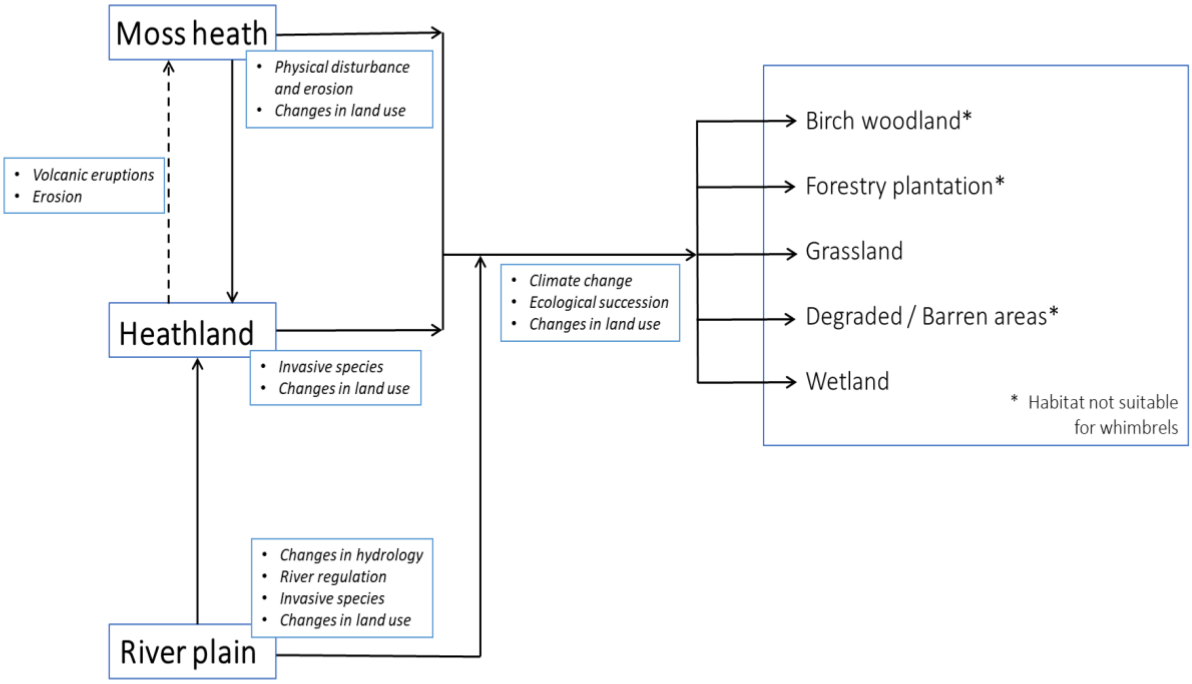

Figure 6. Likely changes in the ecological succession occurring in Iceland and the processes involved in state shifts. The habitats explored in this study are shown in separate boxes and in bold. Other common habitat types which occur further along the succession gradient are also shown and a star (*) indicates habitats not or less suitable for breeding Whimbrels. The arrows indicate the direction the succession process is likely to take and text in italics indicates the different processes that can drive the transition from one habitat state to another. Note the dashed line between heathland and moss heath: under a catastrophic event like a volcanic eruption, an ecosystem will return to barren land. After this, early colonizers of primary succession will establish. Adapted from Barrio et al., 2018.

Conclusions

Differences in Whimbrel abundance were not explained by the process of ecological succession itself, but rather this process is responsible for differences in habitat conditions which in turn determine local Whimbrel abundance. Therefore, threats modifying the direction and strength of the succession process are likely to have cascading effects on the community composition and abundance of species inhabiting these habitats. The seasonal differences in abundance found in this study are a result of the Whimbrel breeding cycle in combination with habitat-specific processes. Moreover, the varying rates of change in abundance during post-incubation suggested higher suitability of heathland and river plain during this period, when food resources might be a limiting factor for chick growth and/or migration fuelling. Under the current climatic crisis, changes in habitat use, and the recent declining Whimbrel population trends reported in other studies, we recommend taking the information presented here into consideration when planning a strategy focused on human-wildlife coexistence before strict and costly conservation efforts become the only option. Prioritizing the protection of river plain and heathland habitats is likely to be imperative for Whimbrel population persistence.

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Appendices

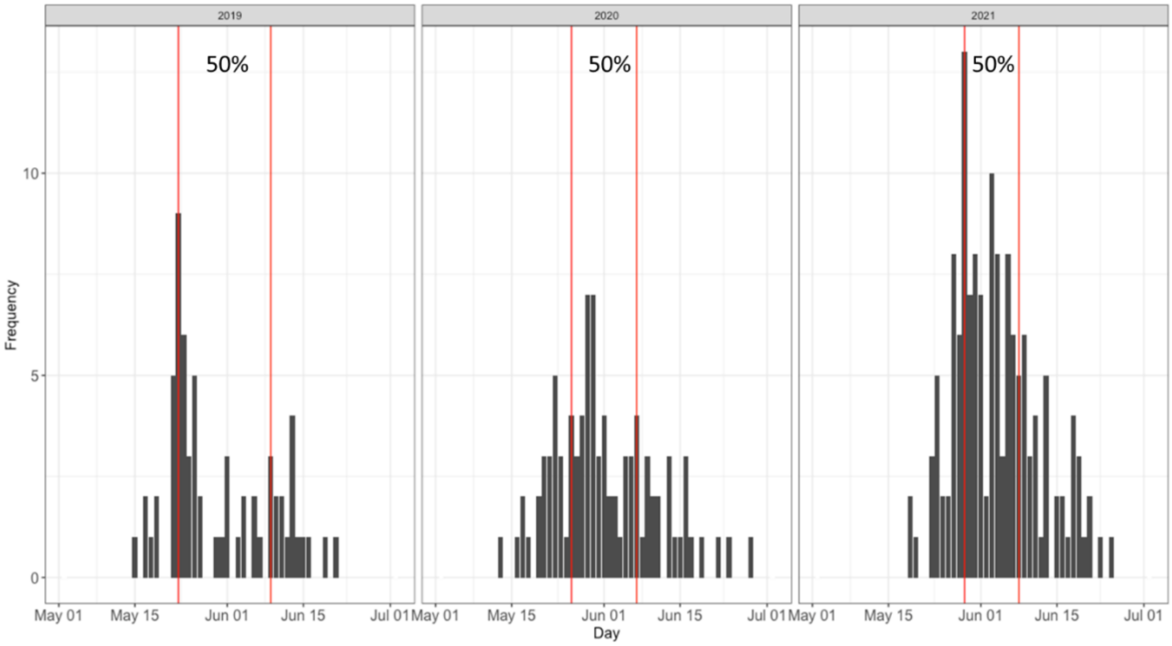
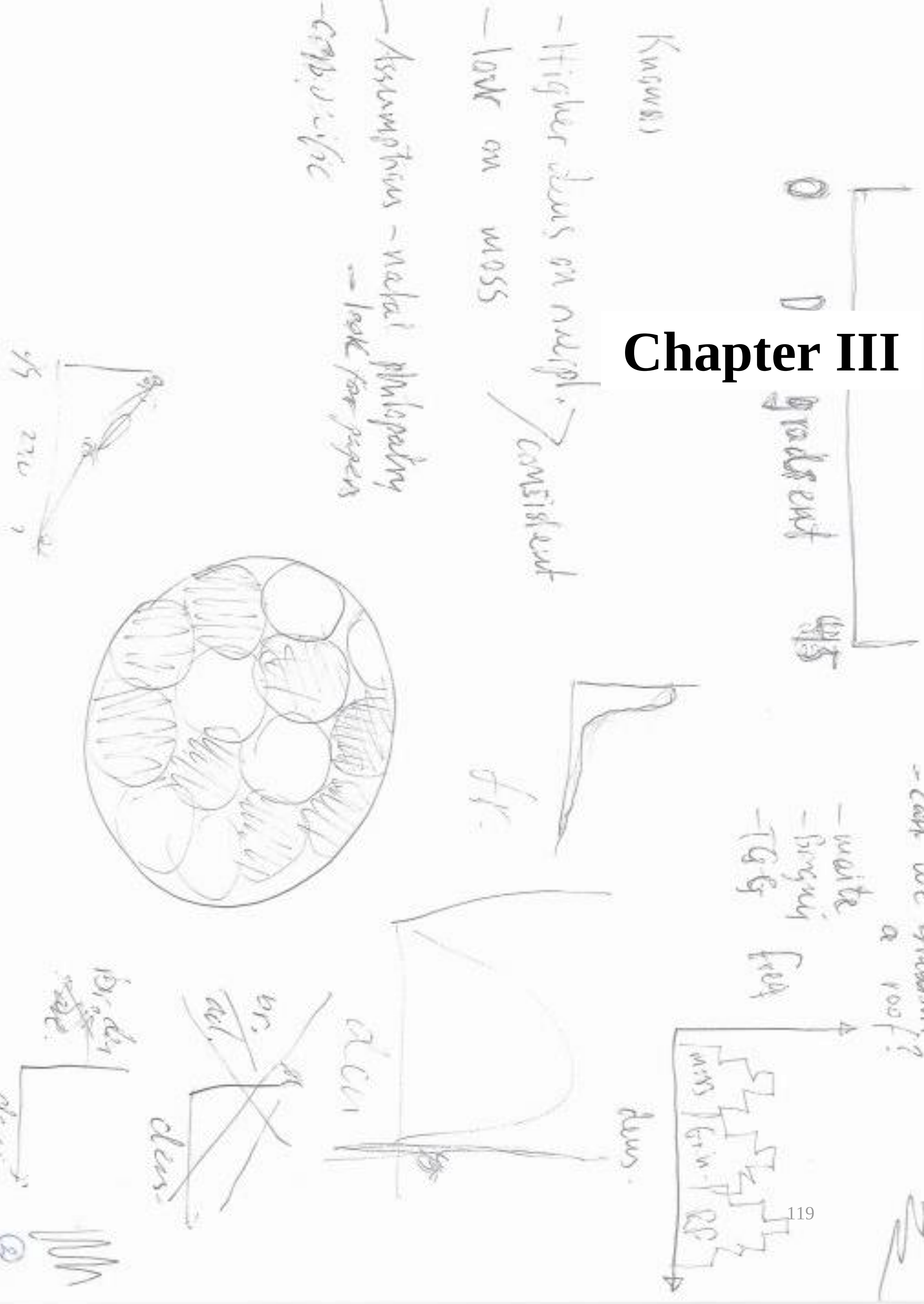


Figure S1. Frequency distribution of Whimbrel laying dates for the three years of study. Dates corresponding to the second and third quartiles are within the red lines and correspond to 50% of the dataset for the first egg laid.


Knows
- Higher dens on nupl.
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Chapter III

Chapter III. Do habitat quality and breeding success explain variation in breeding density of a sub-Arctic wader?

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Summary

Spatial variation in density is often mediated through differences in habitat quality in combination with intrinsic factors in the population and the species' biology. However, as density is not always correlated with habitat quality, measuring different demographic rates and their relationship with appropriate components of habitat quality can provide important insights into the underlying processes driving variation in density. Under the current climatic crisis, species inhabiting high latitudes are predicted to be greatly affected. In Iceland, waders breed at varying densities and in internationally important numbers across semi-natural habitats, providing a good opportunity to explore the processes driving variation in density. Using the variation in Whimbrel (*Numenius phaeopus*) density in Iceland across seven sites and three years, we examined the relationships between adult and brood abundance with availability of potential invertebrate prey and potential predator pressure; and explored whether breeding success (brood:pair ratio) was related to local breeding density. Variation in adult abundance was not explained by prey abundance or predator pressure during incubation, but sites with higher invertebrate abundance during the chick-rearing had higher brood abundance. Although sites with higher adult density produced more broods, breeding success (brood:pair ratio) was similar across breeding densities. Given that Whimbrels are philopatric and long-lived, the variation in breeding density may be maintained by the higher number of broods produced at sites with higher density, possibly due to the higher abundance of potential prey for chicks. At the same time, given the strong habitat preference of the species, density dependent mechanisms might explain the apparently similar breeding success across breeding densities. These results highlight the importance of conserving higher density sites which produce substantially more offspring per unit area.

