Master's thesis



Exploring the Migration and Reproduction of Common Ringed Plovers (*Charadrius hiaticula*) Breeding in Iceland

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Declaration

I hereby confirm that I am the sole author of this thesis and it is a product of my own academic research.

James Fletcher

Abstract

Several migratory bird species rely upon coastal habitats throughout their annual cycle and connect several countries through their migration routes. Humans similarly make use of coastal areas due to their high productivity and resource levels, which has resulted in a level of exploitation that has in some cases damaged ecosystems irreparably. The Common Ringed Plover Charadrius hiaticula, is a long-distance migratory wader that undertakes a seasonal migration between its breeding grounds most commonly in the arctic and sub-arctic, and its wintering grounds in temperate and tropical latitudes, and like many wader species, it has experienced declines in population size across its range. With relatively little being known about the migration and variation in breeding success of Icelandic breeding Common Ringed Plovers, this study investigated (1) whether leap-frog migration is present within the Common Ringed Plover breeding in Iceland, (2) if carry-over effects occur during spring migration and affect breeding success, and (3) if timing of egg laying date vary between populations of Common Ringed Plover in the South and Westfjords of Iceland. By using data retrieved from geolocators fitted to individuals over a four-year period it was possible to estimate locations of winter sites and migration timings. While it has been observed in other Common Ringed Plover populations, a leap-frog migration pattern was not identified between the Icelandic breeding populations. Generalised linear models were used to identify relationships between several stages of spring migration and breeding success, with only the duration of time spent at stopovers found to be affected by the departure date from the wintering sites. Nevertheless, further research should be conducted into potential carry-over effects as more data may be required to explore this further. It was found that lay dates of first nesting attempts varied significantly between breeding sites and years of the study, with lay dates in the South being later in the beginning of the study but advancing beyond those at the Westfjords breeding grounds – which remained at similar dates over the 16 years of data. Despite varying from previous knowledge of later breeding attempts at more northerly latitudes, this could possibly be explained by variation in snow melt, habitat quality and prey abundance between the sites; with the possibility of time constraints preventing the advance of lay dates in the Westfjords.

Útdráttur

Farfuglategundir eins og sandlóan Charadrius hiaticula nota strandbúsvæði allan árshringinn og tengja fjölda landa með því að nota stöðvarnar þar á farleiðum sínum. Á svipaðan hátt notar mannfólk strandsvæði vegna mikillar framleiðni þeirra og auðlindagnóttar, en þetta hefur leitt til stigs af hagnýtingu sem hefur í sumum tilfellum skaðað vistkerfi varanlega. Sandlóan leggur í árvisst ferðalag frá varpsstöðvum sínum á og við Norðurheimskautið til að hafa vetursetu á tempruðum og hitabeltissvæðum. Líkt og stofnar margra vaðfuglategunda hefur stofnstærð sandlóunnar minnkað á öllu útbreiðslusvæði hennar. Þar sem tiltölulega lítið er vitað um farhætti innlenda varpstofns sandlóunnar, beindist þessi rannsókn að (1) hvort svæðahopp sé að finna meðal íslenska varpstofnsins, (2) hvort merkja megi yfirfærsluáhrif á varptíma og hugsanleg áhrif þeirra á farsæld varpsins, (3) hvort munur sé á varp- og álegutíma milli varpstofnanna á Vestfjörðum og Suðurlandi. Með því að nota gögn úr dægurritum einstakra fugla, sem safnað var á fjögurra ára tímabili, var hægt að áætla svæðin þar sem sandlóan hefði vetursetu og tímasetja farflug hennar. Þrátt fyrir að þekkjast meðal annarra sandlóustofna fundust engin merki um svæðahopp hjá íslenska varpstofninum. Almenn línuleg módel voru notuð til að greina samband milli tímasetninga farflugsins að vori og farsæld varpsins, sem leiddu í ljós að tímasetning brottfarar frá vetrarsvæðunum hafði einungis áhrif á tímann sem fuglarnir vörðu á viðkomustöðum á leiðinni. Engu að síður þyrfti að rannsaka frekar möguleg yfirfærsluáhrif þar sem fleiri gögn yrðu notuð. Mikill munur á dagsetningum á fyrstu tilraunum til hreiðurgerðar kom í ljós á því sextán ára tímabili sem vöktun stóð yfir. Í upphafi hennar hófst hreiðurgerð seinna á Suðurlandi en Vestfjörðum en færðist framar eftir því sem á leið og í lok vöktunarinnar hófst hreiðurgerðin fyrr hjá sunnlenska stofninum, en þeim vestfirska sem hafði ekkert færst til allan tímann. Þrátt fyrir að sýna aðra niðurstöðu en fyrri rannsóknir á síðbúnum varptíma á norðlægari slóðum, mætti skýra þessa breytingu með snemmbúnari leysingum, gæðum varpsvæða og framboði á æti og að lengri vöktun þurfi til að sjá hvort tímasetning hreiðurgerðar sé að færast framar á Vestfjörðum einnig.

"Obedience to gravity. The greatest sin."

Simone Weil

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1 Introduction

Migration is a phenomenon that takes place across the globe and is undertaken by billions of individuals across the animal kingdom (Wilcove & Wikelski, 2008), and encompasses annual, seasonal or even daily movements of organisms (Alerstam & Bäckman, 2018). Animal migrations take place in all the major animal groups including mammals, birds, fish and insects (Li *et al.*, 2014). Notable migrations that have been tracked and studied include the Monarch Butterfly *Danaus plexippus* which undertake a journey from Canada to Mexico for winter before returning north in spring, a migration that encompasses 4800km and as many as 5 generations (Reppert & de Roode, 2018). In Africa, Wildebeest *Connochaetes taurinus* undertake an almost circular migration during the dry season as they roam the Serengeti/Mara in search of grass and water in a journey spread over two countries and thousands of kilometres (Serneels & Lambin, 2001). While in the oceans, Humpback Whales *Megaptera novaeangliae* migrate over 8000km from the cold waters of their summer feeding grounds to warmer waters of the tropics in winter in order to raise their calves (Pomilla & Rosenbaum, 2005).

In birds, up to half of all species are migratory (Bildstein, 2006), and migration is generally undertaken in response to changes in conditions, resources or social interactions and usually results in a movement between two distinct habitats (Ramenofsky & Wingfield, 2007). Migratory birds commonly develop different migration patterns both between and within species (Newton, 2020). In this study one such migration pattern that will be looked at in more detail is leap-frog migration. Leap-frog migration occurs in species where a more northerly breeding population migrates beyond the complete range of their more southern breeding counter parts — effectively leap-frogging a portion of the population (Newton, 2020). Leap-frog migration has been observed in a number of avian species such as Bulwer's Petrel *Bulweria bulwerii* and the Fox Sparrow *Passerella iliaca* (Ramos *et al.*, 2015; Bell, 1997), and in waders in particular has previously been observed in Bar-Tailed Godwits *Limosa lapponica* and Common Ringed Plover *Charadrius hiaticula* (Duijns *et al.*, 2012; Hedh & Hedenström, 2016). Even though the leap-frog pattern has been observed in these species in other regions, migration patterns may vary across a species range (Buehler & Piersma, 2008).

Migrations between breeding and wintering grounds are rarely undertaken as one movement, with individuals using sites in between to stop for refuelling or for other functions (stopover sites) (Newton, 2007). Many migrant species utilise coastal areas during at least one phase of migration (Seitz *et al.*, 2014; Frederick, 2001). Hence, migratory species are particularly vulnerable to pressures across a range of locations in different parts of the world (Newton, 2004), particularly those relying on coastal habitats. In fact, stopovers account for the majority of migration duration (Hedenström & Alerstam, 1997), and can be linked to processes at the breeding or wintering grounds, through carry-over effects.

Carry-over effects occur when previous experience in an individual's life history influences the behaviour or performance in following life stages (O'Connor *et al.*, 2014). There is a potential for carry-over effects to be cumulative in migratory species. The routes taken, distances travelled and timing of stages during migrations differ greatly between populations as well as species (Buchan *et al.*, 2021). This can cause variation in carry-over effects such as departure and arrival times, breeding success and even survival rates (Buchan *et al.*, 2021). It is not just timing that can cause these variations however, in some species the habitats utilised during migration and wintering periods can influence body condition, and as such cause variation in important dates for migration (Newton, 2004). At a time in which migrants are generally in decline (Sanderson *et al.*, 2006), it is important to understand the locations and timings that are important across the annual cycles of migrants in order to identify threats and pressures which can be used to direct conservation efforts (Wilcove & Wikelski 2008).

In order to investigate carry-over effects and the links between breeding and non-breeding grounds, researchers have been marking and tracking individual birds to record detailed information throughout the year, using unique combinations of colour rings, but also other tracking devices such as geolocators. Geolocators are very light devices (ca. 0.5g) that continuously record light-intensity and allow geographical locations to be estimated remotely (Bridge *et al.*, 2011). With that information, several links between annual stages can be made (Carneiro *et al.*, 2021), and ultimately help to understand if and when individuals and populations are limited; knowledge that can inform conservation policies.

Coastal areas offer important habitats that support unique levels of biodiversity (Clausen & Clausen, 2014; Kingsford *et al.*, 2016), and provide ecosystem services such as carbon sequestration, nutrient cycling and also improving air and water quality (Kingsford *et al.*,

2016). However, coastal areas also tend to be populated by humans, which threaten habitats through land reclamation and destruction (Sutherland *et al.*, 2012). Coastal wetlands are some of the most heavily used and exploited ecosystems, yet management of these areas across the globe is more often than not done poorly (Doney *et al.*, 2012; Barbier *et al.*, 2019). It is therefore necessary to call attention to the importance of effective management of coastal sites, due to the significant role they play in the various life stages of multiple species. A number of species rely upon coastal areas to breed and raise their young; while many others utilise coastal habitats multiple times a year at different stages of their annual cycle as they undertake seasonal migrations (Puthur *et al.*, 2021).

Iceland is a country of particular importance for birds. It supports internationally important numbers of some species (Jóhannesdóttir *et al.*, 2014), including waders (*Charadriiformes*) (Delany & Scott, 2002; Gunnarsson *et al.*, 2006; Náttúrufræðistofnun Íslands, N.D.a). These wader species are migratory, and it is estimated that as many as 5 million individuals (adults and juveniles) depart Iceland each year during autumn migration (Guðmundsson, 1998). Most of these will use coastal habitats as non-breeding sites (during winter and stopover; Delany *et al.*, 2009). Wader species are particularly threatened and several have been decreasing (Liley & Sutherland, 2007), with a number of wader species in Europe being classified with declining populations (IUCN, 2021). Iceland ranks as the second most important area for breeding waders in Europe (Gunnarsson *et al.*, 2006; Thorup, 2004; Jóhannesdóttir *et al.*, 2014), therefore playing an important role in the conservation of this group of birds.

This project aims to delve into the annual cycle of the Common Ringed Plover, a widespread species in Iceland, that migrates to continental Europe and Africa during the non-breeding period (Delaney *et al.*, 2009), and has experienced a recent decline (Robinson, 2005; van Roomen *et al.*, 2022). Common Ringed Plover are primarily coastal birds, and as such rely upon coastal areas and habitats during both breeding and non-breeding life stages (Wiersma *et al.*, 2020). Using data from two breeding populations, one in the South and another in the Westfjords of Iceland, the objectives of this study are to determine if leap-frog migration is present, while also identifying potential patterns in the migrations of these individuals. Furthermore, the project aims to compare the breeding success between both populations, investigate whether carry-over effects arise during spring migration, and explore variation in timing of nesting.

1.1 Research Questions & Hypotheses

In order to achieve these aims, this project will look to address and answer the following questions:

1. Is leap-frog migration present within the Common Ringed Plover breeding in Iceland?

 H_0 – The Icelandic Common Ringed Plover will show a leap-frog migration pattern, with individuals from the north-western population wintering further south than the southern conspecifics.

H₁ – Icelandic Common Ringed Plover will show no differences in wintering locations.

2. Do carry-over effects occur during spring migration and affect breeding success?

 H_0 – Carry-over effects will occur between consecutive stages during spring migration and will impact breeding success.

H₁ – Breeding success will not be influenced by previous spring migration events.

3. Does timing of egg laying date vary between populations of Common Ringed Plover in the South and Westfjords of Iceland?

H₀ – Common Ringed Plovers breeding in south Iceland will begin laying eggs earlier.

H₁ – Timing of egg laying will not differ between Common Ringed Plover populations.

