The stopover behaviour of Common Snipe *Gallinago gallinago* migrating through North Ronaldsay, Orkney

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Abstract

Investigating the mechanisms governing migratory strategies in birds is key to understanding how populations will respond to climate change. Populations of Common Snipe *Gallinago gallinago* migrate from Scandinavia, Russia, and Iceland to wintering locations in the United Kingdom, Ireland, and southern Europe. The stopover behaviour of snipe following more northerly migration routes, which involve sea crossings, is relatively unknown, despite these individuals clearly experiencing different conditions compared to birds following continental routes.

Using past migrant bird census data collected by North Ronaldsay Bird Observatory, I modelled the effects of weather and time of year on the number of snipe present on North Ronaldsay. I found that snipe migrate through North Ronaldsay in considerably greater intensities during the autumn migration period, although high counts may occasionally occur during the spring. Snipe counts increased during periods of increasing precipitation, higher temperatures, and reduced wind speeds, although wind direction had little noticeable effect on snipe numbers.

I carried out a radio telemetry study to investigate factors affecting snipe stopover durations and spatial behaviour on North Ronaldsay. Whilst the premature detachment of tags and small sample size reduced the power of statistical tests carried out, I found that snipe exhibited large variation in their stopover durations, with some birds staying for extended residency periods. Snipe exhibited a distinct routine in their spatial use of the island, often using areas of increased cover during the day before moving to more exposed habitats at night.

I provide further indications of high flexibility of migration strategies in inland wetland birds and suggest that small island stopover sites may provide additional functions for migratory birds beyond resting and refuelling. I demonstrate how future studies can make use of long-term census data collected by bird observatories in the study of stopover behaviour, which is currently an underutilised resource.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged as references.

1.0 Introduction

1.1 Overview

Migration is observed in multiple animal taxa and allows individuals to exploit temporary variations in resources at different locations, therefore increasing their fitness (Alerstam et al., 2003; Dingle and Drake, 2007; Winger et al., 2018). Due to the large distances covered by many birds during migration, most bird species are unable to complete their migration in a single flight as they lack sufficient energy reserves (Klaassen, 1996). Consequently, birds often break their migrations into multiple flights, interspersed by stopover periods. Previous research has shown that stopover periods contribute to a larger proportion of the total energy and time expenditure during a bird's migration than flight periods themselves (Hedenström and Alerstam, 1997). Therefore, ensuring these periods are used in the most optimal way is essential for maximising a bird's fitness during migration.

Here we present a review of existing literature on the topic of stopover ecology and bird migration strategies. We will first cover the function of stopover periods and factors affecting bird migration strategies, before exploring how these concepts apply to inland wetland species and the use of small island stopover sites by birds. We then explore how movement activity and habitat use may vary during stopover and outline the focus of the subsequent data chapters of this thesis.

1.2 The function of stopover periods

Optimal migration theory investigates the relative importance of various selective pressures on migrating birds, including time, energy and predation risk (Alerstam and Lindström, 1990). Stopover behaviour is one of the key measures used by optimal migration models, since this has a large bearing on the overall speed and timing of migration and subsequent fitness effects and may reveal which factors a bird is likely to be optimising during its migration (Alerstam, 2011). Birds experience a range of costs and benefits both during and as a consequence of stopover periods and understanding the tradeoffs between these allows improved knowledge of birds' behaviour during migration (Schmaljohann et al., 2022).

The principal function of stopover periods is widely considered to be replenishing energy stores lost during previous flights (Alerstam, 2011). Most bird species cannot feed during migratory flights and rely entirely on stored energy during these periods (McWilliams et al., 2004). Subcutaneous fat stores form the primary source of energy for birds during migratory flights, along with smaller amounts of protein (Jenni and Jenni-Eiermann, 1998). These energy stores are accumulated via increases in food consumption and significant changes to birds' physiology during pre-flight periods (Bairlein, 2002; McWilliams et al., 2004), although the endogenous mechanisms allowing such rapid increases in lipid storage in birds during these periods are still not fully understood (Araújo et al., 2019). Before the onset of long migratory flights, deposited fat stores can make up a significant proportion of a bird's total body mass; Garden Warblers *Sylvia borin* have been recorded increasing their body mass by between 50-100% through accumulation of fuel stores at staging sites before crossing the Sahara during spring migration (Ottosson et al., 2005). In contrast, birds often arrive at stopover sites in a fat-depleted state with a very low body mass (Moore and Kerlinger, 1987). Before crossing regions containing no sites suitable for refuelling, birds must ensure they accumulate sufficient fat stores to produce a flight range capable of reaching their next destination (Hedenström and Alerstam, 1997). Consequently, arrival body condition and accumulated fat stores are key factors in the departure decisions of migrants at stopover sites and have a significant effect on stopover duration (Schaub et al., 2008; Anderson et al., 2019; Schmaljohann and Klinner, 2020).