Keywords

Shorebirds; density dependence; breeding success; predator attacks; food resources; invertebrate abundance

Introduction

The mechanisms by which individuals distribute themselves in heterogeneous landscapes remain central to population ecology. Resources are unevenly distributed across habitats and their availability and quality vary spatially following e.g., primary productivity, latitudinal gradients, topography and historical processes, which result in differences in species density (Cook, 1969; Johnson, 2007). Moreover, species-specific behaviour can play a crucial role in determining the density of individuals through for example competitive exclusion hindering access to resources, like territoriality and hierarchy (Fretwell & Lucas, 1969; Sutherland, 1996; Liley and Sutherland 2007; O'Neil et al., 2020), or conspecific attraction for which the presence of conspecifics is used as a positive cue for resource availability (Stamps, 1988; Gill, 2019; Jeglinski et al., 2023). Therefore, local population density can result from the combination of density independent factors driving abiotic conditions and local resources such as food abundance, and density dependent factors modifying access to these resources and affecting individual fitness through population numbers (Nicholson, 1935; Sutherland, 1996; Johnson, 2007).

In non-experimental studies in the wild, identifying these density dependent factors and the mechanisms behind them can be challenging, as the relationships between density and demographic rates are often masked by feedback processes. For example, *per capita* reproductive output may decrease with breeding density negatively affecting the population growth rate. This mismatch between reproductive output and density might arise through increases in competition for resources, or changes in other components of the habitat (e.g., increased predation or parasitism). For this reason, density may not always adequately reflect abundance of resources and other habitat components, habitat quality hereafter, ultimately associated with increased reproduction and survival (Van Horne, 1983; Battin, 2004; Johnson, 2007; Bock and Jones, 2012; Mott et al., 2023). Moreover, multiple mechanisms can act simultaneously (Rodenhouse et al., 2003) and their effects can be very subtle and difficult to detect depending on the scale studied (Hubbell et al., 1990; Krebs, 1995). Therefore, measuring different demographic parameters and their relationships with variation in habitat quality may yield valuable insights into population regulation (Johnson, 2007; Mott et al., 2023).

The increasing temperatures (Post et al., 2019) and extreme weather events (Saha et al., 2006) experienced after the Industrial Revolution, coupled with habitat loss and degradation are altering species composition, population densities, and their relationship with the habitat they occupy (Post et al., 2009; Post et al., 2019). These changes are predicted to be especially harsh and fast in the Arctic and Sub-Arctic (Collins et al., 2014; Post et al., 2019; Shukla et al., 2019), breeding grounds of many migratory waders (Charadrii) which are generally declining and many are severely threatened (Meltofte et al., 2007; Pearce-Higgins et al., 2017; Wauchope et al., 2017; Rosenberg et al., 2019; Smith et al., 2020). For example, changes in environmental factors increased predation rates on sub-Arctic wader nests in Sweden (Machín et al., 2019), and reduced chick growth rates of waders in Arctic Canada (McKinnon et al., 2012), while warming-induced shrub and tree encroachment in sub-Arctic Canada is predicted to decrease nesting habitat for breeding Whimbrels (*Numenius phaeopus*; Ballantyne & Nol, 2011).

Very large numbers of individuals of several wader species such as European Golden Plover (*Pluvialis apricaria*) and Whimbrel breed in Iceland, which is one of the most important breeding grounds for waders in Europe (Gunnarsson et al., 2006; Jóhannesdóttir et al., 2014). Within Iceland, waders show great variation in local breeding density, with individual species densities ranging from ca. 1-2 pairs/km^2 to over 40 pairs/km^2, and many reaching their highest abundance in the southern lowlands of the country (Gunnarsson et al., 2006; Jóhannesdóttir et al., 2014; Méndez & Gunnarsson, 2020). This wader hotspot is characterized by a mosaic of different semi-natural open habitats of varying quality like heathlands, wetlands, and agricultural fields (Gunnarsson et al., 2006; Jóhannesdóttir et al., 2014; Cerezo-Araujo et al., *under review*), making this a suitable model system to investigate the relationship between breeding density, demography and variation in habitat quality. However, these open landscapes have undergone severe anthropogenic changes in land use such as wetland drainage and increased human infrastructure, reducing the extent and quality of these habitats (Jóhannesdóttir et al., 2014; Pálsdóttir et al., 2022). Whimbrel, an open landscape specialist, is commonly found breeding at different densities, particularly in river plain and heathland habitats and the southern population has recently shown signs of a rapid decline (Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Cerezo-Araujo et al., *under review*). Although Whimbrel breeding density varies greatly between habitats, the drivers of this variation and the demographic and conservation implications are currently unknown. In this study, we investigated the relationships between breeding density, breeding output, and habitat quality in the Icelandic Whimbrel. Our aim was to gain insight into drivers of variation in local breeding density across the landscape and its implication for conservation. Using two components of habitat quality and two demographic rates measured during three years and across seven sites of varying breeding density, we tested whether (i) potential food resources and potential predator pressure explained adult and brood abundance, and (ii) whether breeding success was related to local breeding density.

Material and methods

Study system

Fieldwork

A total of seven study sites, which varied in Whimbrel breeding density, were surveyed during three breeding seasons 2019-2021 in the lowland plains of South Iceland (Fig. 1; Table S1; Jóhannesdóttir et al., 2014; Gunnarsson et al., 2017; Alves et al., 2019; Laidlaw et al., 2020). In 2019, six sites were surveyed once a week during the entire season. In 2020 and 2021, six sites were surveyed once a week from 1st – 20th May and 15th July to beginning of August, and twice a week from 21st May – 14th July. One site had to be replaced after the first year due to infrastructure development in the area (Table S1). The average area of the sites was 1.24 km^2 (±0.25 SE) and ranged from 0.43 to 2.2 km^2 (Table S2). All sites were located below 230 m a.s.l., and their relatively flat and open landscape permitted high visibility (Table S2). We predetermined the area of the sites using an

Icelandic online mapping service (www.ja.is/kort), and elevation was obtained from the Google Earth engine. Access to the sites was granted by landowners.

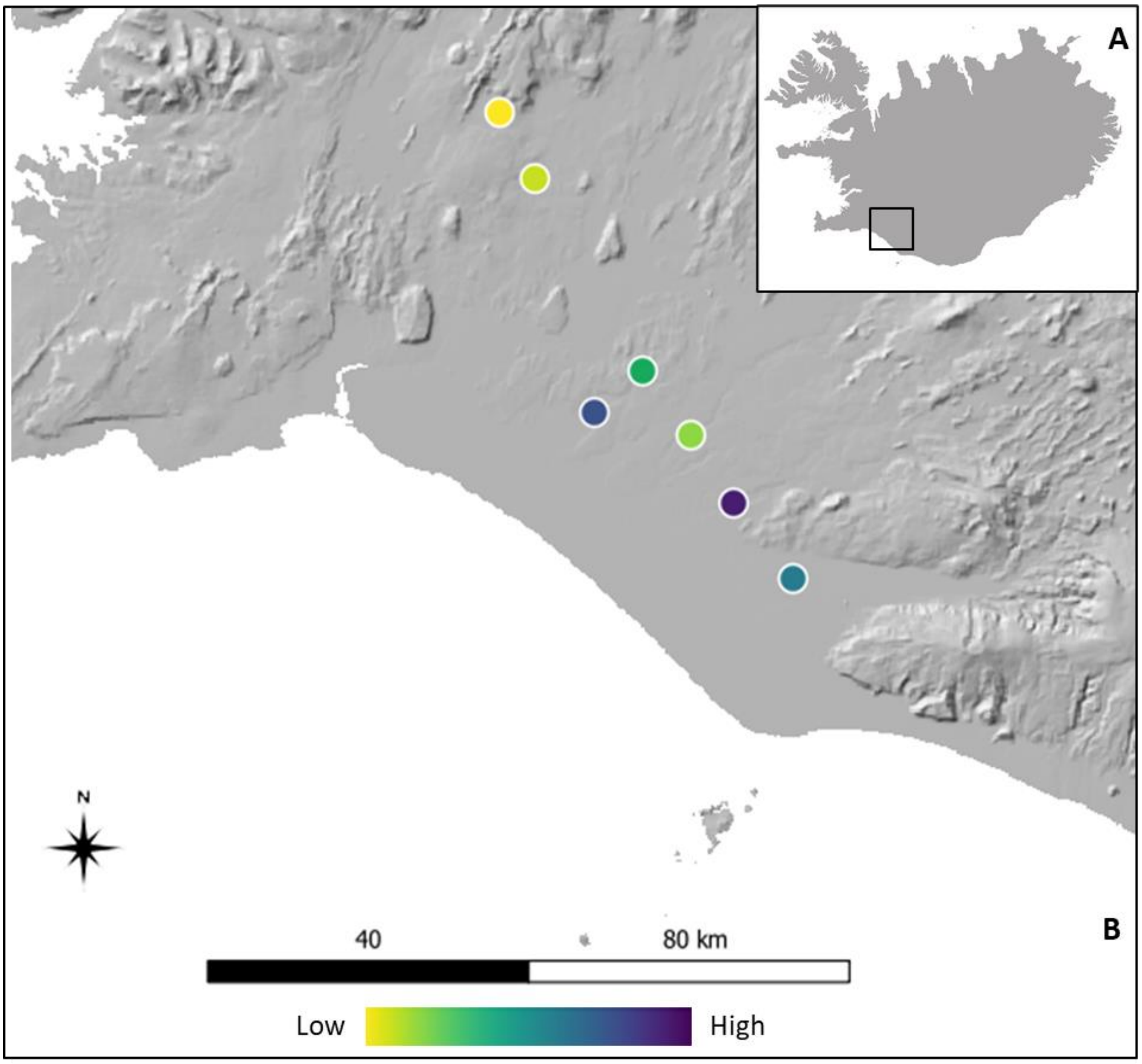

Figure 1. Map of Iceland (A), and the locations of the seven study sites showing variation in mean adult Whimbrel density during incubation (Table S3; range: 5.3 – 52.9 adults/km2) (B).

Adult and brood surveys

Adult and brood Whimbrel counts were performed once or twice a week per site (see Fieldwork section) in the morning hours (starting time range = 7:00 to 11:00; Table S2). The surveys were performed by car and on foot using binoculars (8x42). We drove on dirt tracks at a maximum speed of 10-20 km/h with open windows to aid detection. When the tracks were impassable or when the topography impaired visibility, we walked to cover the whole study site. We counted all adults on the ground and flying low over the site during the breeding season from May to the beginning of August. Double counts were avoided by surveying in one direction and by carefully noting the position of birds passed and those that moved further. Brood counts started in June, when the first Whimbrel nest hatched (Katrínardóttir et al., 2015; Alves et al., 2019; Carneiro et al., 2019; Laidlaw et al., 2020; Cerezo-Araujo et al., *under review*). Broods were counted by either spotting chicks accompanied by adults, or by using the feisty parental behaviour as an indicator of brood presence (Grant et al., 2000; Gunnarsson et al., 2005; Bolton et al., 2012; Katrínardóttir et al., 2015; Gunnarsson et al., 2017; Jarret et al., 2023; Cerezo-Araujo et al., *under review*). Other wader studies have reported declines in chick mortality 7-10 days after hatching (Machín et al., 2019), and hence the presence of a brood after this crucial period likely represents a successful breeding event (Jarrett et al., 2023). We thus did not count the number of chicks per brood to minimize the time spent near them and possible disturbance. Counts were avoided under low visibility due to fog, rain above 1 mm/h and average wind exceeding 7 m/s to minimize disturbance to breeding birds during harsh conditions and to ensure detectability. Most of the surveys (91.5%) were carried out by the same observer.

Habitat quality

To assess habitat quality, we studied two habitat components commonly considered important drivers of nesting effort and breeding output (Mott et al., 2023): potential prey availability and potential predator pressure. Surface-active invertebrates are an important part of the diet of chicks, and it has been shown that daily survival rates for other wader chicks increased with invertebrate biomass (Saafeld et al., 2021). Increased nest predation in Europe has been identified as a potential driver of declining wader populations (Chamberlain & Crick 2003, Milsom 2005, McDonald and Bolton 2008), and predation rates of wader nest in south Iceland have been estimated at ca. 40-50% (Laidlaw et al., 2020; Pálsdóttir *pers. comm.*).