1.2 Document Format

The structure of this paper consists of seven sections. The first and present section introduces the subject area of the thesis and outlines the aims and hypotheses for the study. The next section is a literature review on the topic of this research. The literature review will highlight existing research and information available on the focus areas of this thesis. The fourth section of the paper outlines the methods used for data collection and analysis while also providing an overview of the study sites. Following this, the findings and results of the data used in this thesis will be presented in the fifth section. The findings of the study will then be put into context using existing literature published on Common Ringed Plovers, as well

as drawing comparison to similar papers in other waders and migrants in the discussion (sixth section). The discussion section will also explore the possible implications of this study in terms of the way management and conservation of sites used by migrant coastal birds takes place. Finally, this thesis will conclude with reflections on the outcome of the study, as well as the methods used and possible avenues for future research.

2 Background

2.1 Migration

Migration is generally characterised by organisms' movements in response to changes in conditions, resources or social interactions, and usually occurs between two distinct habitats (Ramenofsky & Wingfield, 2007), allowing individuals to maximise their chance of survival or reproductive success (Chapman *et al.*, 2014). Bildstein (2006) estimates that up to 40% of bird species globally migrate, typically seasonally, with individuals traveling every year from the breeding to the wintering grounds – autumn or post-breeding migration – and from the wintering to the breeding sites – spring or pre-breeding migration (Newton, 2007; Somveille *et al.*, 2015). Migration is central to the lives of a number of avian species, but requires significant time and energy requirements and can account for high levels of mortality due to movements between breeding and wintering areas that are often separated by thousands of kilometres (Robinson *et al.*, 2009a).

The periods when individuals store reserves prior to migratory movements are considerably important and part of migration (Alerstam & Lindström, 1990). When such fuelling periods take place en route, they are usually referred to as stopover or staging areas (Warnock, 2010), and their quality (e.g., in food resources; Aharon-Rotman *et al.*, 2016) is likely to influence migration. Migratory behaviour can vary among populations and individuals at several levels, for example in the number of stopover sites used, migration distance and timing (Þórisson *et al.*, 2012).

2.1.1 Migration Strategies & Patterns

A number of varying migration patterns and strategies have evolved as species exploit optimal conditions and avoid intraspecific competition (Pulido, 2007). The behaviours, patterns and strategies are influenced by these pressures and vary depending on the required distance needing to be covered and latitude of breeding grounds (Hedh & Hedenström, 2016). In order to fully understand the biology of migratory movements and focus conservation efforts, it is important to understand how these strategies and patterns differ both between and within species (Bowlin *et al.*, 2010; Hansson & Åkesson, 2014).

The distances travelled on seasonal migration vary considerably among avian species. Take for instance the Arctic Tern *Sterna paradisaea*, whose seasonal journeys extend from high latitudes in the northern hemisphere to the Antarctic, traveling more than 80,000 km between consecutive breeding seasons (Egevang *et al.*, 2010). Another example of long-distance avian migration is provided by the Bar-tailed Godwit, completing the autumn migration in a non-stop flight of ca. 12,000 km across the Pacific Ocean, during a period of 9 days (Gill *et al.*, 2009). Conversely, in bird species such as the Blue Tit *Cyanistes caeruleus*, some populations undertake much shorter migrations of distances less than 100 km (Nilsson *et al.*, 2008). It has been suggested that longer migrations are often undertaken in birds that breed at higher latitudes (Newton & Dale, 1996). In the Arctic and sub-Arctic, food and resource abundant summer breeding seasons give way into winters unsuitable for certain species, and so it is necessary for those to undertake long migrations to wintering grounds at lower latitudes where resources are more readily available (Hedh *et al.*, 2022).

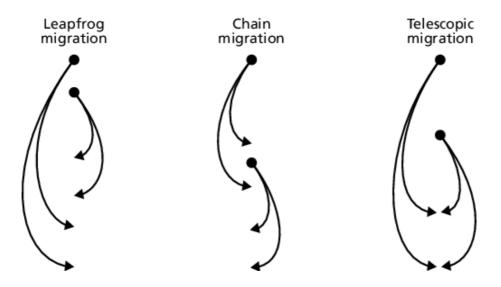


Figure 1: Conceptual illustration of different types of migrations (Chapman et al., 2014).

Populations of species also produce patterns of migration by differing their distribution and movement during migration (Chapman *et al.*, 2014). There are three main migration patterns that have been identified – chain migration, leap-frog migration and telescopic migration – with chain and leap-frog being the two most commonly reported amongst avian species (Skinner *et al.*, 2022; Smith *et al.*, 2003). Leap-frog migration occurs where northern populations of a species migrate further and spend the winter at latitudes further south than more southerly breeding subsections of the population (Figure 1; Newton 2007). The breeding populations at more northerly latitudes migrating to the southernmost wintering

grounds results in populations covering vastly different distances during the migratory period (Alerstam & Hedenström, 1998; Skinner *et al.*, 2022). Since this pattern of migration was first recognised, it has been theorised that the evolution of the pattern and winter displacement of populations can be put down to avoiding intraspecific competition (Drent & Piersma, 1990). Clear evidence of leap-frog migration has been observed in a number of wader species including Bar-tailed Godwits and Common Ringed Plover (Drent & Piersma, 1990; Duijuns *et al.*, 2012; Newton, 2020).

The Bar-tailed Godwit is known to breed predominantly on low arctic tundra, with breeding grounds located in Siberia and northern Scandinavia. When it comes to migration, the northern Scandinavian birds commonly winter in UK and along the northern coastlines of western and central Europe. The Siberian population, by contrast, will often be found wintering in western Africa, with these birds travelling past both the breeding and wintering grounds of the northern Scandinavian birds (Drent & Piersma, 1990). The Common Ringed Plover is a well-documented leap-frog migrant and provides a good example of the strategy. This migration pattern has been observed in populations in Scandinavia; where birds breeding in the south of Sweden migrate to the Iberian Peninsula for winter while individuals breeding in northern Sweden migrate beyond the entire range of the southern birds to spend winter in western Africa (Hedh *et al.*, 2022). Populations of Common Ringed Plover breeding in Iceland and Greenland have also been documented to winter in west Africa, while individuals that breed in the UK will often only travel as far as the coasts of central and western Europe to spend the winter – being "leap-frogged" by the Icelandic/Greenlandic breeding population (Delaney *et al.*, 2009).

Chain migration occurs when breeding populations within a species maintain their latitudinal position relative to each other at the wintering sites (Figure 1; Skinner *et al.*, 2022). It is theorised that chain migration may develop when larger individuals from breeding grounds at more northerly latitudes are able to outcompete individuals from southern populations at the northern wintering sites, forcing the smaller sized individuals from the southern population to winter further south (Norris *et al.*, 2006). Chain migration has been observed across a range of species including Northern Gannets *Morus bassanus*, Eurasian Sparrowhawk *Accipiter nisus* and Eurasian Curlew *Numenius arquata* (Fort *et al.*, 2012; Newton, 2020).

Northern Gannets utilise a major flyway that runs along the coasts of Western Europe and Africa for their post breeding migration. Chain migration has been observed in the Northern Gannets, with birds breeding in Norway wintering in Northern Europe, UK breeding individuals wintering between Northern Europe and North-West Africa, while Gannets breeding in France wintered off Northwest Africa. In this case the distance between the breeding colonies and wintering grounds of each breeding population has been observed to be very similar (Fort *et al.*, 2012). The Eurasian Curlew has a breeding range that extends from Spain over to Russia in the East and encompasses the UK and Arctic breeding grounds. Following migration, Curlews have been observed to spend the wintering period at sites along the Atlantic coast, using sites that are located around the North Sea to down as far as North Africa. Chain migration has been observed in Eurasian Curlew populations as wintering birds maintain the latitudinal sequence of their breeding grounds. This mean that individuals that winter at more northern latitudes will also breed further north, while those that breed further south will also utilise more southern wintering grounds (Pederson *et al.*, 2022).

Telescopic migration describes a pattern of migration in which species that breed at different latitudes migrate to the same or similar latitudes for the wintering period where the two separate breeding populations will coexist for a season (Figure 1; Borras *et al.*, 2011; Chapman *et al.*, 2014). Examples of telescopic migrations have been observed in Graycrowned Rosy Finches *Leucosticte tephrocotis* in North America, Yellow Wagtails *Motacilla flava* in Africa and the Eurasian Skylark *Alauda arvensis* in Europe (Borras *et al.*, 2011; Newton, 2020).

In the case of the Yellow Wagtail, there are a large number subspecies that when combined have a large breeding range that extends across the continents of Africa, Europe and into Asia. Despite this large breeding range, the wintering range following migration is limited to Africa and parts of southern Asia. This species provides an example of telescopic migration because individuals from across multiple breeding sites use the migratory period to condense into a smaller range of wintering grounds in a much more limited area (Ferlini, 2020). This is similar but on a smaller scale in the Eurasian Skylark. The Skylark breeds extensively across Europe with breeding grounds extending as far north as Scandinavia. Individuals then undertake what is a relatively short journey in migration terms to winter in south western Europe and north Africa. Once again this is an example of telescopic migration

as a large and expansive breeding range is condensed into a smaller range of wintering sites, with individuals from across the breeding range often wintering at the same sites (Hargues *et al.*, 2007).

When populations of the same species utilise sites at different latitudes (as is the case with all the aforementioned migration strategies; Figure 1), they are likely to experience varying conditions, food availability and predation risk. The different lengths of season that are inevitable at different latitudes will provide different opportunities in terms of accumulating energy and timing departure from wintering ground, resulting in two populations of the same species that organise their annual cycles in a different manner with regards to length of spring migration and arrival date (Hedh *et al.*, 2022).

2.1.2 Migration Timing

An earlier arrival at breeding grounds is a particularly important factor that is thought to increase breeding success (Morrison *et al.*, 2019). Arriving earlier at breeding sites can often secure breeding individuals' higher quality territories and better chance at procuring a mate for the season (Kokko, 1999), while also opening up opportunity for a higher number of nesting attempts in event of predation or failure (Morrison *et al.*, 2019). Therefore, in order to maximise the probability of breeding successfully, it is expected that the speed of migration is faster in spring due to the pressure of arriving early; a pressure which is amplified at high latitudes (Northern Hemisphere), where the window of optimal conditions for breeding is narrower (Carneiro *et al.*, 2021, Hedh *et al.*, 2022). However, arriving too early can pose risks, particularly at high latitudes. Unfavourable weather events such as snowfall can mark the very early periods of the breeding season which also poses a risk to early arriving birds (Marcström & Mascher, 1979).

It has been reported that arrival time can differ between sexes within species, and protandry – where males arrive to breeding grounds earlier than females – has been well documented in many migratory species (Mills, 2005; Alves *et al.*, 2012; Carneiro *et al.*, 2019). Protandry in spring migration has been found to be driven by an earlier increase in migration restlessness in males, resulting in earlier departure from wintering grounds and arrival at breeding grounds being up to eight days earlier than females in long distance migrants (Briedis *et al.*, 2019). Intrasexual competition is thought to be a driver behind this strategy, with earlier arriving males able to stake claim to the best and most productive territory

(Morbey & Ydenberg, 2001). It is also possible that males aim to arrive first in order to increase their chances of securing a mate for the season (Mills, 2005). Surplus male birds have been observed at breeding grounds along with territorial males with no mate midway through the breeding season, suggesting that there may be a shortage of females across a number of species and therefore by arriving at breeding grounds earlier male birds are giving themselves a longer period of time to find a mate (Francis & Cooke, 1986).

2.1.3 Carry-Over Effects

Later breeding attempts generally prove to be less successful than those earlier in the season (Rowe et al., 1994), but it may be stages much earlier in the annual cycle that determine how early breeding attempts may take place. Birds that arrive at breeding grounds in poor condition are less likely to immediately invest resources into reproduction; instead opting to replenish their body condition as a means of self-preservation (Lehikoinen et al., 2006). Individual condition upon arrival at breeding site can be influenced by the environmental conditions and habitat productivity experienced at wintering grounds, stopover sites and during periods of movement (Finch et al., 2014; Buchan et al., 2021). During migrations, stops are often required for birds to feed and rest, and so highly productive habitats are essential in maintaining body condition for the remainder of the migration (Balachandran, 2012). A particularly important date is the date of arrival at the breeding grounds, as generally birds with earlier arrival times lay earlier and have a higher probability of success (Morrison et al., 2019). However, the date of arrival may depend on previous annual stages, such as the date of departure from the wintering sites (Þórisson et al., 2012), which in turn can vary with conditions on food resources (Dalby et al., 2014). Hence, the performance of an individual at a given annual stage may be influenced by its experience at previous stages, a phenomenon usually termed as "carry-over effects" (O'Connor et al., 2014). It is thought that the build-up of carry-over effects may be cumulative from various stages of the annual cycle (Buchan et al., 2021), and therefore it is possible that a low-quality habitat at a stopover site or adverse weather conditions during migration could result in reduced reproductive success or survival (Robinson et al., 2009a).