We sampled invertebrate abundance as potential prey availability using six pitfall traps per site filled with water (25%), clear antifreeze for preservation (75%), and soap to break the surface tension of the water. The round plastic containers were 9.5 cm in diameter and had a cover (12 cm in diameter) 5 cm above them to prevent rainwater from overflooding. Since the study sites were relatively homogeneous in terms of habitat type and structure, two sets of three independent traps each were placed ca. 10 m apart in a row, close to the entry and exit to the site to facilitate their collection and replacement. Locations did not change from year to year. Pitfall traps were placed at the end of May and beginning of June coinciding with the beginning of the incubation period (Carneiro et al., 2019; Laidlaw et al., 2020), and were emptied every seven days until the last week of July or first week of August, covering the brood-rearing period. Samples were analysed under a magnifying glass and large crawling and flying invertebrates (≥ 3 mm), considered most important in the diet of large waders, were sorted to Order level and counted (Schekkerman et al., 2007).

To measure potential predator pressure, every time an intruding predator was noticed and/or observed within a study site, the number and species were recorded. We then estimated potential predator pressure as the frequency of predator intrusions per hour during the surveying period for all years and sites (information on surveying time is given in Table S2). Main predators of nests and chicks in south Iceland are Common Raven (*Corvus corax*), Arctic Skua (*Stercorarius parasiticus*), large gulls (*Larus* spp.) and Arctic Fox (*Vulpes lagopus*). Occasional predators are Great Skua (*S. skua*), Merlin (*Falco columbarius*), Gyrfalcon (*F. rusticolus*), Short-eared Owl (*Asio flammeus*), Mink (*Neogale* *vison*), and feral cats (*Felis catus*) (Jónsson & Gunnarsson, 2010; Carbonell-Ellgutter et al., 2020; Jónsson et al., 2023; Pálsdóttir et al., *unpublished*). Avian predators were considered a threat when they showed signs of searching behaviour, irregular flight, or hovering, but we excluded Arctic Skuas showing alarming behaviour close to their own nests, as they were breeding in some of the study sites. Birds flying high and directionally were omitted (Jónsson & Gunnarsson, 2010), while all mammalian predators were considered a potential threat. The study sites are open areas with unobscured horizon and thus the predator intrusion events were easily detectable, and all predator detections were done by the same experienced observer. Moreover, waders and other birds such as Arctic Terns (*Sterna paradisaea*) and Arctic Skuas strongly react to predators aiding their detection.

Data analysis

To investigate how differences in habitat quality across sites and during the breeding season affected adult (first model) and brood abundance (second model) of Whimbrels, we used generalized linear mixed effect models, GLMM (R package *lmer4* v.1.1-33, Bates et al., 2017).

The response variable in the first model, adult abundance (i.e., number of adults; see Table 1 for definitions), was defined as the maximum number of adults counted per week and site during the incubation period when numbers are generally most stable (from the third/fourth week in May to the second week in July; Cerezo-Araujo et al., *under review*). Invertebrate abundance (i.e., mean number of invertebrates ≥ 3 mm per trap and week, in log scale), and Intrusions/h (i.e., number of intrusions per hour spent on a site) recorded each week during the incubation period were included as explanatory variables. We used invertebrate abundance as a proxy of invertebrate biomass (Gillespie and Fontaine 2017) as both have been shown to be correlated in other wader studies (Schekkerman et al., 2003; Reneerkens et al., 2016). Year was included as a covariate to account for annual variation in adult abundance and Area (km^2 of the site in log scale) was included as an offset term to account for its potential effect on abundance (i.e. larger sites are more likely to host more birds). Site and sampling Week were included as random terms to account for non-independence of counts. Negative binomial error distribution and logit link were used for this first model to account for overdispersion of the dataset. We did not test the importance of independent potential prey species separately due to insufficient information on prey use and preference for Whimbrels during the breeding season (Guðmundson, 1957).

Table 1. Variables name and definitions.

Variable name	Definition
Adult abundance	Highest number of adult Whimbrels observed per week, site, and year during incubation. Used as response variable to model variation in adult abundance across sites with different components of habitat quality (model 1, Table 1A).
Mean adult density	Mean of the three highest adult counts during incubation/km^2 per site and year. Used as explanatory variable in models 2 and 3 (Table 1B; Table 2).
Brood abundance	Highest number of broods observed per week, site and year. Response variable to model variation in brood abundance across sites of different components of habitat quality and mean adult density (model 2, Table 1B). Used as a measure of weekly variation in breeding output.
Breeding success	Brood:pair ratio, or proportion of pairs with successfully hatched broods, calculated using the mean of the three highest observations of brood abundance divided by the potential breeding pairs per site and year. Used as a measure of *per capita* breeding output (model 3, Table 2).
Potential breeding pairs	Mean of the three highest adult observations during incubation /2, rounded to the nearest integer, per site and year. Used to calculate the brood:pair ratio in model 3 (Table 2).

The response variable in the second model, brood abundance (i.e., number of broods; Table 1) was defined as the maximum brood count per week and site, and therefore served as a measure of weekly breeding output. Since monitoring was continuous (i.e., from May to August), we included data from the first brood detection for all years. This occurred on the 24th of June 2019 (week 26), 25th June 2020 (week 26), and 24th June 2021 (week 25) (Fig. S2). Hence, all observations from week 25 for each year were included in the dataset. Invertebrate abundance (in $\log_e$ scale), Intrusions/h during the chick-rearing period and Mean adult density were included in the model as explanatory variables. Year and Week were included as covariates to account for the temporal variation in brood abundance, and Area (log scale) was included as an offset. Mean adult density for each site and year was expressed as the mean of the three highest adult counts during incubation divided by the area (km^2) of the site (Table 1). We used adult density during incubation instead of number of adults observed during the brood surveys because adult abundance during chick-rearing is known to vary in some habitats (Cerezo-Araujo et al., *under review*), which could potentially bias our results. Week was considered as a covariate in this model to account for broods hatching at different times and having repeated observations throughout the period, and Site was included in the model as random effect. Negative binomial error distribution and logit link were used for this second model.

Finally, we investigated if differences in breeding success could be explained by variation in adult density (third model). The response variable Breeding success, expressed as the brood:pair ratio, was used as a measure of *per capita* breeding output, Table 1 (Grant et al., 2000; Jarrett et al., 2023). To calculate this, we used the ratio of the mean of the three highest brood observations per site and year during the last part of the breeding season (week 28; Fig. S1) and the number of potential breeding pairs per site and year (i.e., mean number of broods/potential breeding pairs per site and year). As Whimbrels do not exhibit sexual dimorphism, potential breeding pairs was measured as the mean of the three highest adult counts during incubation divided by two, rounded to the nearest integer (Table 1), as this better reflects the number of pairs that attempt to breed on a site (Cerezo-Araujo et al., *under review*). The explanatory variable was Mean adult density (Table 1), while Year was included as a covariate and Site was included as random effect. Binomial error distribution and logit link function were used for this model.

Data analysis and visualization was performed in R v.4.1.1 (R Core Team, 2021). We checked model performance by inspecting residuals, overdispersion, QQ-plots and fitted values (R package *performance* v.0.10.3, Lüdecke et al., 2021), and model results were reported using a gradual language of evidence for which p-values below 0.001 indicate a very strong evidence of the effect of the explanatory variable on the response variable, and p-values close to 0.05 were interpreted as having weak evidence supporting this relationship (Muff et al., 2021).

Results

A total of 941 invertebrate samples were collected and analysed over the three study years. Invertebrate abundance peaked in the beginning of June in 2019 (week 24), and in the beginning of July in both 2020 and 2021 (weeks 27 and 26 respectively, Fig. S1.A). The number of invertebrates (≥ 3 mm) sampled ranged from 0 to 426 per trap per week, and the mean number of invertebrates per sample during incubation and chick-rearing for all sites and years was 23.55 (±2.50 SE) and 22.89 (±2.23 SE) invertebrates per trap per week respectively. A total of 16 different groups were identified. Arachnida (Aranea and Opiliones), Coleoptera, Diptera, Hymenoptera, Hemiptera, Orthoptera and Lepidoptera were the most abundant groups. Arachnida comprised more than 50% of the total abundance per site and year in most cases, and up to 75% of the samples collected in sites of lowest Whimbrel density (Table S3), and ranged from 27.7% to 95.8% during incubation and from 42.0% to 96.3% during chick-rearing (Fig. S2).The invertebrate community sampled during incubation and chick-rearing was similar but the relative proportion of different groups in the samples varied (Fig. S2). Diptera were more frequent during incubation than during chick-rearing ranging from 0.3% to 70.3% and from 0% to 18.5% respectively; and Coleoptera reached up to 29.68% during incubation and 35.5% during chick-rearing (Fig. S2).

A total of 338 predator intrusions were recorded during the three years of study, and the number of intrusions/h did not show a distinct peak during the Whimbrel’s breeding season (Fig. S1.B). The number of intrusions recorded during a survey ranged from 1 to 10, and the mean number of intrusions/h for all sites and years during incubation and chick-rearing was 0.51 (±0.06 SE) and 0.31 (±0.04 SE) respectively. The mean number of intrusions/h across the different sites ranged from 0.0 to 4.0 during incubation and from 0.0 to 2.1 during chick-rearing (Table S3). Most avian predators were recorded at all sites, while mammalian predators were recorded only in three sites coinciding with medium Whimbrel breeding densities (Table S4; Table S3). Arctic Skua and different species of large gulls (Gulls hereafter) were the most observed predators during incubation, with 60.2% and 52.3% of the total number of intrusions respectively, while Arctic Skua, Common Raven and Gulls carried out ca. 50% of the intrusions in most sites during chick-rearing (Table S4).

Mean adult abundance per week recorded during incubation was 27.27 (±2.84 SE), and ranged from 0 to 130 individuals across sites, with the highest numbers recorded at the largest site (Table S3). The mean potential number of breeding pairs per year on a site was 21.5 (±7.32 SE) and ranged from 2 to 65 between sites. Mean brood abundance per week, site and year was 3.14 (±0.5 SE; Table S3). Brood abundance peaked during week 29 in all years (Fig. S1. D), five, two and three weeks after the invertebrate peak in 2019, 2020, and 2021 respectively (Fig. S1. A). The highest number of broods recorded during a single survey was 28 on the largest site (Table S3).

We did not find evidence supporting a relationship between adult abundance and potential prey abundance, nor between adult abundance and potential predator pressure during the incubation period (Table 2; Fig. 2). Adult abundance was higher in 2020 and 2021 when compared to 2019 (Table 2). On the other hand, we found moderate evidence for a positive relationship between brood abundance and potential prey abundance sampled during chick-rearing, and very strong evidence for a positive relationship between brood abundance and adult density during incubation (Table 2; Fig. 2). Variation in brood abundance was not explained by variation in potential predator pressure (Table 2; Fig. 2). Brood abundance was similar during the three years of study, but we found very strong evidence for a weekly increase from hatching to the end of the season as more broods were added to the system (Table 2).

Table 2. Model results from two GLMMs. Left: relationship between adult abundance and habitat quality expressed as potential predator pressure and potential prey abundance (log scale). Right: Relationship between brood abundance, habitat quality, and adult density (Table 1), during the final part of the breeding season. Reference: Year = 2019.

	Adult abundance				**Brood abundance**			
Predictors	Estimate	Std. error	z value	p value	Estimate	Std. error	z value	p value
Intercept	2.493	0.350	7.121	**< 0.001**	-3.191	0.666	-4.791	**< 0.001**
Intrusions/h	-0.019	0.072	-0.267	0.790	0.207	0.174	1.192	0.233
Invertebrates /sample	0.013	0.051	0.263	0.792	0.313	0.146	2.142	**0.032**
Adult density	*na*	*na*	*na*	*na*	0.055	0.013	4.373	**< 0.001**
Week	*na*	*na*	*na*	*na*	0.249	0.048	5.195	**< 0.001**
Year								
2020	0.422	0.098	4.294	**< 0.001**	0.365	0.263	1.388	0.165
2021	0.502	0.091	5.524	**< 0.001**	0.343	0.279	1.230	0.219
Random effects	Groups	Variance	Std. deviation		Groups	Variance	Std. deviation	
Site	7	0.656	0.810		7	0.714	0.845	
Week	8	0.022	0.148		*na*	*na*	*na*	
Number of observations: 105					Number of observations: 116			

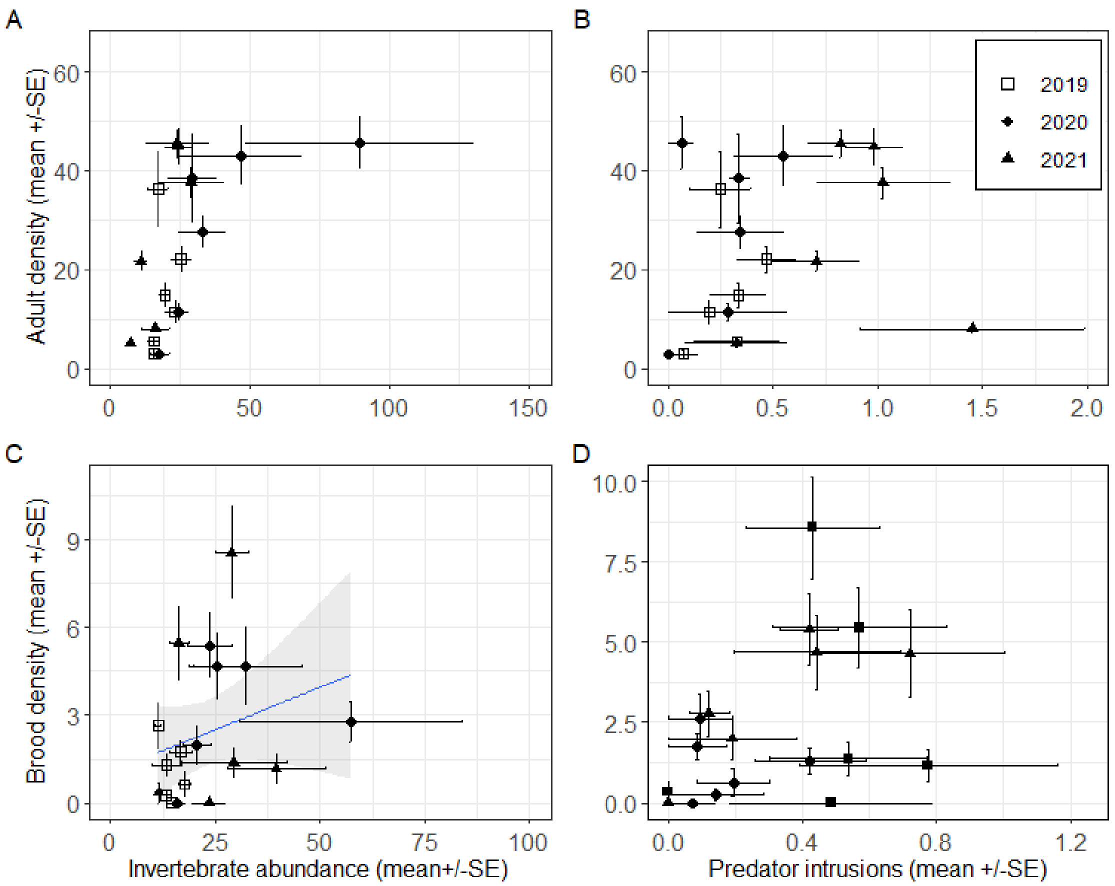

Figure 2. Relationships between available prey abundance (mean invertebrate abundance per sample ±SE, A, C), potential predator pressure (mean number of intrusions/h ±SE, B, D), and abundance of adult Whimbrels during incubation (mean nr. /km2 ±SE, A, B) and brood abundance, mean nr. /km2 ±SE, C, D) per year and site. Significant relationships from the GLMMs are expressed with a regression line and shaded area represents the standard error.

Finally, we did not find evidence for differences in breeding success at different adult density nor over time (Table 3; Fig. 3), indicating that the brood:pair ratio was similar on a gradient of adult density and over the years of study (Table 3).

Table 3. Model results investigating the relationship between breeding success (brood:pair ratio), adult density during incubation and year (see Table 1 for description of the variables). Reference level: Year = 2019.

		Breeding Success			
Predictors		Estimate	Std error	z value	p value
Intercept		-1.914	0.653	-2.932	**0.003**
Year					
	2020	0.574	0.445	1.290	0.197
	2021	0.488	0.467	1.046	0.296
Adult density		0.010	0.020	0.487	0.626
Random effects		Groups	Variance	Std deviation	
Site		7	0.399	0.6316	
Number of observations: 18					

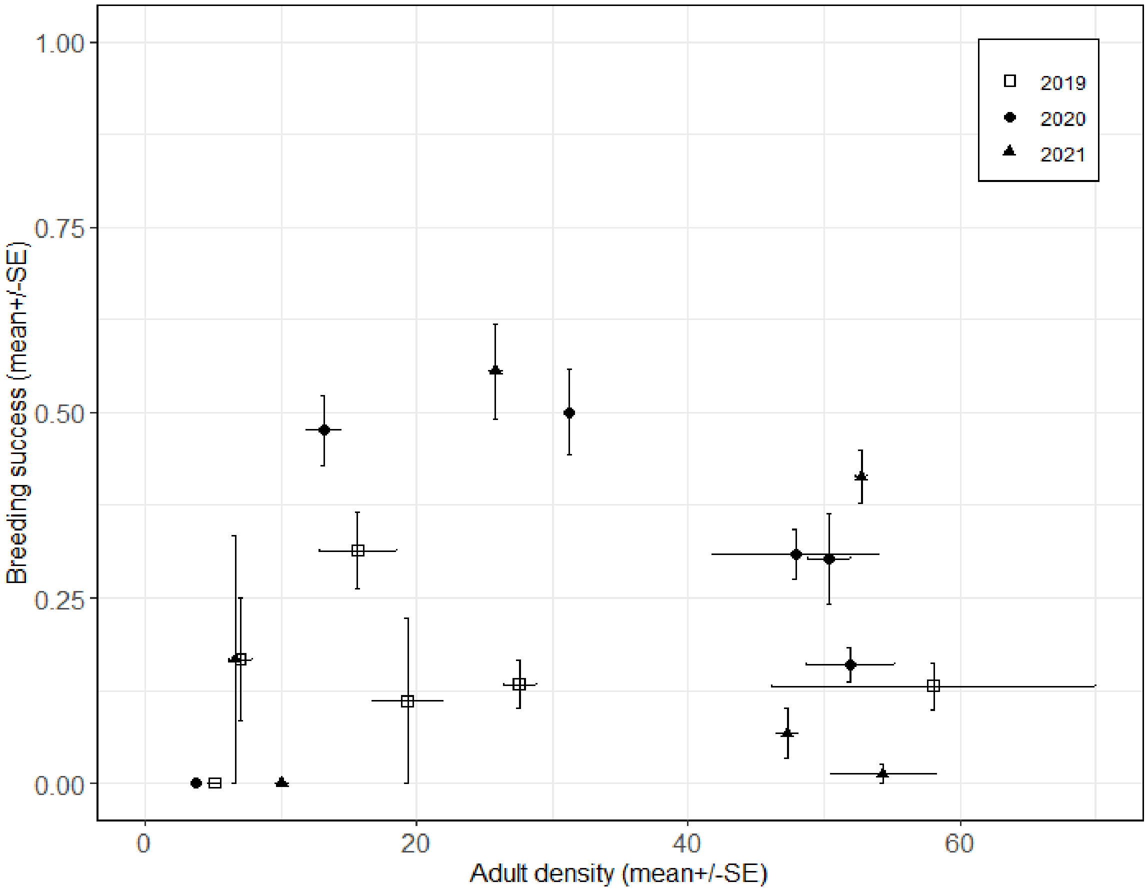

Figure 3. Relationship between breeding success (mean brood:pair ratio ±SE) and mean adult density (±SE) per site and year (see Table 1 for description of the variables). Some SE bars are smaller than the symbol size: for points with mean breeding success = 0.00 and breeding success >0.5, SE bars of mean adult density range from 0.0 – 0.5.

Discussion

Species distributions result from the spatiotemporal variation in resources in combination with factors intrinsic to populations such as density dependent effects that might arise at some point and space (Newton, 1998). Understanding how species are distributed is important for conservation, as management can then be targeted towards more efficient strategies focusing on key habitat components and/or demographic rates regulating the variation in species density across landscapes (Santini et al., 2023). In this study we explored the relationship between demographic rates and two components of habitat quality and investigated breeding success across a unique gradient of Whimbrel breeding density found in South Iceland.

Variation in adult abundance was not directly explained by differences in potential prey abundance sampled during incubation, but brood abundance was higher at higher invertebrate abundance sampled during chick-rearing. These results suggest that while potential prey abundance within breeding sites might not be very important for adult Whimbrels, it is likely so for chicks, as reported for similar species (Silva-Monteiro et al., 2023). Limited information exists regarding prey use and preference of Whimbrels in Iceland, but a study based on stomach content of 20 adult individuals found remains of berries, Coleoptera, Lepidoptera and Diptera (Guðmundson, 1957), and another that examined faecal contents found remains of Aranea and other invertebrates (Gunnarsson, 2000). Moreover, preliminary results from a third study investigating the diet of Whimbrel chicks in Iceland showed that Coleoptera, Bibionidae, seeds of *Empetrun nigrum* and Hymenoptera in faeces was very common (frequency of occurrence >50%), and that food could limit growth rates of chicks (Carneiro, *pers. comm.*). Given this, we could not assess the importance of specific invertebrate groups in explaining the variation in adult and brood abundance. Further work is hence needed to better understand chick diet and prey preference and to further assess the importance of different habitats in relation to breeding output. Whimbrels are highly mobile and breeding adults frequently travel away from their breeding territories during the breeding season, as recently revealed by individual GPS tracking in this population (Carneiro et al., *unpublished*). Therefore, selection of breeding sites and the subsequent variation in breeding density across the landscape might be explained by availability of food resources needed to sustain the precocial chicks that are not fed by parents and must forage locally by themselves on invertebrate prey and berries (Lappo et al., 2012; Silva-Monteiro et al., 2023; Carneiro et al., *in prep*), in combination with the philopatry of the species (Skeel, 1983). Moreover, variation in brood abundance (used as a measure of breeding output) was partly explained by differences in adult density, with brood abundance increasing with adult density. A similar result was also reported during a long-term study that found a positive relationship between brood and adult Whimbrel abundance at a small spatial (patch) scale across South Iceland (Cerezo-Araujo et al., *under review*). This highlights the importance of sites with higher adult density for conservation, as higher number of broods are produced on sites with more breeding adults.

Potential predator pressure, mostly recorded from avian predators, did not explain differences in either adult or brood abundance. Whimbrel predators do not normally focus on adults but instead on nests and chicks, thus the lack of a relationship with the former is not surprising. Regarding the latter, the result could stem from differences in parental aggressive behaviour and breeding density within sites, combined with differences in predator pressure throughout the breeding season, on the predator's numbers and *modus operandi*. Waders are more aggressive around the hatching period (Andersson et al., 1980; Królikowska et al., 2016), and thus predation effort on eggs during early incubation might be more successful than predation on small chicks later on. Nest predation rates for waders in south Iceland are typically 40-50% (Laidlaw et al., 2020; Pálsdóttir, *pers. comm.*) and survival rates (probability from hatching to fledging) of Whimbrel chicks were 36-40% on a heathland site and 50-55% on a river plain site (Gunnarsson, 2000). Following this, preliminary results from a more recent study (2021 to 2023) reported a 30-45% fledging success for Whimbrels in South Iceland (Carneiro, *pers. comm.*). Lower predation rates for species nesting at high densities have been described both for some big-sized wader species (Berg 1996; Valkama et al., 1999; Hötker and Segebade 2000; Sálek & Smilauer 2002; McDonald and Bolton 2008) and for wader species breeding sympatrically (Thorup 1998; McDonald and Bolton 2008) although such a relationship was not evident in our data. Some wader species breeding at high latitudes have also been observed nesting close to avian predators trading off predation risk to their own kind by protection from third parties (Norrdahl et al., 1995; McDonald and Bolton 2008). Whimbrels are known to breed close to Arctic Skuas in Shetland and Iceland (Grant 1989; Gunnarsson 2001; Jónsson and Gunnarsson, 2010) and breeding Arctic Skuas were present in three of our sites coinciding with highest Whimbrel densities. It is thus possible that even though high breeding densities may attract more predators, breeding presence of the aggressive Arctic Skua might aid more effective defence especially against other avian predators of similar size like Common Raven or gulls.