2.2 Coastal Habitats & Ecosystems

2.2.1 Diversity & Importance

There are numerous different ways in which countries throughout Europe define coastal habitats (Seitz *et al.*, 2014). Natural features such as estuaries, lagoons, intertidal bays and mudflats are synonymous with coastlines across Europe and often boast a wide range of

habitats from saltmarshes and irregularly flooded wetlands to rocky shores, tidal creeks and sandflats (Airoldi & Beck, 2007; Seitz *et al.*, 2014). While coastal ecosystems such as wetlands are distinct and relatively independent in their own right (Watanabe *et al.*, 2018), they form a bridge between ecosystems on land and sea providing a channel for material and nutrient exchange as well as movements of fauna (Barbier, 2017). In 1997, Costanza *et al.* (1997) reported that coastal ecosystems only covered an estimated 6% of the total global surface area, yet despite not being large they are characterised by a high degree of species diversity (Watanabe *et al.*, 2018) and accounted for ca. 38% of all global ecosystem services (Constanza *et al.*, 1997). However, coastal environments are not limited to narrow stretches between land and sea, with Barbier (2017) stating that they can in fact stretch from up to 100 kilometres inland.

Coastal ecosystems are complex systems and the cycling of material, dispersal of biotic particles and food webs present throughout creates a highly productive habitat that can be utilised by multiple species in many different ways (Watanabe *et al.*, 2018). The abundance and variation of habitat and nutrients present in these ecosystems make coastal areas a great environment for nursery grounds, spawning and feeding grounds for a number of species (Seitz *et al.*, 2014). Habitats in coastal areas such as wetlands also provide a vital service through carbon sequestration and storage (Sapkota & White, 2020). While coastal areas offer less global coverage than terrestrial forests their contribution to carbon sequestration and storage as 'blue carbon' is much greater per unit area (McLeod *et al.*, 2011).

Other important services are also provided by coastal ecosystems such as pollution control, flood and storm protection and shoreline stabilisation (Barbier, 2017). Coastal areas have always been key population centres for humans with over a third of the global population being located within coastal zones (Barbier, 2017). Around 10% of the world's population reside in the low elevation coastal zone – coastal areas at an altitude of 10 metres or lower – and as result are particularly exposed and vulnerable to storm surges and extreme wave events (McGranahan *et al.*, 2007). Habitats such as marshes, beaches, dunes and mangroves offer coastal protection by helping to dissipate wave energy while also increasing the deposition of sediment suspended in the water and reducing the level of erosion (Spalding *et al.*, 2014). This creates a buffer zone between the populous areas and the sea that protects human activities along the coast from extreme weather (Barbier, 2017), with one study based

in the UK reporting that saltmarshes reduced wave height by up to 61% and total wave energy by an average of 82% prior to breaking (Möller *et al.*, 1999).

Coastal ecosystems are also utilised directly by humans; with the varied flora and fauna providing opportunities for harvesting and hunting while these areas also provide opportunities and spaces for activities such as birdwatching and other forms of recreation due to their aesthetically pleasing nature (Barbier, 2017). The wide range of ecosystem services provided by wetlands and coastal habitats are vitally important and far outweigh the services provided by terrestrial ecosystems (Davidson, 2019), however coastal ecosystems in particular are being poorly managed putting the longevity of these ecosystem services at risk (Barbier, 2019).

2.2.2 Threats & Pressures

High levels of human related activities have been concentrated along coastlines and in coastal areas; with the extensive anthropogenic activities exerting detrimental pressures on the environment (Watanabe et al., 2018). Human endeavours in coastal areas often result in the removal, change or complete destruction of habitat with prolonged residency increasing the runoff of pollutants into coastal waters (Halpern et al., 2008). As a result, marine ecosystems are some of the most exploited ecosystems globally (Barbier, 2017). To add to the already high population density present in coastal areas, there has been substantial growth in the number of people living in and around coastal habitats (Airoldi & Beck, 2007). Rapidly growing population sizes in these areas go in tandem with extended coastal developments which in turn can create issues with pollution, eutrophication and invasion and colonisation of non-native species which put these habitats at high risk of being impaired or even destroyed (Lotze et al., 2006; Watanabe et al., 2018). Anthropogenic influence causes both direct and indirect pressures to coastal habitats (Newton et al., 2020). Direct pressures such as land use change can severely degrade and reduce coastal areas, with one such example coming from the Huang He Delta Wetland in China where intensive agriculture and urban development halved the area of wetlands between 1976 and 2008 (Chen et al., 2011). Another example is the proposed airport designed to alleviate the full capacity Lisbon airport, in Portugal, which is planned for a peninsula within the Tagus Estuary – a large and internationally important wetland for migratory birds (Alves & Dias, 2020). Indirectly, humans influence on climate can lead to sea level rise and effects on coastal habitats.

The global loss of coastal wetland ecosystems has been occurring at a rapid pace with reports suggesting that since 1970 there have been losses of up to 35%, but it is not just the losses that cause the issues, with the quality of the remaining coastal wetlands also taking a big hit because of human led drainage, increased pollution and unsustainable use (Davidson, 2019). The evidence alarmingly supports the findings of Halpern *et al.* (2008), with their suggestion that when looking into coastal and marine ecosystems there is "no area unaffected by human impact", but recorded changes in temperature, precipitation and sea levels suggest that climate change and the effects of global warming are likely to pose an increasingly large threat to the coastal habitats and ecosystems that remain in the future (Robinson *et al.*, 2009b; Barbier, 2019). Fifty percent of saltmarshes and 35% of mangroves worldwide have been lost, destroyed or already suffered significant degradation over the past few decades as a result of human activities (Barbier, 2019). It has been suggested that due to human development and interference, up to 86% of the coastline of Europe is at a moderate risk or higher of being subject to unsustainable coastal development and construction (Seitz *et al.*, 2014).

While healthy coastal habitats are highly diverse, the extreme degradation of these sites that has taken place over a number of decades has reduced the quality of habitat to a point where many are no longer adequate nursery, feeding or breeding grounds and as a result the services these ecosystems provide have suffered consequences (Seitz *et al.*, 2014). It is not just the biological impacts that are being felt because of both the decline in abundance and quality of coastal habitats and ecosystems. From an anthropogenic perspective, deterioration and loss of these areas can result in declining water quality, loss of recreational opportunities as well as the loss of shoreline stabilisation, protection from flooding and storm events and control of erosion that are provided by coastal habitats such as wetlands and saltmarshes (Barbier *et al.*, 2019).

Through management efforts, humans have attempted to improve the state of coastal habitats and combat the degradation the ecosystems within are suffering. However, many of these practices do not go far enough leaving the delicate habitats and species that rely on them under threat (Seitz *et al.*, 2014). Detailed knowledge on the ecology of species using coastal habitats is fundamental for informed conservation measures.

2.2.3 Birdlife in Coastal Habitats

Coastal habitats support a wealth of species of both flora and fauna, many of which rely on these areas during their life cycle (Seitz *et al.*, 2014). Coastal wetland habitats provide areas of refuge to as many as 400 species of waterbirds globally (Puthur *et al.*, 2021). The avifauna in these habitats often consists of large numbers of gulls, terns, waterfowl and waders (Bildstein *et al.*, 1991). The utilisation of these coastal areas by a number of different avian families highlights how significant these areas and the conditions they provide are for birds during breeding, staging and migratory periods (Clausen & Clausen, 2014). Waders, in particular, rely on coastal habitats at various stages of their life cycle and utilise these areas across the globe (Delany *et al.*, 2009). A number of coastal wetland habitats see an increase in use by avian species during migrations and during the wintering season (Bildstein *et al.*, 1991).

A number of reasons have been outlined as to why coastal habitats are so important for bird species, with the high primary and secondary productivity of these sites being a key factor (Frederick, 2001). Coastal sites are often a place where freshwater and saltwater mix, with the combination of a nutrient influx from freshwater environments and the wide variety of submerged and aquatic vegetation present providing an attractive nursery ground for marine creatures in early life stages (Seitz et al., 2014). This in turn creates a highly diverse and rich habitat that is more productive than rocky shores or sandy beaches for foraging waders, proving to be a more attractive choice of habitat (Frederick, 2001). The tidal nature of coastal habitats is also a trait that is beneficial to foraging birds and therefore makes these sites preferable to inland wetlands. While inland marshes can be subject to complete drying depending on the season and weather, coastal habitats are exposed on a predictable basis each day allowing for regular access to concentrated shallow pools and flats for feeding (Kingsford & Johnson, 1998). The lack of seasonal drying makes coastal sites preferential to inland wetland habitats for breeding birds too, with water being a natural deterrent for many species that would predate upon vulnerable chicks, eggs or nesting adults (Frederick, 2001). Millions of individual birds globally depend heavily upon coastal areas and habitats at varying stages of their annual cycle (Clausen & Clausen, 2014). While many of the bird species that inhabit coastal wetland areas travel vast distances annually during migration, the requirement to use these wetland areas to make use of the high productivity classifies these birds as "wetland dependent" (Balachandran, 2012).

2.3 Study Species Overview

The Common Ringed Plover *Charadrius hiaticula* (hereafter referred to as Ringed Plover) is a small wader which is a native breeder across Europe, Asia and North America; but can also be found across Africa and into parts of the Middle East during the winter (Delany *et al.*, 2009). During the breeding season these birds are commonly found on the coast along sand or shingle beaches, but are also known to utilise short grassland and artificial habitats such as gravel pits and farmland; with some individuals being recorded breeding inland at altitudes of up to 1200m (Wiersma *et al.*, 2020). Over the winter months, Ringed Plovers often make use of the coastline utilising estuaries, tidal mudflats and exposed coral reefs (BirdLife International, 2022). However, they can also be found further inland outside of the breeding season, with sightings recorded at habitats including short grassland, farmland, gravel pits and sewage works (BirdLife International, 2022; Hockey *et al.*, 2005). A member of the *Charadriidae* family of Lapwings, Dotterels and Plovers, Ringed Plovers measure around 18-20 centimetres in length with a 48 – 57 centimetre wingspan and weighing between 42 – 78 grams (Mullarney & Zetterstrom, 2009).

Ringed Plovers are monogamous (Þórisson *et al.*, 2013), with chicks fledging after around 24 days and becoming independent from their parents soon after this (Wiersma *et al.*, 2020). Ringed Plovers, similarly to other waders, divide incubation and chick rearing responsibility equally between the sexes (Wallander, 2003). Sexual maturity is reached by the time the bird is one year old and on average Ringed Plovers lifespan is five years (Robinson, 2005). Recorded individuals have been observed to live upwards of 10 years, with an individual in Norway being recorded at 14 years (Norwegian Polar Institute, N.D.) and an individual in the UK reaching 21 years (Robinson, 2005). Ringed Plovers are classified as least concern on the IUCN red list with global population estimated to be between 450,000 and 1.4 million individuals (IUCN, 2021).

Adults of the species in summer breeding plumage have a bold black breast band along with a white belly and brown back. They have a white forehead which is restricted by a black band that extends around the eye and with a second black band extending from the base of the beak joining the former around the ear coverts. Ringed Plovers have striking orange legs and feet, with a bill that is orange at the base and is capped with a black tip (Figure 2A; Toochin, 2019). Both sexes of the species are similar in plumage, however the females have a less prominent breast band than their male counterparts. Breeding plumage is held for 6 months between March and September (Sibley, 2000), in winter months Ringed Plovers hold their basic plumage which is very similar to breeding plumage but the black is replaced by a brown and colouration of the plumage is generally duller (Figure 2B; Mullarney & Zetterstrom, 2009). Juveniles of the species resemble wintering adults in plumage; however, the breast band is often incomplete with the back of the bird being a mottled brown (Figure 2C; Hayman *et al.*, 1986).