The consistently high Whimbrel breeding densities reported across Iceland in habitats such as river plain (Gunnarsson et al., 2006; Katrínardóttir et al., 2015; Cerezo-Araujo et al., *under review*) suggests that some fitness benefit might be associated with breeding in such habitats (Gunnarsson et al., 2005). However, a positive relationship between breeding success and adult density was not apparent in our data indicating that the probability of raising a brood is not different across a range of breeding densities. A similar result was reported in a previous study that compared hatching success between sites of different Whimbrel density (Katrínardóttir et al., 2015). These two results might suggest the presence of some density dependent mechanisms buffering breeding success at high breeding density and masking the fitness benefits of breeding in certain habitats of high conspecific density. Such a pattern can be driven through density-related differences, for example in predation pressure, competition for resources or interference competition at high densities (Goss-Custard, 1980; Page et al., 1983; Vahl et al., 2005 Møller et al., 2018).

Our results have some methodological limitations. First, the apparent lack of a relationship between brood abundance and potential predation pressure could be affected by the sampling methodology. The presence of an observer might have hindered predator presence and intrusions of some predators like Arctic Fox and American Mink; and the timing of the observations did not capture nocturnal events, the active period of some predators particularly that of Arctic Fox (Laidlaw et al., 2020; Pálsdóttir et al., *unpublished*). Moreover, accurately recording predatory events is notoriously difficult owing to the low predator encounter rates and more so for mammalian predators of a more secretive nature, highly mobile or with large home-ranges (Gese, 2001). Future research could thus incorporate more standardized techniques for predator monitoring such as fixed point-count observations of predation events, traps such as cameras or smell stations with footprint tracking on trails to assess predator presence or temperature loggers on nests to assess predation and timing of occurrence.

Second, our measure of the brood:pair ratio might not have fully captured the variation in breeding success. Recording the number of chicks over time and the number of chicks fledged by the end of the season is a more accurate estimate (Jarrett et al., 2023), and would have been preferable given the single annual reproductive attempt and the fixed clutch size of Whimbrels. However, this was impractical in our case given the number and extension of the study sites. Despite this, our measures of breeding output are robust as the number of broods is frequently used to gain insight into spatial variation in wader breeding success in large waders (Gunnarsson et al., 2017; Jarrett et al., 2023; Cerezo-Araujo et al., *under review*), and the brood:pair ratio is commonly used during the study of other wader species and waterfowl (Elmberg et al., 2003, 2005; Grant et al., 2000; Gunnarsson et al., 2005; Pagano et al., 2014; Jarrett et al., 2023). Moreover, the fact that another study on the same system reported similar hatching and fledging success between sites of different Whimbrel density (Katrínardóttir et al., 2015) also highlights this point. In our case, given the survey frequency, the time spent on the study sites, and the difficulties of locating small chicks in certain habitats, we had to trade-off these variables and minimize disturbance to breeding birds and possible attraction of predators.

To conclude, spatial variation in Whimbrel breeding density across the Icelandic landscape is probably maintained by a combination of the philopatric nature of the species, some potential fitness benefit associated with breeding in certain habitats, and the higher brood numbers produced at higher adult density, plausibly as a result of the higher invertebrate abundance within these sites. Finally, the implications of our findings for conservation are important in the light of global status of waders (Smith et al., 2020) and the current threats to Icelandic wader breeding habitats (Jóhannesdóttir et al., 2014; Pálsdóttir et al., 2022). With increasing anthropogenic changes to internationally important semi-natural wader habitats in Iceland, conservation conflicts will become more common, and decisions on habitat management and species conservation will have to take place. The results of this study further emphasise two points: (i) the need to prioritise the conservation of high-density wader breeding sites that produce more broods per unit area despite the possible density dependent mechanisms affecting breeding success; and (ii) the increasingly urgent need to perform similar studies on other wader populations in Iceland and elsewhere to identify key breeding sites and habitats for population persistence.

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Appendices

Table S1. Fieldwork methodology for the years of study.

Year	2019	2020	2021
Sites (replaced)	6(1)	6	6
Fieldwork starts - ends	15.05 - 02.08	01.05 - 01.08	02.05 - 30.07
Sampling per week:			
Adults & broods	Once	Once/Twice*/Once	Once/Twice*/Once
Invertebrates	Once	Once	Once
Predation intrusions	Opportunistically	Opportunistically	Opportunistically

*twice a week from 21st May to 14th July

Table S2. Information about the study sites surveyed. Mean starting time of the surveys per site is given in hours, and SE is given in minutes. Effort in the field is given in minutes. Differences in effort are due to the different extent of the sites, the tracks within them and additional tasks performed (collection and/or replacement of pitfall traps, nest searching, and nest monitoring).

	Coordinates	Elevation (m)	Area (km^2)	Starting time		Effort in the field (min)	
				Mean (h, min)	SE (min)	Mean (SE)/km^2	Range
Apavatn	64.142501, -20.695732	224.75	1.09	8:47	27	88.02 (4.8)	30-185
Drumbabót	63.728296, -20.141549	41.16	2.20	9:42	15	136.0 (6.3)	135-600
Helluvað	63.858140, -20.340119	38.80	2.13	11:15	60	77.6 (9.22)	87-270
Lyngdalsheiði	64.212177, -20.821905	127.72	1.17	08:57	25	73.3 (6.0)	30-230
Raftholt	63.933924, -20.475244	116.30	0.67	08:05	13	155.0 (9.5)	45-250
Rangá	63.784972, -20.213912	46.23	0.98	09:51	20	231.0 (13.8)	60-510
Sel	63.886275, -20.593547	19.02	0.43	07:06	5	205.0 (11.2)	60-195

Table S3. Variable information for the different study sites surveyed. See Table 1 for definitions of mean adult density during incubation and brood abundance. Information regarding invertebrate abundance and intrusions/h is given relative to the incubation and chick-rearing periods.

	Adult density incubation		Brood abundance		Invertebrate abundance				Intrusions/h			
					Incubation		*Chick-rearing*		*Incubation*		*Chick-rearing*	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Apavatn	10.10	0.99	0.96	0.31	17.60	2.46	18.50	1.89	0.78	0.27	0.25	0.12
Drumbabót	41.90	4.45	15.70	2.98	25.70	2.92	22.00	2.83	0.65	0.10	0.43	0.08
Helluvað	15.60	2.82	4.80	0.58	23.00	3.52	16.60	2.62	0.20	0.13	0.09	0.09
Lyngdalsheiði	5.13	0.45	0.23	0.13	12.60	1.57	14.20	0.94	0.16	0.10	0.03	0.03
Raftholt	24.70	1.86	2.62	0.71	19.10	2.91	19.90	2.30	0.48	0.11	0.39	0.12
Rangá	52.90	4.17	3.67	0.37	35.70	11.60	32.80	10.50	0.43	0.11	0.24	0.09
Sel	48.10	1.55	2.29	0.61	35.00	10.60	35.60	8.71	0.85	0.22	0.75	0.22

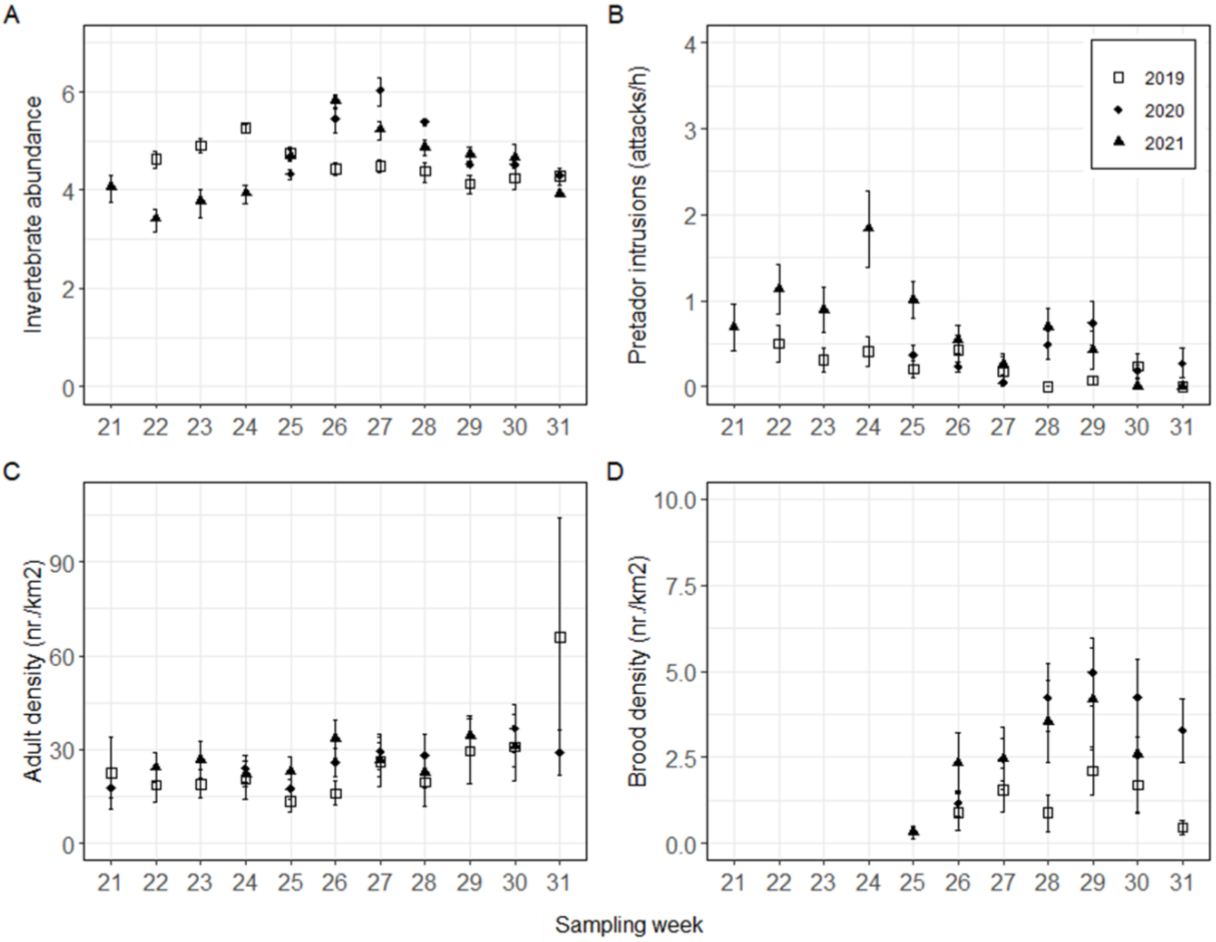


Figure S1. Seasonal variation in: A. mean invertebrate abundance per trapping week (mean number of invertebrates on a log scale +/-SE). B. mean number of predator intrusions (mean number of predator intrusions/h +/-SE). C. Mean adult density (mean number/km^2+/-SE), and D. mean brood density (mean number of broods/km^2 +/-SE) for all sites and years of study. Week 21 = 18- 20th of May, depending on the year. Week 23 = first week of June; week 27 = beginning of July.

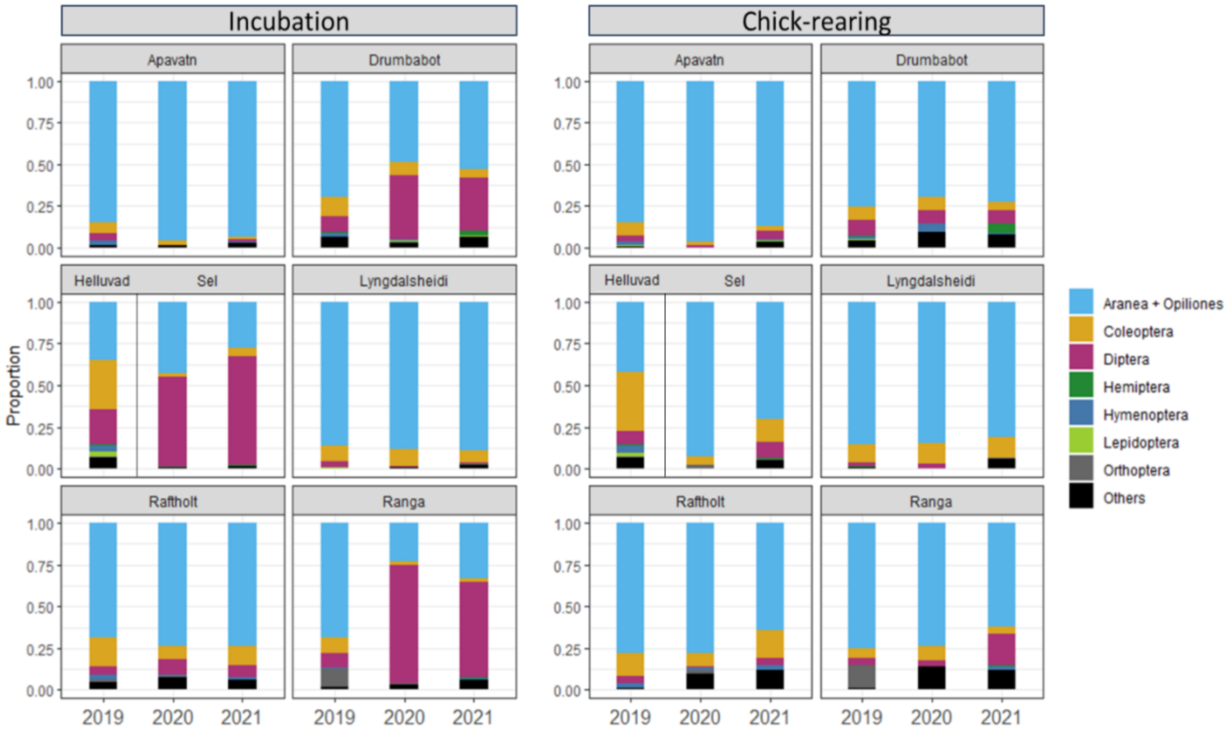
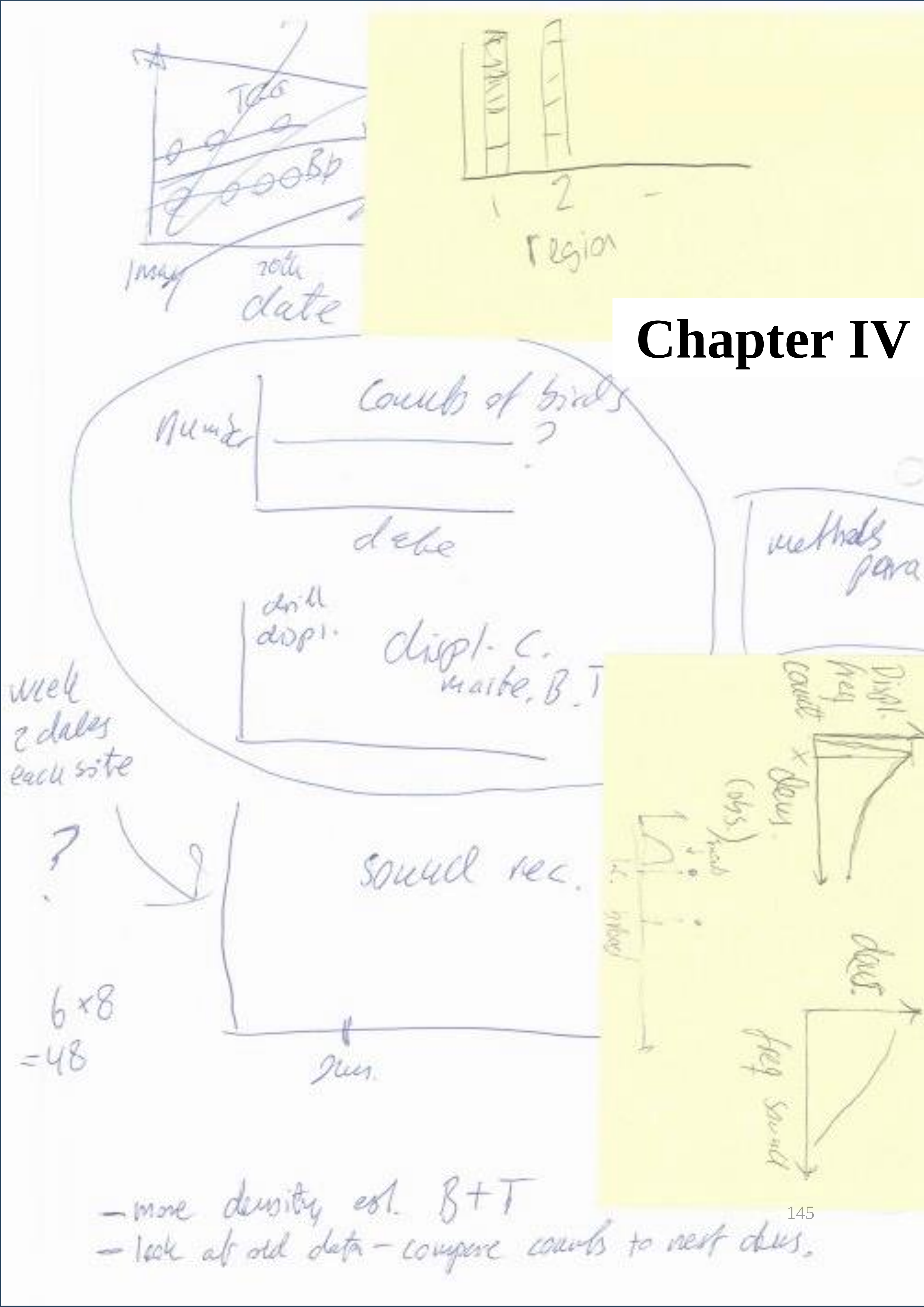


Figure S2. Proportion of different invertebrate orders in the pitfall traps found for each site and the three years of study during incubation and chick-rearing.

Table S4. Proportion of different potential predators intruding per site and effort in the field during incubation and chick-rearing. The Gull category groups the different species of gulls observed that were not identified to species level. Mean effort in the field per visit is expressed in hours/km^2 while SE is given in minutes/km^2. Number of visits represents those during which predator intrusions were observed.

	Proportion of potential intruders										**Effort in the field**		
	Incubation					**Chick rearing**							
	Gull	**Raven**	**Arctic skua**	**Fox**	**Mink**	**Gull**	**Raven**	**Arctic skua**	**Fox**	**Mink**	**Mean h/km^2**	**SE min/km^2**	**Total nr. visits**
Apavatn	52.30	20.50	27.30	0.00	0.00	10.00	40.00	50.00	0.00	0.00	1.60	5.36	44
Drumbabót	13.60	26.30	60.20	0.00	0.00	16.00	30.70	53.30	0.00	0.00	2.69	3.40	56
Helluvað	50.00	50.00	0.00	0.00	0.00	50.00	50.00	0.00	0.00	0.00	1.44	3.58	10
Lyngdalsheiði	0.00	50.00	50.00	0.00	0.00	0.00	50.00	50.00	0.00	0.00	1.30	10.81	55
Raftholt	40.00	6.67	46.70	6.67	0.00	37.50	8.33	45.80	8.33	0.00	3.04	14.06	55
Rangá	36.70	10.10	51.90	0.00	1.27	42.60	11.50	44.30	0.00	1.64	5.09	9.81	57
Sel	44.40	36.10	19.40	0.00	0.00	46.20	30.80	19.20	0.00	3.86	3.88	9.56	44


TBG
Bp
date
1
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drill displ.
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maybe B T
methods
para
week
2 dates
each site
?
sound rec.
6×8
=48
Displ. freq count × days
(obs.)
days
freq sound
– more density est. B+T
– look at old data – compare counts to next days.

Chapter IV

Chapter IV. Serenade of a Whimbrel: understanding the function of display behaviour in a sub-Arctic territorial wader

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Summary

Animal sounds contain important information used in intra- and inter-species communication. For species exhibiting elaborate and energetically expensive signals such as aerial displays accompanied by a call, the nature of the message being transmitted is honest and usually reflects individual fitness. Display events that combine flight and calls and are executed during the breeding season have traditionally been associated with two main functions: repelling rivals and/or attracting mates. In waders, the distinction between the two could not only rely on the timing of the breeding season at which displays occur but also on the frequency at which displays occur in relation to local breeding density. Here, we investigated the function of display behaviour in the Icelandic Whimbrel throughout the breeding season and along a breeding density gradient. We used a site-based approach in the southern lowland plain in Iceland where Whimbrel breeding density and display frequency were recorded for two years. Although Whimbrels showed display behaviour throughout the entire season, display frequency was higher at low densities during pre-incubation but similar at different densities during incubation and post-incubation. Our results indicate that this behaviour is context-dependent and pluripotent, supporting the importance of mate attraction at low conspecific density during pre-incubation, while other functions such as resource defence may be important throughout the breeding season.

Keywords

Shorebirds; mate attraction; territory defence; bioacoustics; *Numenius phaeopus*

Introduction

Animal communication occurs through a combination of visual, chemical, physical and acoustic signals aimed to modify the behaviour of the receiver (Marler, 1957; Rogers & Kaplan, 2003). The signals can be directed towards other species, such as the warning coloration of poisonous frogs, or towards conspecifics via territory scent marking of some mammals (Rogers & Kaplan, 2003). Many animals, especially birds, rely heavily on a combination of visual and acoustic signals to broadcast a message through patterns, colours, and displays (Slabbekoorn, 2004). The goal of the message is to meet both biological and social demands and this is reflected in the nature of the signal (Burger & Olla, 2013). If the signal used is costly to maintain due to high physiological expenditure (e.g. trade-off with energy or immune system), it is considered as honest and correlates with the size, physical health and strength of the sender (Koch & Hill, 2018), as occurs in Black-tailed godwits, *Limosa limosa*, whose plumage colouration reflects an individual's immune state and physical condition (Pardal et al., 2018). If the transmission distance between the sender and the receiver is short, the use of body language, displays on the ground, morphological ornaments and elaborated songs will be of advantage (Rogers & Kaplan, 2003). In such cases, high-frequency acoustic signals and complex song structures, typical of songbirds, will be well transmitted (Burger & Olla, 2013). On the other hand, if the signal is expected to encounter barriers (i.e., geographical or back-ground noise) or the transmission distance is large, the use of displays at several meters above the ground and/or acoustic signals of high energy, low frequency, simple and repetitive, such as the ones performed by waders (Charadrii), may be useful (Rogers & Kaplan, 2003; Burger & Olla, 2013). Moreover, environmental conditions, habitat structure and anthropogenic noise also influence the nature of the signals by altering their transmission efficiency (Boncoraglio & Saino, 2007; Snell-Rood, 2012; McMullen et al., 2014).

Acoustic avian studies have often focused on songbirds and less attention has been given to other groups such as waders. Many species of waders inhabiting open and often windy landscapes perform displays consisting of both a loud repetitive call accompanied by an elaborated aerial flight. These displays (call and flight) often range over large areas (Holmes, 1973; Lanctot et al., 2000; Burger and Olla 2013) making individual-based studies highly challenging without individual identification or new technological advances like 3D acoustic tracking (Dutilleux et al., 2023). Since the repetitive calls and elaborated flights in waders are energetically expensive activities (Butler & Woakes, 1990), these aerial displays are considered honest signals (Dabelsteen, 1978; Mather & Robertson, 1992; Searcy et al., 2006) and therefore their function must be important. The function of such aerial displays (displays hereafter) during the breeding season has traditionally being associated with attracting mates and/or defending territories (Miller, 1984; Lanctot et al., 2000). Therefore, the frequency at which displays occur during the breeding season, the breeding status of the individual displaying, the biology (e.g., mating strategy, philopatry) (Lanctot et al., 2000) and morphological characteristics of the species (Møller, 1991; Hedenstrom & Møller, 1992; Figuerola, 1999) will determine its function. If displays are solely used to attract mates, display frequency in monogamous species should decrease as birds pair up and start breeding (Lanctot et al., 2000). However, if displays also function to defend other resources such as territories, displays are likely to be performed well into the breeding season, even throughout incubation and brood-rearing (Schwarz, 2016).