Figure 2: Ringed Plovers pictured in adult breeding plumage with bold black breast band (A), adult winter plumage with brown colouration of the breast band (B) and juvenile plumage mottled brown with dull features (C). (Photos; A: Daniel Jauvin, August 2018, Quebec, Canada. B: Ian Davies, December 2014, Oromia, Ethiopia. C: Suzanne Labbé, September 2016, Quebec, Canada).

2.3.1 Range

Ringed Plovers breed across Arctic and temperate regions (Figure 3). The species spreads across Europe with populations in western Europe and breeding birds found as far east as eastern Russia. Northern Canada hosts Ringed Plover populations as both a passage and breeding species, while Greenland and Iceland are used during the summer months for breeding (Delaney *et al.*, 2009; Bird Life International, 2022). Across the majority of their range Ringed Plovers are migratory birds, with the United Kingdom hosting a resident population all year round (Þórisson *et al.*, 2013; BirdLife International, 2022), while also supporting migratory populations of Ringed Plover during the breeding season and winter

months (Figure 3). Migratory populations from Canada journey across the North Atlantic to join the Western European populations wintering in Africa. While West Africa is a common destination for wintering Ringed Plovers, they have also been found to winter across continental Europe in the Mediterranean Basin and Iberian Peninsula. Small numbers of Ringed Plover have been found to migrate via China and Japan although the species is mainly a vagrant to South East Asia (Wiersma *et al.*, 2020). Within Iceland, Ringed Plovers are widespread native breeders (Figure 4). While the majority of breeding populations in Iceland can be found in coastal areas, there are numerous instances of breeding at sites inland with breeding even taking place in areas of the highlands (Þórisson *et al.*, 2013).

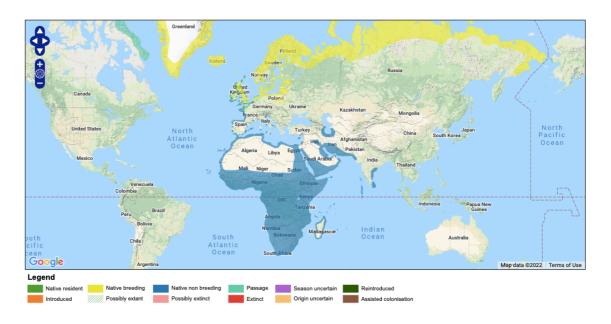


Figure 3: Global distribution range of the Ringed Plover (Charadrius hiaticula) (BirdLife International, 2022).



Figure 4: Iceland distribution range of the Ringed Plover (Charadrius hiaticula) (BirdLife International, 2022).

2.3.2 Subspecies

The Ringed Plover species is currently split into three widely recognised subspecies: hiaticula, tundrae and psammodromus (Thies et al., 2018). The hiaticula subspecies encapsulates populations breeding in the UK, Ireland and parts of continental Europe. This particular subspecies can be found wintering across Western Europe and West Africa after undertaking an autumn migration (Figure 5; Delany et al., 2009). Individuals of the tundrae subspecies are often slightly smaller than their hiaticula cousins. While being smaller, this subspecies also has a less extensive orange colouration of the bill, darker, duller upperparts and a narrower white patch behind the eye which enables them to be distinguished from the hiaticula subspecies (Wiersma et al., 2020). The tundrae subspecies of Ringed Plover includes birds breeding in northern Scandinavia, Finland and Russia, with these birds migrating to winter across continental Europe, Western Africa and parts of the Middle East (Figure 5; Delany et al., 2009).

The Icelandic population of Ringed Plover is included in the *psammodromus* subspecies along with breeding populations from Canada, Greenland and the Faeroes (Delany *et al.*, 2009). This particular subspecies is very similar to birds of the *tundrae* subspecies in both size and appearance, although may be distinguished from this subspecies in breeding plumage due to having a narrower white band on the forehead – a trait which is especially

noticeable in females (Wiersma *et al.*, 2020). The *psammodromus* subspecies is migratory, joining its relatives on the coasts of western Europe and Africa over the winter months (Figure 5; Delany *et al.*, 2009). Estimates suggest that the Icelandic population of *psammodromus* accounts for half the breeding population of the subspecies (Delany *et al.*, 2009) with Guðmundsson (2002) reporting there to be around 50,000 breeding pairs breeding in Iceland in 2002; however, more recent reports have indicated that this number has dropped to around 23,000 breeding pairs in recent years (Guðmundsson, 2002; Skarphéðinsson *et al.*, 2016).

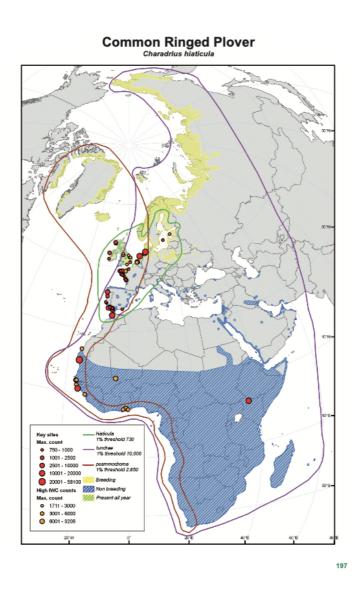


Figure 5: Distribution of breeding and wintering grounds of the three subspecies of Ringed Plover (Delany et al., 2009).

2.3.3 Breeding

The beginning of the breeding season for Ringed Plovers varies depending on the location of the breeding grounds. For populations breeding in areas around the North Sea egg laying can commence as early as April compared to breeders in Greenland where egg laying is unlikely to begin until around the fourth week in June (Wiersma *et al.*, 2020). The Icelandic population Ringed Plovers have been recorded as laying eggs and beginning incubation in mid-May (Þórisson *et al.*, 2013), however earlier nesting attempts have also been observed (this thesis) and nesting attempts continue through June and into July (Wiersma *et al.*, 2020). Ringed Plovers are territorial birds and show both high site fidelity and natal philopatry. Adults will nest in a shallow scrape on the ground that is usually lined with pebbles, debris or vegetation (Figure 6; Stenzel & Page, 2019). The female Ringed Plover will usually lay a clutch of between 2 and 4 eggs with eggs being laid at an interval of 1-3 days, although in some instances nests have been recorded with 5 eggs (Winkler & Walters, 1983).



Figure 6: Three examples of Ringed Plover nests with clutches of 4 eggs lined with different materials, gravel (A), vegetation/debris and gravel (B) and seashell debris (C) (Photographs by author, 2021).

Ringed Plovers lay eggs measuring 36 mm × 26 mm on average. The eggs are pyriform and olive-grey in colour with black speckles helping to camouflage the eggs against the substrate of the nests (Figure 6; Norwegian Polar Institute, N.D.). Both adults incubate the eggs over a period of up to 27 days, bringing total time from the laying of the first egg to hatching to around 30 days (Wiersma *et al.*, 2020). With both adults being present throughout the duration of the incubation period, shifts on the eggs are shared evenly although it is possible that males have a tendency to cover more of the night-time incubation period (Stenzel & Page, 2019; Wallander, 2003). Pairs that successfully fledge their first brood will often

attempt to double brood, with minimal clutch overlap due to the second clutch being started shortly after the first young have fledged (Wallander & Andersson, 2003). Double brooding is a rare occurrence in waders (Dowding *et al.*, 1999). Most wader species will replace a lost clutch, but are highly unlikely to lay a second clutch if the first survives (Cramp & Simmons, 1985).

2.3.4 Diet

In summer, Ringed Plovers typically move to areas away from their breeding territory to feed, and can often be found in small flocks of up to 50 individuals when feeding (Wiersma et al., 2020). Often these birds will be found feeding on coastal flats, however they will also venture away from the coast and can be found feeding in agricultural areas and areas of short grassland including maintained areas such as playing fields (Wiersma et al., 2020). As a result of this range of habitats, the Ringed Plover's diet during the breeding season includes a number of invertebrate species including small crustaceans, molluscs, polychaete worms, isopods, amphipods, various insects (e.g., ants, beetles, flies and their larvae) and millipedes (del Hoyo et al., 1996). During the winter, the Ringed Plover primarily feeds on marine worms such as polychaete worms, as well as various small crustaceans and molluscs (Robinson, 2005). Ringed Plover have not been found to specialise their diet during the winter, however they are likely to vary their diet depending on the most common prey species in the area (Pienkowski, 1982). They are foraging birds that will search for food and feed at any time of day or night. Ringed Plovers will sometimes use the foot-trembling technique on the substrate to bring their prey towards the surface where they then have a peck rate of up to one peck per second to catch their prey (Wiersma et al., 2020).

3 Methods

3.1 Study Sites

Data used in this project was collected from two sites within Iceland, the Westfjords and the South. The Westfjords are a very mountainous region, with the coastline made up of fjords indenting into the land; while the South is a much flatter region, made up mostly of heath and farmland. Within the study sites, large areas were surveyed regularly each year in order to locate nesting Ringed Plover.

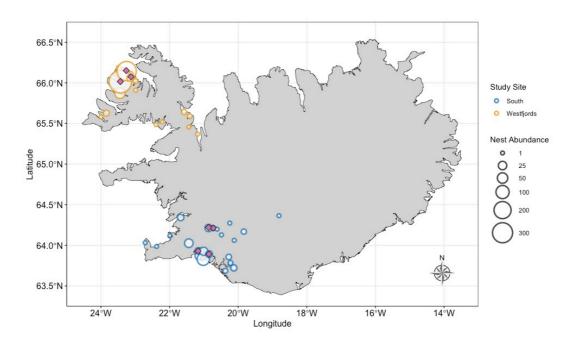


Figure 7: Map of Iceland with location and number of Ringed Plover nests recorded in both study sites, marked by circles, as well as deployment areas for geolocators, marked by purple diamonds.

Three of the areas surveyed for nests in the Westfjords and four such areas in the South were chosen to monitor and tag individuals with geolocators (see below). Bolungarvík, Önundarfjörður and Skutulsfjörður were the areas used in the Westfjords to deploy the geolocators, while Kaldaðarnes, Súluholt, Laugarvatn and Laugarvatnsvellir were chosen as deployment areas in the south of Iceland (Figure 7). The monitored area in Önundarfjörður focused largely on a vegetated coastal plain situated adjacent to a mudflat and is an area that

has been identified as a key site for Ringed Plovers and other migratory birds (Þórisson *et al.*, 2013). Three patches of habitat made up the Bolungarvík study area, including sandy patches near the coast, gravel patches further inland and vegetated patches on a golf course. In Skutulsfjörður the area chosen for monitoring and geolocation deployment was a reclaimed area of landfill consisting of both gravel patches and rough grassland. Both the areas of Kaldaðarnes and Súluholt that were monitored were made up of large patches of gravel surrounded by swathes of farmland with Ringed Plover nests being located across the gravel patches. The Laugarvatn study area was made up of low-quality heathland and vegetation with a similar habitat situation being found at the fourth study area surveyed across the south in Laugarvatnsvellir.

3.2 Data Collection

Data collection for this project was carried out by researchers at Rannsóknasetur Háskóla Íslands á Suðurlandi (University of Iceland South Iceland Research Centre). This includes all ringing and marking of birds that was undertaken, as well as the deployment and retrieval of all geolocators.

Nesting data was collected from 2004 up until 2020. During the breeding season (from May to July), each of the areas within the two study sites were searched for nests. Ringed Plover nests were often located by surveying the area for adult birds and observing behaviour indicating that a nest was nearby. After retreating to a distance where the bird returned to normal behaviour, the individual was then watched until it returned to the nest to identify the location. Observed adults were also checked for metal and colour rings during observation.

Ringing birds is a simple but effective way of tracking movements, especially in migrants, and has been carried out in Iceland since the early 1920's (Náttúrufræðistofnun Íslands, N.D.b). Some Ringed Plovers have been fitted with individual combinations of colour rings for the purpose of several studies, allowing for identification of individuals from a greater distance. The combinations are comprised of four rings, placed one on the tibia and one on the tarsus of each leg (Figure 8). Over the years, a network of volunteers has reported marked birds abroad, which allows for verification of data retrieved from the geolocator tags (see below).



Figure 8: Ringed Plover fitted with a metal and colour rings on legs, and with a geolocator tag visible between feathers on back (deployed using a leg-loop; photo: Francisco Tornero Iranzo, Galicia, Spain. August 2019).