Based on these premises, we further hypothesize that for monogamous and highly philopatric waders, the frequency of display behaviour should change in relation to the density of conspecifics at which display frequency occurs, since density can affect individual fitness and behaviour (Fretwell and Lucas, 1969; Pulliam and Danielson, 1991; Sutherland, 1996). Moreover, since density might not be a good indicator of resource abundance within a site such as mates and/or territories (Van Horne, 1983), the frequency of displays might not be positively correlated with local density, as has been shown for other vertebrate species (Höglund and Robertson, 1988). Accordingly, at low conspecific density where territories might be largely available but mating opportunities rare, higher display frequency should be indicative of mate attraction (Table 1). On the other hand, at high conspecific density with potentially higher competition for resources, higher display frequency should be expected (Currie and Valkama, 2000; Lanctot et al., 2000; Johnson and Walters, 2011), thus allowing further inference regarding the function of displays based upon the relationship between breeding density and display frequency, given the species biology (Table 1; Currie and Valkama 2000).

Table 1. Potential differences in display frequency, based on conspecific density, timing of the breeding period, and limiting resources. The number of symbols indicate predicted high (+++) or low (+) display frequency. At high density, if display behaviour functions to attract mates, it should be highest at the beginning of the season and decline as the breeding season progresses. However, if it functions for territory defence, display frequency should be high and constant throughout the breeding season due to competition. At low density, if display behaviour functions to attract mates, its frequency should be highest during pre-incubation and decline after. At low conspecific density territory availability is less likely to be a limiting factor and thus display frequency should be relatively low throughout the breeding season.

	Pre-incubation		**Incubation**		**Post-incubation**		**Limiting resources**
	Mate attraction	**Territory defence**	**Mate attraction**	**Territory defence**	**Mate attraction**	**Territory defence**	
High density	+++	+++	+	+++	+	+++	Territories and mates
Low density	+++	+	+	+	+	+	Mates

In order to investigate these hypotheses, we used the Whimbrel, *Numenius phaeopus*, as a model system. Whimbrels are large and long-lived waders, highly philopatric, territorial and monogamous that show mate fidelity from year to year (Mallory, 1982; Carneiro et al., 2021). The bulk of the population of the subspecies *islandicus* breeds in Iceland below 200-300 m a.s.l. and are especially abundant in the southern lowland basin (Gunnarsson et al., 2006; Jóhannesdóttir et al., 2014; Katrínardóttir et al., 2015; Méndez and Gunnarsson 2020; Cerezo-Araujo et al., *under review*), where the population seems to be declining (Cerezo-Araujo et al., *under review*). There, Whimbrels are found in different semi-natural open habitats breeding on a density gradient from ca. 2 pairs/km^2 up to 45 pairs/km^2, one of the highest densities recorded worldwide (Gunnarsson, 2000; Kátrínardóttir et al., 2015;

Jóhannesdóttir et al., 2018; Cerezo-Araujo et al., *under review*). Whimbrel vocal repertoire was described 50 years ago by Skeel (1978) in Canada, but little is known about the behavioural function of their stereotypical display song, which is performed over large areas, at high flight altitude of ca. 300 m, and can last as much as 10 minutes despite being highly variable in duration. These characteristics make individual identification of displaying birds extremely difficult, especially if the study sites are large, density is high, and birds are not marked. Despite this, given that the Whimbrel is a long-lived and highly philopatric species, evidence of a floating population does not exist and return rates in South Iceland are relatively high (Katrínardóttir et al., 2015), so most individuals will be the same between consecutive years. Therefore, using a site-based approach can give valuable insight on the function of this behaviour, particularly in relation to variation in breeding density. To do so, we studied variation in Whimbrel display frequency throughout the breeding season over a wide range of breeding density. More specifically, we investigated whether the frequency of Whimbrel displays varies with adult density depending on the timing of the breeding season, in order to make inferences about the function of aerial display data.

Material and methods

Fieldwork

Six study sites were selected based on variation in Whimbrel breeding density in the lowlands of South Iceland ranging from 2 to ca. 30 pairs/km^2 (Table 2). The sites were monitored throughout the breeding season from May to the end of July for two years, 2020 and 2021, with permission to access sites provided by landowners.

All sites were surveyed weekly during the start (from 1st to 25th May in 2020, and from 2nd May to 4th June in 2021), and at end of the breeding season (from 18th to 30th July in both years); and twice a week in between, during the middle the season (from the 5th June in 2020 and 26th May in 2021 to 18th July; differences due to colder weather, Alves et al., 2019; see methods for further details) to get better estimates of breeding Whimbrel abundance when numbers are more stable (Cerezo-Araujo et al., *under review*).

On each visit, we performed adult counts and acoustic surveys. Adults were counted following pre-defined routes within the sites driving on gravel tracks with open windows and at a speed of 10-20 km/h. Areas of the site where the topography impeded driving were surveyed on foot to properly cover them. Counts were done in one direction, always the same one, to avoid double-counting and using binoculars (8x42) (Cerezo-Araujo et al., *under review*). Acoustic surveys were done at three to five fixed points-counts per site, depending on the topography of the site, to properly cover the area of study. On each point, we counted the number of displays for a period of three minutes, thus, our measure of Display frequency was the number of displays per point and per three minutes. A display consists of a Whimbrel flying up at high speed and at an acute angle, and slowly gliding down while emitting at least two consecutive flute calls followed by a trill call (Skeel, 1978). In some instances (i.e., very bright light or cloudy), the individual displaying could not be seen, but if the call sequence (flutes plus trill) was clearly heard, it was considered a display. The acoustic surveys were performed between 6:00 and 10:00 when birds are most active (Davidsdottir, 2010; Jóhannesdóttir et al., 2019), and the starting time was constant but sometimes had to be adjusted due to unfavourable weather conditions (Table 2). Fieldwork was avoided in fog, rain exceeding 1 mm/h and wind exceeding 7 m/s to minimize disturbance to breeding birds and to avoid potential noise interference during the acoustic surveys. The area of the study sites in km^2 was measured with a tool from an Icelandic online map engine (www.já.is/kort) (Table 2).

Table 2. Information on study sites in South Iceland and details of acoustic surveys.

Site	**Coordinates**	**Area (km^2)**	**Mean adult density (±SE pairs/km2)**		**Acoustic sampling points**	**Number of surveys**		**Mean starting time (± SE min)**
			2020	**2021**		**2020**	**2021**	
Rangá	63.784972, -20.213912	0.97	24.6 (±2.53)	27.2 (±1.94)	4	18	20	09:28 (±3.2)
Drumbabót	63.728296, -20.141549	2.20	19.2 (±2.30)	25.8 (±0.46)	5	19	19	09:32 (±2.2)
Sel	63.886275, -20.593547	0.43	25.2 (±0.77)	23.6 (±0.38)	3	19	19	07:32 (±3.2)
Raftholt	63.933924, -20.475244	0.67	15.6 (±0)	12.9 (±0.24)	4	17	19	08:04 (±4.5)
Apavatn	64.142501, -20.695732	1.09	5.81 (±0.15)	4.74 (±0.40)	4	16	19	07:54 (±4.2)
Lyngdalsheiði	64.212177, -20.821905	1.17	2.14 (±0.42)	3.42 (±0.24)	3	17	20	07:59 (±6.0)

Data analysis

To investigate if the frequency of displays changes with breeding density within and between different periods of the breeding seasons, we used a generalized linear mixed effect model (GLMM, R package *lme4*, Bates et al., 2015) with negative binomial error distribution to account for overdispersion of the dataset. Display frequency was included in the model as the response variable, while Breeding period (categorical), Adult breeding density (continuous, pairs/km^2) and their interaction were included as explanatory variables, along with Year (categorical) to account for potential annual differences. Point nested within Site was included as a random effect to account for the non-independence of the data. We split the breeding season into three periods, pre-incubation, incubation and post-incubation, according to the year-specific frequency distribution of laying dates obtained from a wader nest monitoring programme in South Iceland (Alves et al., 2019; Carneiro et al., 2019; Laidlaw et al., 2020; Cerezo-Araujo et al., *under review)*. The first and last quartiles (Q) of laying dates were excluded to avoid early breeders and re-nesters, so that the incubation period spanned from Q2 to 29 days (number of days for an egg to develop and for the chick to hatch) after the final date on Q3 (Cerezo-Araujo et al., *under review*). Pre-incubation period spanned from the first field survey (1st and 2nd of May 2020 and 2021 respectively) to the date before the incubation period started in each year (25th and 28th of May in 2020 and 2021 respectively), and post-incubation spanned from the day after the last incubation date (7th and 8th of July in 2020 and 2021 respectively) to the end of the field season when the last survey was performed (30th July both years). Adult breeding density was obtained for each site and year by dividing the mean of the maximum three counts of Whimbrel pairs recorded during incubation, when abundance is more stable, by the area of the site in km^2 (Cerezo-Araujo et al., *under review*). We first considered modelling the *per capita* display frequency by also including the number of Whimbrels counted during each visit as an offset but given the positive relationship between the number of adults recorded on a visit and breeding density per site ($r = 0.475$, $p< 0.005$), we omitted it to avoid model penalisation. Finally, to test for differences in display frequency between the three different periods of the breeding season we performed a pairwise comparison using estimated marginal means (R package *emmeans*, Lenth et al., 2023).

Data analysis, visualization and model validation were done in R v.4.1.1 (R Core Team, 2021; R package *performance*, Lüdecke et al., 2021). Results were reported as recommended by Muff et al., (2021). According to the authors, significance scores above 0.05 were interpreted as having little evidence of the effect of the explanatory variable(s) on the response variable, and values above 0.001 were considered as a-very-strong-evidence supporting the effect of the explanatory variable(s) on the response.

Results

The total number of displays per point sampled in each of the six sites ranged from 0 to 10, and the mean display frequency per point, day and site ranged from 0.86 (±0.12 SE) to 2.22 (±0.15 SE). Mean adult breeding density ranged from 2.1 to 25.2 pairs/km^2 in 2020, and from 3.4 to 27.2 pairs/km^2 in 2021 (Table 2).

Although displays were seen and heard throughout the entire breeding season, we found evidence for a higher display frequency during pre-incubation than during incubation (Table 3; Fig. 1), but no differences between incubation and post-incubation (Table 3; Fig. 1). We also found evidence for a negative relationship between the frequency of display and adult breeding density during pre-incubation, indicating higher frequency of displays at low Whimbrel density (Table 3; Fig. 2). However, this relationship was absent during incubation and post-incubation (Table 3; Fig. 2). Finally, we found differences between years, with 2021 having on average lower frequency of displays (Table 3), and the pairwise test showed no differences in display frequency among the three different periods of the breeding season (Table 4).

Table 3. Results of the GLMM exploring the effects of breeding adult density, period of the breeding season, year and the interaction between adult density and breeding period on the frequency of display behaviour. Reference levels are Year = 2020 and Breeding period = Incubation.

Predictors	Estimate	Standard error	z value	p value
Intercept	0.161	0.245	0.657	0.512
Breeding period				
Post-incubation	0.128	0.224	0.571	0.568
Pre-incubation	0.532	0.218	2.439	**0.015**
Adult density	0.016	0.013	1.246	0.213
Year 2021	-0.241	0.088	-2.743	**0.006**
Adult density: Breeding period				
Adult density: Post-incubation	-0.005	0.012	-0.430	0.667
Adult density: Pre-incubation	-0.027	0.011	-2.377	**0.017**
Random effects	Variance	Standard dev.	Groups	
Site	0.075	0.274	6	
Point: Site	0.030	0.173	24	
Number of observations: 817				

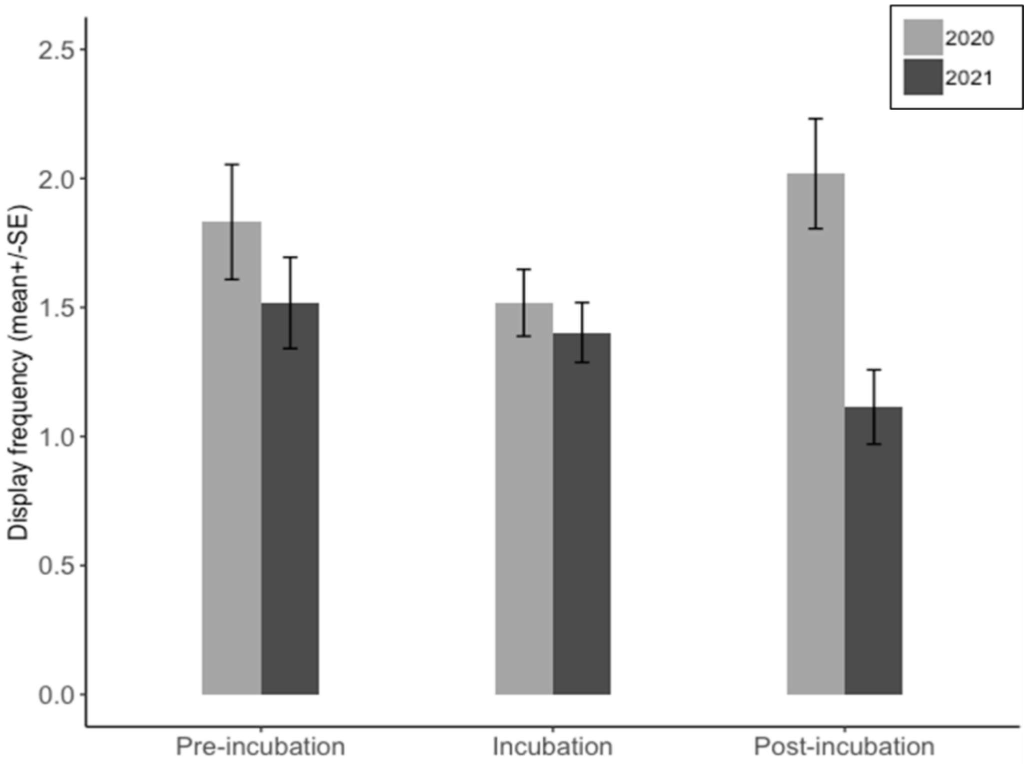

Figure 1. Frequency of displays for the different breeding periods expressed as mean number of displays per point and year (±SE).