Once the nest location was identified, the position of the nest cup was taken using GPS. This ensured the location of the nest was recorded as accurately as possible and allowed for easy relocation of the nest without having to mark it with any object. Clutch size was recorded for each nest, and the incubation stage of the eggs was estimated by floating them in water; as embryos within the eggs develop and the air cell grows during incubation the density of the egg changes allowing them to float (Brua & Machin, 2000). Incubation stage can then be estimated based on the location of the egg in the water column and the angle at which the egg sits (Liebezeit *et al.*, 2007). Lay date was converted to Julian Date from the start of each new year in order to make annual data sets easily comparable. From the estimated incubation stage an estimate for the lay date of the first egg in the clutch was calculated by back dating, using an assumed 30-day nesting duration from the first egg being laid to hatching (Wallander & Andersson, 2003, Þórisson *et al.*, 2013).

In each year of the study, most nests were monitored to observe the outcome of the nest with the fate of the nest being recorded as one of three categories; successfully hatched, failed to hatch or unknown outcome. Nests were classified as having successfully hatched in cases where at least one egg had hatched. Fledging success was not monitored or recorded. In cases where the nest was revisited in advance of the predicted hatch date and no eggs were present it was assumed that the nest had been predated and therefore recorded as failed to hatch, after inspecting the nest cup for eggshell fragments indicative of hatching.

3.3 Deployment & Recovery of Geolocators

Adult birds were caught on the nest during incubation, using a Moudry TR60 trap (www.moudry.cz). While most individuals trapped only had eggs to tend to, three females and two males were caught while tending to chicks with one male caught while attending both chicks and eggs. Once captured, each individual was weighed, with the sex of the bird being determined using plumage or observation during coitus (Meissner *et al.*, 2010, Þórisson *et al.*, 2013). All captured birds were individually marked with a combination of colour rings. Additionally, between 2016 and 2019, 55 Ringed Plovers were fitted with geolocators across the South and Westfjords of Iceland (Table 1).

Geolocators are small lightweight data loggers that record light levels from the surrounding area at regular intervals for the duration of their battery life. Patterns of ambient light recorded by the geolocator can be analysed to estimate locations and movement patterns of animals during migrations. Information such as day length, solar noon and solar midnight can be used in the analysis to predict these locations, however noise in the collected data from unpredictable shading can result in errors (Lisovski *et al.*, 2015; Lisovski *et al.*, 2019).

The geolocator tags (hereafter referred to as tags) used in this project were produced by Migrate Technology LTD and attached to the birds using two methods. Birds captured in 2016 were fitted with Intigeo-W65A9-SEA tags weighing 0.70 g on a flag on the tibia. Birds captured between 2017 and 2019 had Intigeo-P65A2 tags weighing 0.71/0.87 g attached to their back, with a leg-loop fitted to secure the tag in place (Figure 8). The tags were programmed to collect a reading of light intensity every 5 minutes over a period of a 1-2 year battery life (Fox, 2021). Therefore, it is necessary to retrieve the tags the following year. In order to retrieve the tags, the birds were recaptured using the same nest trap method as mentioned above.

Table 1: Number of tags deployed and retrieved per site, area and year, between 2016 and 2019. Note that all retrieved tags were removed from the bird in the first year after deployment.

Site	Area	Year	Tags Deployed	Tags Retrieved	Percentage Retrieved
Westfjords	Bolungarvík	2019	8	6	75.00%
	Önundarfjörður	2019	12	5	41.67%
	Skutulsfjörður	2019	2	1	50.00%
		Total	22	12	54.55%
South	Kaldaðarnes	2016	6	5	83.33%
		2017	6	1	16.67%
		2018	2	0	0.00%
	Súluholt	2016	4	2	50.00%
		2017	8	3	37.50%
		2018	4	0	0.00%
	Laugarvatn	2018	2	0	0.00%
	Laugarvatnsvellir	2019	1	1	100.00%
		Total	33	12	36.36%
		TOTAL	55	24	43.64%

Out of 22 tags deployed in the Westfjords, 12 were retrieved; while 12 out of the 33 tags that were deployed across the South of Iceland were retrieved (Table 1). Of the tags that were deployed but were not retrieved, one tagged individual was found deceased in August 2016 around two months after being caught. Six of the individuals tagged in the Westfjords have been sighted since being fitted with geolocators, but attempts to recapture the birds to retrieve the tags have proved unsuccessful.

3.4 Light Data Processing

While all data collection for this project was carried out by researchers at Rannsóknasetur Háskóla Íslands á Suðurlandi (University of Iceland South Iceland Research Centre), the data processing and analysis for this project was all undertaken by the author.

Once tags were retrieved data was downloaded and automatically adjusted for clock drift, using IntigeoIF (Fox, 2021). In instances where the tag had failed or run out of battery resulting in an incomplete dataset it was not possible to adjust for clock drift (n = 7). The data from the failed tags was visually inspected and no obvious signs of gradual longitudinal movement at stationary sites was noted, indicating that insignificant clock drift had occurred. Two of the seven tags with incomplete datasets had failed early into the recording period (2 and 6 months later), producing a limited dataset. Therefore, these two tags were excluded from analysis. The exclusion of these 2 tags left a total of 22 tags from which data was used in analysis.

The downloaded light-level data was analysed using the 'GeoLight' package in R (Lisovski et al., 2015) and following indications in the light-level geolocation analyses manual (Lisovski et al., 2019). Since geolocators are activated before deployment and deactivated after retrieval, excess data collected during these periods was removed. Tag data was also filtered to remove extended periods of time spent within the breeding grounds, where location of the bird is known; this was carried out using data collected by volunteers reporting sightings of Ringed Plover within Iceland. In some cases, there were no recorded sightings of individuals in Iceland following deployment or prior to retrieval of the tag (n = 11). In these instances, the data was filtered to the calculated average date of last and first sighting in Iceland from all tagged birds (23rd June & 20th May respectively).

During the three weeks surrounding the spring and autumn equinoxes day lengths are similar across the globe, a phenomenon which can cause errors of thousands of kilometres in latitude estimates (Porter & Smith, 2013). To account for this, data was filtered to exclude location estimates on dates surrounding both the spring and autumn equinox. All positions recorded in the period 5 days prior and 20 days after the autumn equinox were excluded, while also excluding all recorded positions in the 20 days prior and 5 days after the spring equinox (Hedh *et al.*, 2022). These periods were excluded due to known sun outages which occur

prior to the March (spring) equinox and following the September (autumn) equinox in the northern hemisphere (Ma *et al.*, 2018).

A threshold value of 3 lux was used to estimate sunrise and sunset events. After estimation, sunrise and sunset times were inspected manually and adjusted to account for false events, such as night-time light noise or periods of shading during the day. Stationary periods during the bird's migration were differentiated from periods of movement using the 'changeLight' function with probability of change q = 0.9 and the minimum stationary period was set to 2 days. The 'changeLight' function uses the extracted sunrise and sunset times to define stationary periods based on probability of change (Lisovski & Hahn, 2012). Both study sites where geolocators were deployed are situated in areas with constant daylight during the summer months. As this period coincides with the breeding season and the deployment and retrieval of geolocators, calibration of the data at the breeding grounds was not possible. Instead, the sun elevation angles were calculated during periods of residency outside the breeding season using the Hill-Ekstrom calibration (Lisovski et al., 2012). The Hill-Ekstrom calibration calculated a sun elevation angle corresponding to the threshold light value of 3, however when the calculated sun elevation angle based on the threshold value does not match the true elevation angle there is a risk of increased error in latitudes due to over or underestimating the elevation angle (Lindström et al., 2016). To account for this, a range of sun elevation angles were tested (steps of 0.25 degrees) with latitude estimates being inspected in order to find the optimal elevation angle that minimised variation in latitude estimates. This resulted in a range of sun elevation angles between -3.25 and -4.5 across all tags.

Once the optimal sun elevation angle had been found for each individual tag, the 'mergeSites' function (with a distance threshold of 250 km) was used (Lisovski & Hahn, 2012). This function merges stationary periods in case some consecutive sites were separated by outliers or strong shading events, and allows to determine the arrival and departure date at each site. Hence, it was possible to calculate the duration of stay for the bird at each of its stopover and wintering sites for each individual.

The sighting data recorded by a network of volunteers allowed for verification of the accuracy of defined sites. For birds that had recorded sightings outside of Iceland (n = 6) the locations and timings of these sightings was compared to the locations and timings of stationary periods produced by 'mergeSites' to ensure that the correct location and time period was being estimated for the individual.

3.5 Data Analysis

3.5.1 Migration Patterns

Winter locations were extracted from geolocator analysis and plotted on a map with the aim of investigating the occurrence of leap-frog migration within the Icelandic population of Ringed Plover. Winter locations were defined as the longest stationary period that occurred following autumn migration and before any large northerly movements suggesting spring migration. Once winter locations were defined and mapped, the distance between each individuals breeding and wintering ground was calculated. This was done using the 'distHaversine' function from the 'Geosphere' package in R allowing for the "Great Circle" distance to be calculated using the Haversine method (Hijmans, 2021). In order to test if the mean latitude of winter locations for individuals from the South and Westfjords breeding sites were equal a Mann-Whitney U test was performed. In a leap-frog migration pattern, it is expected that northerly breeding populations will spend the winter at lower latitudes than more southern breeding populations (Newton, 2020).

3.5.2 Carry-Over Effects

To investigate if events during spring migration and breeding were influenced by previous stages, a number of key dates and periods of time were looked at. Key dates or periods of time were classified as 1) departure date from wintering grounds, 2) total time spent at stopovers, 3) total number of stopovers, 4) date of arrival in Iceland and 5) lay date of first egg. A sixth parameter of hatch success was also used to investigate for possible carry-overs into the breeding season. As a result of recorded positions during the period surrounding the spring equinox being excluded, data from any individual that was apparently not stationary during the equinox period was not used for this analysis. This left a total of seven tags from which these key events and periods could be extracted.

Simple linear models were used to test for relationships between different stages of the spring migration. In these models key events prior to arrival in Iceland were used as fixed factors. Six linear models were run in total, in which the dependent key date/time period was regressed on a preceding key date date/time period from the spring migration to test for possible causal relationships. The six linear models run were in order to test for associations between 1) departure date from wintering grounds and the number of stopovers en route to Iceland, 2) departure date from wintering grounds and total stopover duration during spring migration, 3) total stopover duration and number of stopovers, 4) departure date from

wintering grounds and arrival date in Iceland, 5) stopover duration and arrival date in Iceland, and 6) number of stopovers during spring migration and arrival date in Iceland.

Three simple linear models were also carried out to test if lay date was influenced by previous events in the individual's life history. For these models the lay date of the first egg was always used as the dependent variable, with 1) departure date from wintering grounds, 2) total time spent at stopovers and 3) date of arrival in Iceland being used as fixed factors.

In order to investigate whether the laying date affected hatching success (coded as 1 - success, 0 - fail), a generalised linear model with binomial regression distribution was carried out. Lay date was used as the fixed factor for this model; however, this factor was scaled in order to normalise the data and allow for comparison. Random effects of both year and individual were used to account for potential biases that could result from multiple nests from the same individual bird and multiple nests on the same date in different years.

3.5.3 Timing of Breeding

To identify any trends or changes in lay date over the years, a linear model was performed, which would also indicate the presence of possible differences in lay date between the two study sites. For this analysis lay date was used as the response variable, with both year and study site used as fixed factors while the interaction between these two factors was also investigated. Only the first nesting attempt per induvial was considered in the above analysis, in order to only analyse the known first breeding attempt and to avoid potential bias by including any re-nesting attempts in the analysis.

All analysis of data was carried out in R 4.0.5 (R Development Core Team, 2013), with all models being checked using the 'Performance' package in R (Lüdecke *et al.*, 2021).

4 Results

Over the 16 years in which nest data for Ringed Plovers was collected a total of 979 nests were observed and recorded across both study sites. Of this total, 749 nests were located and recorded in the Westfjords with yearly figures ranging from 8 observed nests (2016 & 2018) to 144 nests (2007; Figure 9). In the South, a total of 230 nests were located and recorded. Yearly figures for located nests ranged from 1 nest (2010 & 2014) to 30 nests (2016). In 2013 no nests were located in this study site (Figure 9).

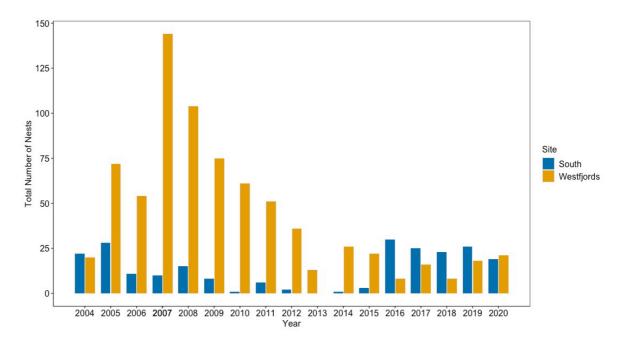


Figure 9: Annual variation in the frequency of Ringed Plover nests found in the Westfjords and South of Iceland from 2004 - 2020.

In the Westfjords, a total of 605 nests were monitored for their success and 336 nests (44.86%) hatched, with annual estimated hatch successes ranging between 0% (2016, 2017 & 2018) and 100% (2013) in observed nests (Figure 10). In the South, a total of 143 nests were monitored, with 86 nests successfully hatching (37.55%). The annual hatch success rates ranged between 0% (2010, 2012 & 2014) and 100% (2011; Figure 10) in observed nests. No nests were observed in the South during 2013.

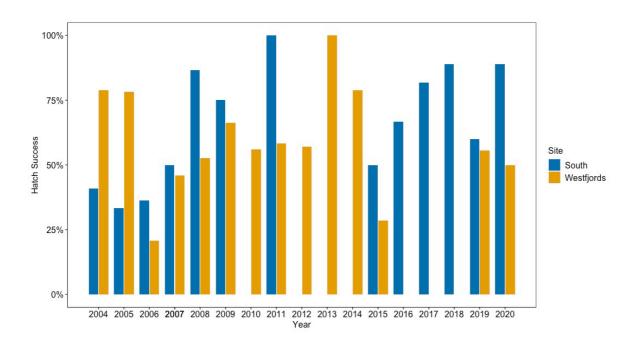


Figure 10: Annual variation in the proportion of Ringed Plover nests that successfully hatched in the Westfjords and South of Iceland from 2004 - 2020. Nests with unknown outcomes were excluded.

4.1 Migration Patterns

During autumn migration, individuals that had spent the preceding breeding season in the South of Iceland spent the winter 3530 km away (SD = 1280 km, n = 11) on average. Meanwhile, individuals who had spent the breeding season in the Westfjords travelled 4124 km (SD = 1218 km, n = 11) on average during autumn migration.

The majority of Westfjords breeding Ringed Plover were found to have wintered below 40°N latitude, with one individual being an exception to this, wintering in Western Europe (49.4°N; average wintering latitude of 29.99°N, SD = 11.72; Figure 11). Breeding Ringed Plover in the South of Iceland wintered around the coast of Western and South Western Europe in France, Spain and Portugal, but also further south in West Africa (most likely in Mauritania and Senegal; average wintering latitude of 33.23°N, SD = 11.69; Figure 11).

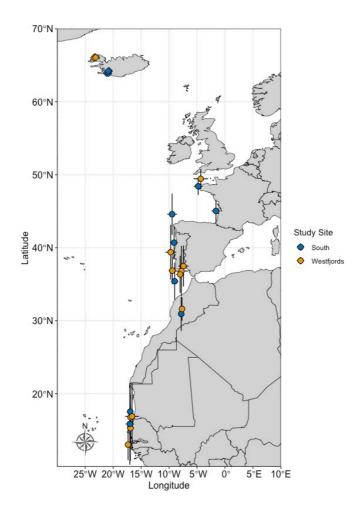


Figure 11: Wintering areas (circles) for individual Ringed Plovers breeding in the South and Westfjords of Iceland (diamonds). Error bars represent the latitudinal and longitudinal SD of the average positions, and diamonds represent the breeding areas.

A Mann-Whitney U test indicated that the wintering latitudes of birds breeding in the Westfjords (median = 36.34°N) were not statistically different to those birds breeding in the South (median = 35.41°N); W = 71, p = 0.511, r = 0.17, n = 22; Figure 12), suggesting no clear leap-frog migration pattern for those populations.

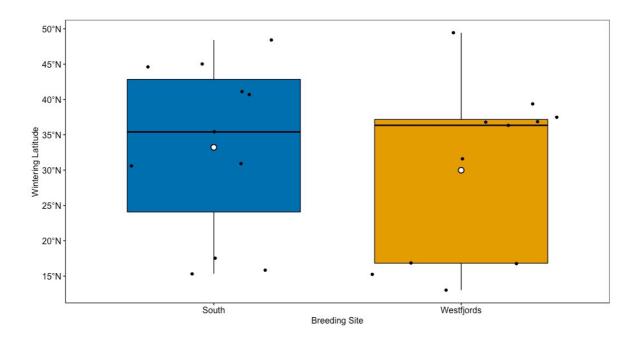


Figure 12: Boxplot representing wintering latitudes between individuals in the South and Westfjords breeding populations. Mean wintering latitude of each population is represented by the white point, coloured sections highlight the interquartile range and bold black line represents the median wintering latitude. Black points show the underlying distribution of the data.

4.2 Carry-Over Effects

The average departure date from wintering grounds was 19 March (SD = 32.24, range: 16 January – 15 April, n = 7). All individuals made at least one stop en route from wintering grounds to breeding grounds in Iceland. The average number of stops taken was 2.6 (SD = 0.98, range: 1 - 4, n = 7), with individuals spending an average of 34 days at stopover sites after departing wintering grounds (SD = 29.82, range 13 - 87 days, n = 7).

The average arrival date of individuals in Iceland was 6 May (SD = 9.11, range: 27 April – 23 May, n = 7). Average estimated lay date for individuals that had been followed throughout the spring migration was 22 May (SD = 5.53, range: 13 May – 28 May, n = 7).

4.2.1 Spring Migration

Six simple linear models were used to test for relationships between different stages of the spring migration in Icelandic Ringed Plovers. The first three of these models were used to identify possible effects of stages prior to arrival in Iceland. No effects were found of departure date from wintering grounds on the number of stopovers, or of the number of

stopovers on the total stopover duration (Table 2A & 2C, Figure 13A & 13C). There was however, a significant negative effect of winter departure date on the total duration of stopovers undertaken during spring migration (Table 2B), suggesting that the later in the year that an individual departs its wintering grounds the shorter its total stopover duration will be (Figure 13B).

The three simple linear models run in order to identify potential carry-over effects of preceding migration events on the arrival date of individuals in Iceland, showed no significant effects of winter departure date (Table 2D, Figure 13D), total duration of stopovers (Table 2E, Figure 13E), and the number of stopovers undertaken during spring migration (Table 2F, Figure 13F).

Table 2: Linear model results analysing the effect of winter departure date on the number of stopovers (A), winter departure date on the total duration of stopovers on spring migration (B), number of stopovers on the total duration of stopovers (C), winter departure date on arrival date in Iceland (D), total duration of stopovers on the arrival date in Iceland (E), and the number of stopovers on the arrival date in Iceland (F). Significance levels are shown for each variable with significant variables in bold.

Model	Coefficients	Estimate	SE	t	р
A	Intercept	3.98075	0.9214	4.32	< 0.01
A	Winter Departure Date	-0.01787	0.01093	-1.653	0.16289
В	Intercept	105.74402	7.31123	14.46	< 0.001
Б	Winter Departure Date	-0.90436	0.08671	-10.43	< 0.001
С	Intercept	-14.3	29.21	-0.49	0.645
	Number of Stopovers	18.95	10.72	1.768	0.137
D	Intercept	124.63404	10.63672	11.717	< 0.001
	Winter Departure Date	0.01732	0.12615	0.137	0.896
Е	Intercept	124.54119	5.97191	20.854	< 0.001
E	Total Duration of Stopovers	0.04237	0.13533	0.313	0.767
F	Intercept	121.05	11.134	10.872	< 0.001
Γ	Number of Stopovers	1.925	4.085	0.471	0.657332

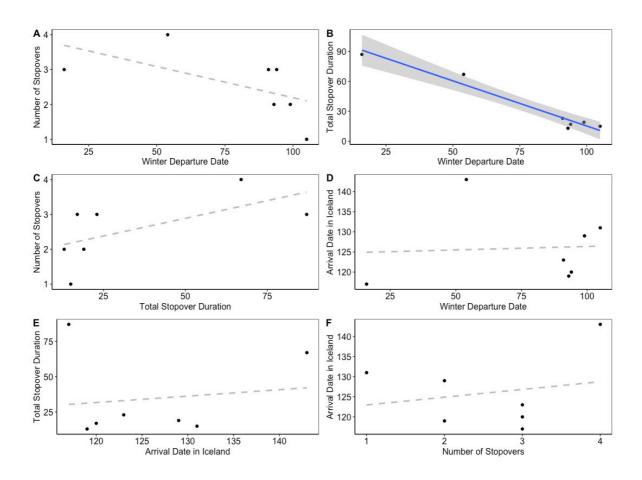


Figure 13: Estimated relationships of life stages during the spring migration of Icelandic Ringed Plover. Dashed lines are used to represent non-significant relationships, while blue lines are used to highlight significant relationships between variables. Grey shading on plot 'B' represents the standard error. Date on axis' is Julian Date and represents a day of the year; e.g., $I = January I^{st} & 365 = December 31^{st}$.

4.2.2 Lay Date

Table 3 shows the results of three simple linear models run to analyse the effects of preceding life stages on the lay date of first nesting attempts in Iceland. There were no apparent effects of winter departure (Table 3A, Figure 14A) and total duration of stopover periods found on lay dates of first nesting attempts (Table 3B, Figure 14B). While there was some suggestion of a relationship between arrival date in Iceland and lay date of first nesting attempts, with individuals arriving later seemingly having later lay dates (Figure 14C), once again it was found that arrival date in Iceland had no effect on lay dates of first nesting attempts (Table 3C).

Table 3: Linear model results analysing the effect of winter departure date (A), total duration of stopovers on spring migration (B) and arrival date in Iceland (C) on the lay date of first breeding attempts. Significance levels are shown for each variable with significant variables in bold.

Model	Coefficients	Estimate	SE	t	р
A	Intercept	135.40363	5.53276	24.473	< 0.001
A	Winter Departure Date	0.08908	0.06562	1.358	0.233
В	Intercept	144.84455	3.39067	42.719	< 0.01
	Total Duration of Stopovers	-0.07017	0.07684	-0.913	0.403
С	Intercept	93.0912	26.2217	3550	< 0.05
	Arrival Date in Iceland	0.3916	0.2076	1.886	0.118

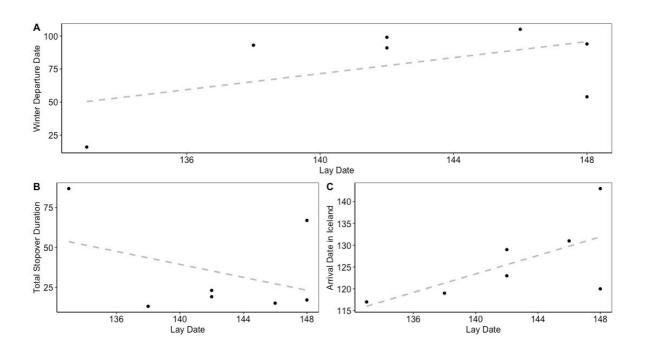


Figure 14: Estimated relationships of preceding life stages during spring migration on the egg laying date of Icelandic Ringed Plover. Dashed lines are used to represent non-significant relationships between variables. Date on axis' is Julian Date and represents a day of the year; e.g., $I = January 1^{st} & 365 = December 31^{st}$.

4.2.3 Hatch Success

The generalised linear model shows that there was no significant association between the date at which the first egg of the nest attempt was laid and hatching success of the nest (Table 4). The model also found that there were no significant associations between the site at which

the nest attempts were made and hatch success (Table 4). There were also no significant effects reported in the interaction between lay date and site on the hatch success of nest attempts (Table 4).

Table 4: Generalised linear model analysing the effect of lay date of nesting attempts and site of breeding ground on hatch success. Significance levels are shown for each variable with significant variables in bold. 'SiteWestfjords' represents the estimation in relation to the South site. ¹ Lay date was scaled to normalise the dataset and allow for comparison.

Fixed Effects	Estimate	SE	p
Intercept	0.974	0.2881	< 0.001
Lay Date ¹	0.2476	0.1878	0.187344
SiteWestfjords	-0.5113	0.2763	0.064243
Lay Date*:SiteWestfjords	-0.2307	0.2087	0.26894
Random Effects		Variance	SD
Individual ID		0.2174	0.4662
Year		0.2873	0.536

While the hatch success of nest attempts at each breeding site showed suggestions of changes – increasing over the breeding season in the South but decreasing as the breeding season progressed in the Westfjords – neither sites' hatch success altered significantly over the duration of the breeding season. The hatch success of nests at both sites was also shown to be similar, with there being no indication of nest attempts at one of the breeding sites significantly outperforming the other (Figure 15).