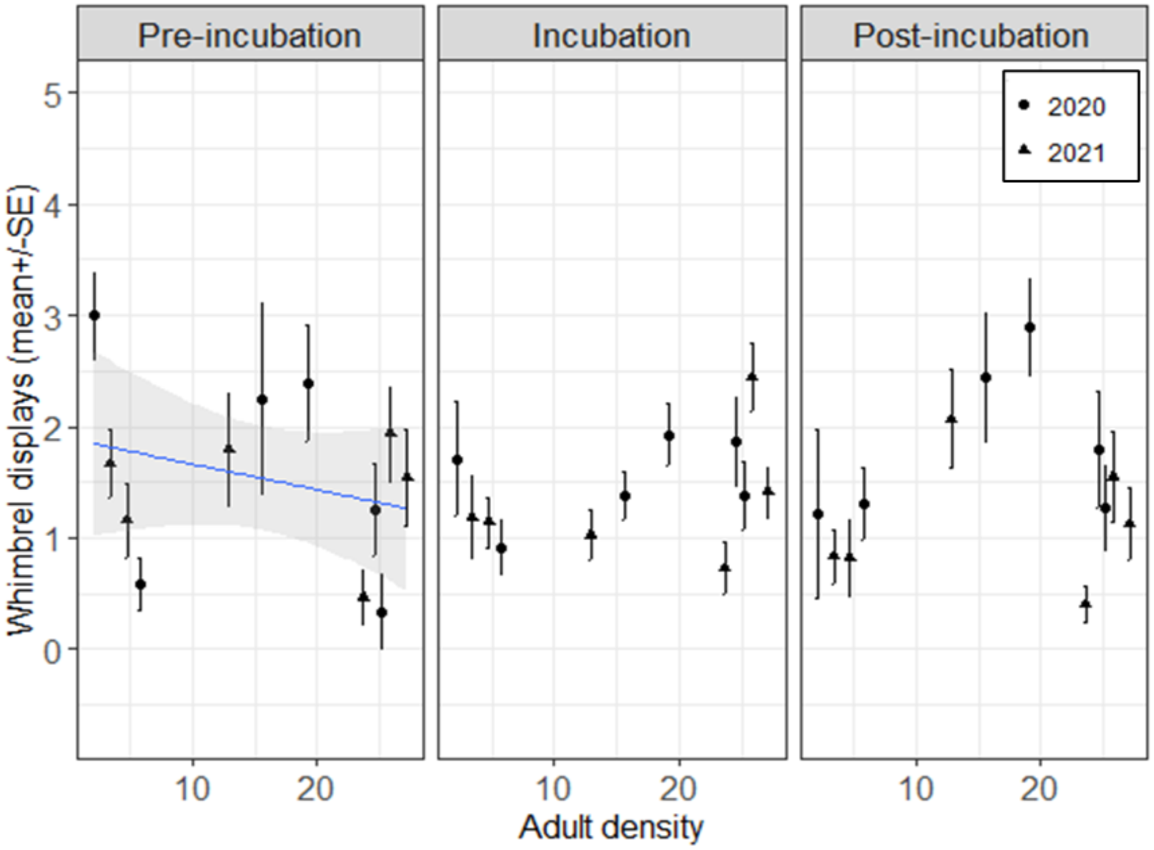

Figure 2. Relationship between display frequency (mean ±SE per point) and adult density (pairs/km^2) for the three periods of the breeding season and the two years of study (symbols). Regression line fitted through the significant relationship (see Table 3).

Table 4. Pairwise comparisons using estimated marginal means testing whether the display frequency differed among the three periods of the breeding season (Pre. – pre-incubation; Post. – post-incubation).

Comparison	**Estimate**	**SE**	**p. value**
Incubation - Post.	-0.042	0.103	0.914
Incubation - Pre.	-0.087	0.106	0.691
Post. - Pre.	-0.045	0.120	0.926

Discussion

The function of display behaviour has been extensively investigated in songbirds, but little attention has been given to other groups like waders. In this study we used a site-based approach to investigate display behaviour in Whimbrels across a gradient of breeding density and throughout the breeding season to gain insights into the function of this behaviour. Birds only sing for those who listen (Autin, 2014): our results show that although Whimbrels display throughout the whole breeding season, they do so more frequently during pre-incubation and at low density of conspecifics.

The higher frequency of displays found during the pre-incubation period could be explained by the tight breeding schedule of Whimbrels and by the energetic requirements of the behaviour itself. Whimbrels are constrained by the short Icelandic summer (Gunnarsson 2010; Carneiro et al., 2019), probably resulting in higher display frequency early in the season, and a subsequent rapid decline after pairing-up, securing territories and once egg-laying starts (Oliver et al., 2018). Moreover, the fact that the aerial display behaviour is energetically costly and time-consuming (Dabelsteen, 1978; Mather and Robertson, 1992; Searcy et al., 2006) also suggests that this behaviour is performed when energy is not directed towards other highly demanding activities such as incubating or brooding. This seasonal pattern has also been observed in other individual-based studies performed on waders like Dunlin, *Calidris alpina*, Western Sandpiper, *C. mauri*, and Curlew, *N. arquata*; and birds of prey like Montagu's Harrier, *Circus pygargus* (Blomqvist et al., 1997; Currie & Valkama, 2000; Lanctot et al., 2000; Arroyo et al., 2013;). For these monogamous species, males displayed more frequently coinciding with the female's fertile period and paired males reduced their display activity during incubation and post-incubation (Blomqvist et al., 1997; Currie & Valkama, 2000; Lanctot et al., 2000; Arroyo et al., 2013). The differences in display frequency throughout the season with significantly higher number of displays during the pre-incubation period might be explained by the timing of male arrival if displays are used for mate attraction (e.g. Eastern Willet, *Tringa semipalmata semipalmata*, Dunlin and Western Sandpiper, Howe, 1982; Blomqvist et al., 1997; Lanctot et al., 2000), by changes in the display function (e.g. Montagu's Harrier; Arroyo et al., 2013), or by changes in the individuals displaying, from all individuals at the beginning of the season to a mixture of unpaired and widowed males later in the season, and as response to conspecific intrusions (e.g. Curlew; Currie & Valkama, 2000). Therefore, the decrease in the number of displays performed by Whimbrels at low breeding densities might indicate a shift in its function from mate attraction, with higher display frequency in pre-incubation, to territory defence, with similar display frequency throughout the rest of breeding season.

Furthermore, the decrease in frequency of displays with adult breeding density recorded during pre-incubation suggests that finding mates in areas with few individuals requires considerably more effort than at high densities, where the chance of finding a mate potentially increases with abundance. It is then possible that display behaviour during pre-incubation at low density of individuals may emphasise the effort needed to attract mates. If instead, its function was of territory defence, higher display frequency should be expected at higher density (Table 1; Currie and Valkama 2000). Alternatively, lower display frequency on sites of higher density may stem from the philopatric and monogamous nature of the species. Individuals pairing up with an old mate may require less information on a mate's status resulting in lower display frequency (Lanctot et al.,

2000) and this may vary with breeding density. Return rates for Whimbrels in Iceland were of 57-78% in sites of breeding density of >10 pairs/km^2 (Katrínardóttir et al., 2015; Méndez et al., 2018b), while for Whimbrels in Canada were of ca. 99% for individuals breeding in areas of 10-11 pairs/km^2 and of ca. 26% for individuals breeding in areas of 1-5 pairs/km^2 (Skeel, 1983). It might be possible then that high return rates on sites of high breeding density could result in a low display frequency upon the encounter of old mates.

The high display frequency during pre-incubation combined with the higher display frequency at lower Whimbrel densities suggest that displays may be particularly important during pair formation, and those performed afterwards may be more important for other functions, likely defending other resources. Accordingly, displays in Whimbrels and similar species may be pluripotent, as the same behaviour might have different functions depending on the context and the receiver (Oring, 1966; Byrkjedal et al., 1989; Whitfield & Brade, 1991; Arroyo et al., 2013; Guindre-Parker et al., 2013; Hebets et al., 2016; Schwarz, 2016). Skeel (1978) described her view on the function of the Whimbrel display behaviour: "(…) von Frisch believed the display to have no role in courtship (…). I feel that the aerial display song of the Whimbrel serves both in attracting a mate and in marking an area, part of which will later become its territory". Our data supports such functions of the aerial displays in Whimbrels which is probably very old since displays in waders show little evolutionary plasticity (Miller & Baker, 2009). At the beginning of the breeding season, this behaviour may be particularly important for mate attraction at low breeding densities whereas other functions, such as resource defence, may be more important later and at higher densities. Meanwhile, the displays observed during incubation and post-incubation most likely function as resource defence independent of the adult density.

Despite this, a key characteristic of pluripotentiality, the receiver, might be more important than we originally thought. An individual-based study in Snow Buntings, *Plectrophenax nivalis*, found that the same display behaviour had different meanings depending on the sex of the receiver (Guindre-Parker et al., 2013). It might thus be possible that the Whimbrel display could function to indicate mate searching towards females at low conspecific density during pre-incubation, while it could function to indicate resource ownership, possibly towards both males and females, at high density throughout the whole season, but we could not formally test this hypothesis due to the nature of our data. Moreover, other types of behaviour could contribute to mate attraction and territory defence. Some *Calidris* species use aggressive chases involved in courtship (Bengston 1970) and on territorial defence (Holmes, 1973). Despite Whimbrels being observed fighting and performing aggressive chases towards conspecifics, we did not assess if the finality of this behaviour was involved with courtship or territoriality and its contribution to display behaviour. Further research based on individual breeding birds is needed to assess the importance of the receiver and the contribution of other types of behaviour.

Finally, for animals like waders whose acoustic behaviour plays an important role in their life cycle, any modification of the landscape that can potentially alter the acoustic information transferred poses a risk. While acoustic behaviour has evolved around natural noise conditions like wind and water, anthropogenic noise risks the communication system. The Icelandic open landscape is undergoing heavy infrastructure development (Jóhannesdóttir et al., 2018; Pálsdóttir et al., 2022) altering environmental conditions and increasing background noise, and many of these changes can have cascading effects on sound transmission and degradation. Given that some wader species such as Whimbrels partly rely on acoustic signals to find mates, degradation of the soundscape may bring important consequences for individual fitness and local populations. Sound barriers might potentially increase the effort that individuals must undertake while displaying, reducing their fitness and the likelihood of finding a mate at low density, and ultimately affecting local breeding output. Reduction in population densities in noisy environments have been reported by several studies (McClure et al., 2013; Ware et al., 2015), and given the important role acoustic behaviour can have on breeding, alteration of the soundscape might bring irreversible consequences for population numbers. Therefore, understanding species acoustic behaviour is important to predict the population-level consequences that changes in the landscape might bring. As such, incorporating this knowledge into landscape planning will potentially facilitate the human-wildlife coexistence.

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