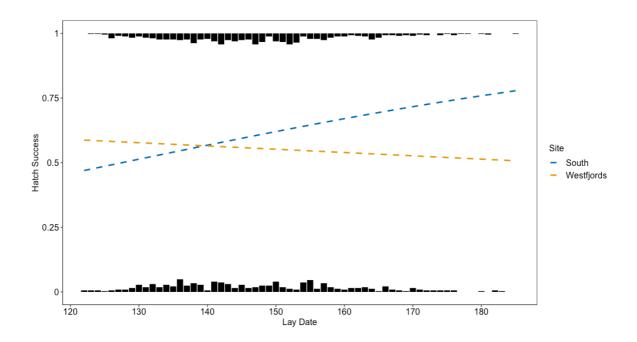


Figure 15: Hatch success of Ringed Plover nests in the South and Westfjords of Iceland based on lay date of the first egg in the clutch (1 = successfully hatched at least 1 egg, 0 = unsuccessful nesting attempt). Black bars indicate the density of nests at each lay date while dashed lines show the predicted hatch success of nests depending on the respective lay date at each site.

4.3 Timing of Breeding

The linear model showed that laying date varied significantly over the years of the study (p < 0.001). Laying date also varied significantly between locations (p < 0.01), and there was a significant effect of the interaction between location and year (p < 0.01). This would suggest that the date of the first nesting attempts of Ringed Plover is likely to be different depending on the year of breeding and the site at which breeding takes place. The model also suggests that the lay date of individuals first nesting attempts changes at different rates between the two sites across the years (Table 5).

Egg laying date was marginally later in the South of Iceland for the first 9 years of the study, but gradually advanced over the course of the 16 years of the study eventually surpassing the lay date of the Westfjords in 2014 with earlier lay dates being recorded in the South for the remainder of the study. Throughout the 16 years of the study the lay date remained fairly constant in the Westfjords (Figure 16).

Table 5: Linear model analysing the effect of breeding site and year of breeding on the lay date of the first nesting attempt for individuals. Significance levels are shown for each variable with significant variables in bold.

Coefficients	Estimate	SE	t	p
Intercept	1720.5712	441.269	3.899	< 0.001
SiteWestfjords	-1351.9736	522.5703	-2.587	< 0.01
Year	-0.7827	0.2191	-3.572	< 0.001
SiteWestfjords:Year	0.6713	0.2596	2.585	< 0.01

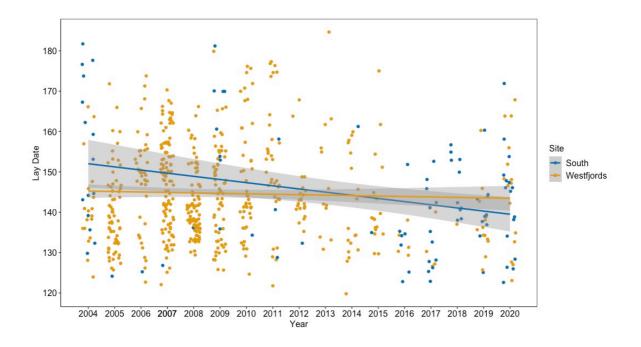


Figure 16: Lay dates of first nesting attempts in the South and Westfjords from 2004 – 2020. Blue and orange lines show the trend in lay date over the 16 years in the South and Westfjords respectively with shading indicating standard error.

5 Discussion

This thesis investigated some aspects of the annual cycle of Ringed Plover populations breeding in Iceland. By using data from two populations, one in the South and another in the Westfjords, it was possible to identify wintering locations and migration patterns (n = 22). Furthermore, the study compared the breeding success of the two populations and identified whether carry-over effects arose during spring migration. Despite being a widespread species in Iceland, relatively little is known about its migration which is necessary knowledge for its conservation.

5.1 Migration Patterns

This study found that there was no significant difference between the wintering latitudes of Ringed Plover populations that breed in the South and Westfjords of Iceland. Although there were some subtle visual trends that suggested individuals breeding in the Westfjords wintered in southern Iberia and West Africa while birds breeding in South Iceland seemed to spread across western Europe, Iberia and the coast of West Africa, this large overlap of wintering locations suggests that the leap-frog migration pattern is not present amongst the Icelandic populations of Ringed Plover.

The absence of leap-frog migration between the two studied populations, contrasts with the pattern found by Hedh *et al.*, 2022 (Figure 17), where leap-frog migration was identified between two breeding populations of Ringed Plover in Sweden. It is possible that the relatively small distance between the two breeding populations tracked in this study prevented the detection of that pattern. The average distance between the study sites in the South and Westfjords of Iceland breeding sites is considerably smaller (~ 250km) than that of the populations compared in Sweden (~ 1300km; Hedh *et al.*, 2022). Another possible contributing factor as to why the two studied breeding populations of Icelandic Ringed Plover do not exhibit leap-frog migration could be due to both populations being formed by members of the same sub-species in Iceland, but not in Sweden.

Despite this observation, the findings of this study do largely support suggestions made in other studies regarding the routes, patterns and wintering grounds used by Ringed Plovers.

Icelandic birds make up part of the *psammodromus* subspecies consisting of birds also breeding in Canada, Greenland and the Faeroe Islands (Delany *et al.*, 2009), and have been previously reported to spend the non-breeding portions of their annual cycle at sites further south than individuals of the *hiaticula* subspecies that breed in more temperate conditions such as those in the British Isles (Taylor, 1980). The results from this study suggest similar patterns in wintering locations to populations from Canada, Sweden and Norway which all identified non-breeding distribution across Western Europe, Iberia and West Africa (Léandri-Breton *et al.*, 2019; Hedh *et al.*, 2022; Lislevand *et al.*, 2017). This study also supports previous reports of the non-breeding distribution of Icelandic Ringed Plover, based on ring recoveries during the autumn and winter period (Pórisson *et al.*, 2012).

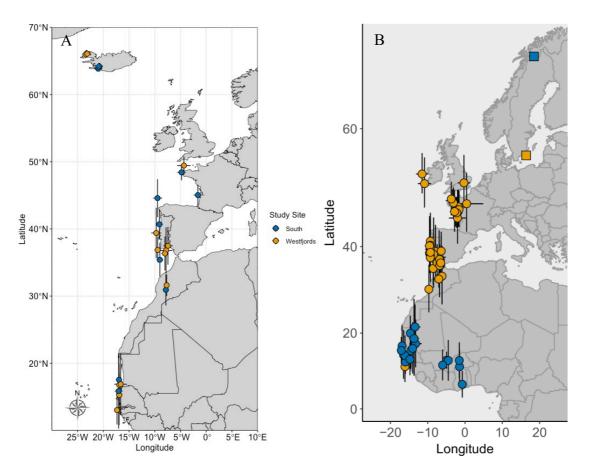


Figure 17: Comparison of winter location maps from two studies of Ringed Plover using geolocators. This study (A), and Hedh et al. 2022 (B).

Geolocators were only fitted to breeding adult birds for the collection of data for this study, and thus it is not possible to suggest that juvenile Ringed Plovers follow the same distribution pattern in their non-breeding periods. Due to sample size constraints, the individual sex of

the birds tracked was also not taken into account during analysis of winter locations, and therefore it could be possible that male and female Ringed Plover from the Icelandic breeding populations show different patterns of distribution as similar patterns have been identified in other wader species (Summers *et al.*, 2013).

5.2 Carry-Over Effects

5.2.1 Late Departures & Stopover Duration

While aiming to identify possible areas where carry-over effects may develop or be present in the spring migration of Icelandic breeding Ringed Plover, six possible relationships were tested for. However, only one significant relationship was found, between the departure date from wintering grounds and the total stopover duration. Late departing individuals tended to spend less time at stopovers than earlier ones (n = 7).

There is considerable evidence of late departing birds having shorter stopover durations, similar to those found in this study. In a study of the spring migrations of Eurasian Teal *Anas crecca*, individuals with earlier departure dates from wintering grounds in Italy were found to undertake longer stopovers than later departing individuals (Giunchi *et al.*, 2019). A similar pattern was observed in the Semipalmated Sandpiper *Calidris pusilla* – a shorebird breeding in the Arctic and sub-Arctic and wintering in South America. In this case short stopovers were performed by individuals migrating with higher fuel loads (Herbert *et al.*, 2022), with higher fuel loads often being a result of extending the period spent at the wintering ground and departing for migration later in the season (Arlt *et al.*, 2015, Dujins *et al.*, 2017). Northern Wheatears *Oenanthe oenanthe* have also been observed to have shorter migrations in later departing birds, which come as the result of shortened stopover periods (Arlt *et al.*, 2015). Despite this being observed, there is no knowledge as to whether stopovers were intentionally shortened in order to achieve the shorter total migration (Arlt *et al.*, 2015).

However, stopover duration can also be longer after a late spring departure (González *et al.*, 2006). One theory behind this was discussed by Paxton & Moore (2015), who state that often late departing spring migrants will utilise lower quality stopover sites, or even visit sites that have been well used by migrants earlier in the season. Therefore, later departing birds often

find depleted resources at stopover sites, leading to longer required periods to refuel for the next stage of the journey (Paxton & Moore, 2015).

One possible reason as to why late departures tend to result in shorter stopover duration in Ringed Plover is related to time constraints at the breeding sites. Individuals within species breeding at more northerly latitudes have a shorter window in which to arrive and breed (Carneiro *et al.*, 2021, Hedh *et al.*, 2022), and therefore must not arrive too late, to increase the chance of a successful breeding season (Morrison *et al.*, 2019). Time and energy considerations are among the most important driving factors for breeding shorebirds in the Arctic and sub-Arctic, due to this narrow opportunity for peak breeding conditions (Johnson & Herter 1990; Warnock & Bishop, 1998). It could then be possible that individuals minimise time at stopovers in order to ensure they do not arrive to breeding grounds too late.

5.2.2 Spring Migration, Arrival & Breeding Success

No other relationships were detected throughout the spring migration and into the breeding period, which was unexpected. When successive stages of a migrant's annual cycle are compared, it is often expected to see links between timings, where a delay in the start of one event commonly delays the onset of the following stage (Marra *et al.*, 2015; van Wijk *et al.*, 2017). In migrant species, the habitats used by individuals throughout the non-breeding period and during migration can impact the birds body condition and thus the timing of migration and breeding success of individuals (Newton, 2004).

There have been several studies – reviewed by McKinnon *et al.* (2013) - in which geolocators have been used to track land bird migrations and where winter departure dates were found to be the strongest predictor of spring arrival dates, with these links between the two stages also being reported by Briedis *et al.* (2018). Links between the departure date from wintering grounds, arrival date at breeding grounds, and breeding success have been drawn in a number of species; including American Redstarts *Setophaga ruticilla* (Tonra *et al.*, 2011), Barn Swallows *Hirundo rustica* (Saino *et al.*, 2004), House Martins *Delichon urbicum* (López-Calderón *et al.*, 2017) and Warbler species (Rockwell *et al.*, 2012; Paxton & Moore, 2015).

It is not just arrival times at breeding grounds that can be influenced by carry-over effects originating in the wintering locations. Individuals with longer migratory distances to travel have also been found to show lower breeding success as well as later arrivals (Buchan *et al.*,

2021). In Brant Geese *Branta bernicla*, the wintering site was shown to have an influence on the lay date in the next breeding season, with this also going on to have an effect on the clutch size (Schamber *et al.*, 2012). Similarly, carry-over effects originating in the previous breeding season have been shown to have an impact on future breeding attempts of migratory birds with long lifespans (Catry *et al.*, 2013). Carry-overs from the wintering period into spring migration and the subsequent breeding season have also been recorded in waders, in particular Eurasian Oystercatchers *Haematopus ostralegus* (Duriez *et al.*, 2012), Blacktailed Godwit *Limosa limosa* (Alves *et al.*, 2013), while also being suggested as a possibility in Ringed Plover (Þórisson *et al.*, 2012).

However, previous studies have also shown no correlations between winter departure and spring arrival dates in species such as Yellow Warblers *Setophaga petechia* and Magnolia Warblers *Setophaga magnolia* (Drake *et al.*, 2014; Boone *et al.*, 2010) as well as in Northern Wheatear (Arlt *et al.*, 2015) and the Great Reed Warbler *Acrocephalus arundinaceus* (Lemke *et al.*, 2013). This is present in wader species too, with Senner *et al.* (2014) reporting that carry-over effects were not present in Hudsonian Godwits *Limosa haemastica* during spring migration as there were no effects of the non-breeding habitat or late departure from wintering ground influencing arrival to breeding grounds, timing of breeding, breeding success of even survival.

It is possible that the long wintering period may prevent carry-over effects from building up during the annual cycle. This has previously been reported in studies by van Wijk *et al.* (2017) and Briedis *et al.* (2018), with both studies reporting similar findings of carry-over effects being developed from the breeding period into autumn migration but no evidence of further effects being present beyond the wintering period. It has therefore been proposed that the wintering period allows for flexibility in migration schedules, acting as a buffer or reset period during which timings may not be so constrained and birds can depart for spring migration without any lasting effects from the previous year (Briedis *et al.*, 2018). With this potential buffer period also having been suggested in waders (Senner *et al.*, 2014), it is possible that the same could be expected of Ringed Plover. As the autumn migration was not investigated, it is currently unknown whether there were carry-over effects present during the post-breeding migration that were then eliminated by the wintering period.

Long distance migrants are often subjected to high selection pressures, and this too can produce an apparent lack of carry-over effects (Conklin *et al.*, 2017). Species that breed at high latitudes undertake long distance flights from wintering grounds to reach their breeding sites. Long distance migrant waders such as Eurasian Whimbrels *Numenius phaeopus* and Hudsonian Godwits have previously been found to not accumulate carry-over effects from the wintering site (Carneiro *et al.*, 2021; Senner *et al.*, 2014), with it being suggested that carry-overs may not be able to persist in a life cycle with such extreme selection pressures (Senner *et al.*, 2014). With Icelandic Ringed Plover also undertaking long distance migrations between wintering and breeding grounds (as seen in this study; Þórisson *et al.*, 2012) it is likely that this species also experiences high selection pressures at every stage of migration and could, therefore, be an explanation for the lack of carry-over effects following the wintering period.

5.3 Timing of Breeding

Although the laying date of first nesting attempts varied among the years, it was shown to advance over the study period for the South, but remained stable for the Westfjords.

Previous studies have suggested that laying dates are found to be later at more northern than at breeding grounds at lower latitudes (Pienkowski, 1984). However, the results from the first 10 years of this study (2004 – 2014) suggest that this may not always be the case with the breeding population of the Westfjords (the most northerly study site) having earlier laying dates of first nesting attempts. Studies comparing differences in lay dates between breeding populations often take place over a larger latitudinal range for example comparing populations in Greenland and the British Isles (Pienkowski, 1984). This has made comparison difficult and supporting evidence hard to come by, however it is feasible that some of the factors contributing to differences in lay date of first nesting attempts over large latitudinal ranges are evident at a smaller scale in the two studied breeding populations in Iceland.

In breeding grounds at high latitudes (which both studied breeding sites are), the lay date of first nesting attempts has been found to be heavily influenced by snow cover and how late the snow melt occurs (Pienkowski, 1984). A possible explanation for the difference in lay date of first nesting attempts between the two breeding sites studied in this thesis is that snow melt occurred later in the year at one of the sites. While Iceland is a relatively small country,

the landmass covers over 3 degrees of latitude and therefore subtle climate differences can occur, with different regions of Iceland being recorded to experience different monthly average temperatures and local amplifications of conditions (Einarsson, 1984; Ólafsson *et al.*, 2007). Differences in conditions at a local and regional level will also be likely to influence vegetation growth and peaks in food abundance (Meltofte *et al.*, 2021). Bird species, particularly migratory species that primarily prey on insects, attempt to time their breeding and laying of eggs to coincide the hatching of chicks with peaks in prey availability and abundance (Meltofte *et al.*, 2021; Shave *et al.*, 2019). These peaks coincide with temperature changes and vegetation growth and so are likely to occur at different times between the South and Westfjords of Iceland, potentially influencing the laying date of first nesting attempts.

The variance in seasonal temperatures and onset of spring occurs at different rates annually and across different latitudes creating climatic constraints (Briedis et al., 2016). Therefore, it is likely that the differences in lay date between sites, variation in lay date between years and different rates of advancement of lay date are due to these changes and the effects on surrounding habitats and ecosystems they have (i.e., date of snow melt, vegetation growth and peaks in prey abundance). However, a possible important factor to consider in the different rates of advance in lay date between the South and Westfjords breeding sites is that timing of breeding may become constrained by arrival date from spring migrations (Shave et al., 2019). Spring arrival of migrants and subsequently laying dates of first nesting attempts have been advancing across the Northern Hemisphere (Rubolini et al., 2007) and as Iceland has experienced unexpectedly warm years in the 21st Century with increasing temperatures expected to continue (Boyd & Petersen, 2006) so are advancements in lay dates of nesting attempts. However, the advancement of arrival dates in Icelandic waders may be driven by new recruits to the population, with individuals showing high levels of consistency in their arrival dates (Gill et al., 2014). This can lead to constraints on laying dates of first nesting attempts if spring arrival is not advancing.

It is also important to note that while the factors offered as suggestions for the results observed in this study have been observed to influence lay dates in previous studies they were beyond the scope of testing in this thesis and are therefore speculatory. Nevertheless, comparison of lay dates to average temperature and date of snow melt at each site would make interesting future studies. Another factor which could play a part in the difference in

lay date between sites but wasn't tested for in this study is disturbance. Disturbance has been observed to influence the nesting habits and success of Ringed Plover (Tratalos et al., 2021) and could possibly be a factor that could influence lay date if occurring at different levels between the sites in Iceland.

5.4 Implications for Future Management & Conservation

In order for management techniques to be effective it is important to understand the challenges that are being faced. While management can aim to protect and conserve wildlife, there are aspects that must be considered other than the species itself. To effectively implement management strategies the needs of every stakeholder must be evaluated and taken into consideration; even if the goal is to protect a vulnerable species. This includes having an understanding of the importance of the site to each stakeholder. Given that we are living in a period of time where the majority of the Earth has been subject to human influence or usage in some way (Hooke *et al.*, 2013), the challenge of management for both humans and wildlife becomes an increasingly prevalent issue.

The increase of anthropogenic impacts is especially felt in coastal habitats, and on waders in particular due to habitat loss and the increased intensification of human activity (Melville, 1997; Hamza, 2020). Wading birds depend upon coastal habitats throughout their life and annual cycles, for breeding, as stopovers during migration and during their wintering period. During these periods not only do they feed, refuel and prepare for the next stage of their annual cycle but they also play a role at a greater scale becoming part of the ecosystem and food chain of these coastal areas (Hamza, 2020). It has been documented that interference and disturbance can impact breeding success of waders (Tratalos et al., 2021), and research has shown that habitat quality as well as success and survival rates can carry-over into subsequent stages of individuals annual cycles and impact them further (O'Connor et al. 2014; Senner et al. 2015). Therefore, an increased importance is placed on knowing locations that are utilised by individual waders at every stage of the annual cycle, to ensure where possible that management strategies are aligned in order to be as effective as possible. Understanding the relationship and impact that shared land use with humans can have on wading birds' populations and success is crucial for successful and effective management (Hamza, 2020).

This becomes of elevated importance due to the results of this study not necessarily matching those of studies of Ringed Plover undertaken and completed in other locations. The continuation of studying the Icelandic population of Ringed Plover would develop upon the findings of this study which has begun to reveal information on the migration and annual cycle of Icelandic individuals; allowing for more detailed and thorough understanding of the behaviour of these birds outside of Iceland. By continuing this form of research over longer periods or larger population samples, more information would be available on which informed management and conservation decisions could be made – not just in Iceland but across the flyway utilised by Icelandic Ringed Plover.

Overall, important steps towards effective management for wading birds can be taken as knowledge on important areas for wader species is increased. With this knowledge it becomes possible to connect countries through these species and provides the opportunity to align management strategies across countries and continents in the case of some species. With migratory species depending on multiple sites in multiple countries the emphasis for effective management in one particular location is somewhat reduced, as this could possibly be completely undone at subsequent stages of the life cycle if there is poor management in place across other areas. With Iceland hosting important breeding populations of a number of wader species that have been subject to land use change and human influence within well used habitat (Gunnarsson *et al.*, 2006), the opportunity is provided to continue with monitoring breeding success, population levels and trends as well as possible conflicts over habitats or land use changes; information which can be used to establish more effective management throughout the flyway of threatened wader species.

6 Conclusion

This thesis aimed to explore some aspects of the annual cycle of Ringed Plover breeding in Iceland by analysing key locations and timings from the migrations of individuals tracked with geolocators and those sighted during the breeding season in Iceland. In order to do so, three research aims were outlined looking to identify whether leap-frog migration was present; whether carry-over effects occurred during spring migration and potentially affected subsequent breeding success; and whether the timing of egg laying date varied between two breeding populations of Ringed Plover in Iceland.

Through analysing geolocator data and identifying wintering locations of tracked individuals it was possible to develop upon knowledge from ring recoveries to further enhance our understanding of the areas utilised by Icelandic birds during the winter. In doing so it became clear that while Ringed Plover have been observed to display a leap-frog migration pattern in other areas of their range this was not present within the Icelandic breeding population.

Minimal carry-over effects were detected throughout the spring migration of Icelandic Ringed Plovers, with only the total duration of time spent at stopover sites found to be influenced by a previous stage of the annual cycle (i.e., winter departure date); breeding success was found to not be influenced by previous stages of the annual cycle, namely spring arrival date and egg laying date, which is not in accordance with previous evidence (Morrison *et al.*, 2019; Þórisson *et al.*, 2013). While the apparent lack of carry-over effects was not entirely expected, it is not an unfamiliar sight in long distance migrants.

Timing of egg laying date was fairly constant at the more northerly breeding site in the Westfjords, while at the breeding site in the South of Iceland lay date had advanced over the course of the 16 years of the study to be earlier than that in the Westfjords (2015 -2020). Initiation of nesting often varies depending on the latitude of the breeding grounds, with this result being in keeping with this. The different latitudes of the sites bring with them different conditions and levels of abundance of prey which individuals us to time their breeding to meet the optimal conditions to try and improve breeding success.

While the results of this study provide an insight into the annual cycle of Icelandic breeding Ringed Plover, the nature of the data used means that further research is required to fully understand the migratory and breeding behaviour of the species. The limited number of tracked individuals leaves the possibility of one individual or a small number of individuals creating a bias within the results. Similarly with the breeding data, while efforts were made in all 16 years from 2004 - 2020 to locate nests and track their progress, some years had more limited datasets than others. As a result of this it is possible that the rate of advance of lay dates is not necessarily representative of the true change, as there were some years where only a small number of nests located and followed throughout the season.

Nevertheless, previous knowledge of Ringed Plover breeding in Iceland was limited and therefore the findings of this thesis can help to piece together a greater understanding of the movements, locations utilised and timings of migration for Icelandic breeding birds. With an increased understanding and knowledge of the species and their migrations, it will become possible to employ conservation and management strategies more effectively in areas that they are required to make a difference. With the landscape of coastal habitats constantly being altered by anthropogenic influences – both directly and indirectly – it is becoming increasingly important to increase knowledge of where migrant species are visiting, however briefly. Doing so will allow for increased protection measures and give species that are declining the best possible chance of survival.

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Appendix A: Ethics Clearance



Research ethics training and clearance

University Centre of the Westfjords Suðurgata 12 400 Ísafjörður, Iceland +354 450 3040 info@uw.is

This letter certifies that James Fletcher has completed the following modules of:

- (X) Basic ethics in research
- (X) Human subjects research
- (X) Animal subjects research

Furthermore, the Masters Program Committee has determined that the proposed masters research entitled Variation of migration patterns and breeding output/performance of the Common Ringed Plover breeding in South and NW Iceland meets the ethics and research integrity standards of the University Centre of the Westfjords. Throughout the course of his or her research, the student has the continued responsibility to adhere to basic ethical principles for the responsible conduct of research and discipline specific professional standards.

University Centre of the Westfjords ethics training certification and research ethics clearance is valid for one year past the date of issue unless otherwise noted.

Effective Date: 18 June 2021 Expiration Date: 18 June 2022

Prior to making substantive changes to the scope of research, research tools, or methods, the student is required to contact the Masters Program Committee to determine whether or not additional review is required.

Data collection for this project was carried out by researchers at Rannsóknasetur Suðurlands/South Iceland Research Centre. This includes all ringing/marking of birds that was undertaken, as well as the deployment and retrieval of all geolocators.