Stopover periods are also used by birds for other functions, although these have received less research attention. Birds which make long, continuous flights across ecological barriers may be required to spend time recovering from the physiological effects of these flights (Linscott and Senner, 2021; Schmaljohann et al., 2022). Whilst it is well established that many birds spend periods of time "resting" during stopover through periods of inactivity (Aborn and Moore, 2004), the underlying physiological processes occurring during their recovery are less well known (Schmaljohann et al., 2022). Recent research has indicated that during stopover birds recover from oxidative damage to lipids that occurs during migratory endurance flights (Skrip et al., 2015; Eikenaar et al., 2020a). Birds' constitutive immune function may also be negatively affected by migratory flights (Owen and Moore, 2008) and improvements in this during stopover have been observed in several species, including the Northern Wheatear *Oenanthe oenanthe* and Red Knots *Calidris canutus* (Buehler et al., 2010; Eikenaar et al., 2020b).

Neurological adaptations such as temporary changes to circadian rhythms may reduce the need for sleep for many migratory birds during migration (Gwinner, 1996) and many birds can perform unihemispheric sleeps during flight (Rattenborg, 2017). However, catching up on lost sleep during migration may still be an important factor for some individuals during stopover due to the detrimental effects of accumulated sleep deficits (Rattenborg, 2006; Linscott and Senner, 2021). There are numerous documented and anecdotal reports of migrating birds sleeping for extended periods upon arrival at stopover sites; during a food choice experiment on migrating passerines on the island of Ventonene in the Thyrennian

Sea, several *Sylvia* warblers were observed falling asleep in the cages used during the experiment (Schwilch et al., 2002). Daytime sleeping has also been recorded in free-flying birds during migration stopover, including Hooded Warblers *Setophaga citrina* (Németh, 2009) and Red-backed Shrikes *Lanius collurio* (Bäckman et al., 2017). Further research into the physiological benefits of stopover periods is required for a more comprehensive understanding of arrival and departure decisions.

Stopover periods may also be used to avoid adverse weather or to time migratory flights with more favourable conditions (Linscott and Senner, 2021; Schmaljohann et al., 2022). This may be of particular importance to soaring birds which require thermal uplift for flight; migrating Black Kites *Milvus migrans* crossing the straits of Gibraltar are required to fly over open water where thermal uplift is much reduced and consequently avoid crossing the sea in strong westerly crosswinds (Mellone, 2020). Certain sites that are not usually part of a bird's migration route may be used as "emergency stopover sites" during periods of severe weather (Shamoun-Baranes et al., 2010). In 2011, headwinds and heavy rainfall coincided with exceptional numbers of Eurasian Spoonbills *Platalea leucorodia* stopping over at three wetlands in northern Spain, despite these sites not regularly hosting large numbers of migrating spoonbills (Overdijk and Navedo, 2012). Passerine species have also been shown to delay their migration as a consequence of weather events; in 2015, Semi-collared Flycatchers *Ficedula semitorquata* fitted with geolocaters delayed continuing their spring migration in response to unusually cold temperatures experienced in the Mediterranean (Briedis et al., 2017). Stopover duration is therefore often dependent on weather conditions experienced before and during stopover periods (Dossman et al., 2016).

Whilst serving essential functions for completing a bird's migration, stopover periods may induce significant costs for birds. Since birds have limited time to gather social information on predators during stopover, they may be at an increased risk of predation during these periods at certain stopover sites (Németh and Moore, 2007). Birds may experience varying predation risk during migration stopover and due to temporal and spatial variation in predator distributions, stopping at certain sites may result in greater predation risk than others. Concentrations of migrating raptors, such as the Sharp-shinned Hawk *Accipter striatus*, present at stopover sites vary with weather conditions, resulting in temporary increases in predation risk for smaller passerine birds (Cimprich et al., 2005). Predation risk may also vary depending on the body condition of individuals; birds arriving in poorer body condition may show an increased risk of predation due to reduced predator vigilance or increased conspicuousness because of their increased need to forage (Dierschke, 2003). Predation risk therefore introduces tradeoffs during stopover periods that affect stopover duration, such as reduced foraging rates due to the need for increased predator vigilance (Ydenberg et al., 2002; Cimprich et al., 2005).

Mistiming stopover periods can result in early or late arrival at breeding or wintering grounds. Whilst early arrival at breeding sites may allow birds to take advantage of reduced competition for breeding territories and mates (Møller, 1994), it may also come with significant fitness costs. During earlier months, the climate may still be unsuitable both for birds to withstand weather conditions themselves and for their food resources to be present in sufficient quantities (Brown and Brown, 2000; Newton, 2007; Visser et al., 2012). Many migratory passerines rely on insect prey for food and mistiming arrival with insect emergence may be fatal for early arriving individuals (Both et al., 2006). In contrast, late arrival on breeding grounds may lead to missing out on mating opportunities due to the increased competition for breeding resources (Kokko, 1999). Additionally, mistiming departure from one stopover site may lead to experiencing costs at subsequent sites, such as missing out on temporary food resources. For instance, late arriving Red Knots stopping over at Delaware Bay show decreased foraging rates and survival due to decreases in abundance of their food source of Horseshoe Crab *Limulus polyphemus* eggs (Baker et al., 2004; González et al., 2006).

To conclude, stopover duration varies between species and individuals due to the tradeoff between costs and benefits experienced during and as a consequence of stopover periods. Processes occurring during stopover periods have a large impact on the overall success of migration and therefore fitness of migratory birds, so are essential considerations when assessing rates of population change in these species. Climate change and human activities are already driving significant declines in many migratory bird species, which are likely to continue in the future (Zurell et al., 2018). Recent technological advances, such as the advent of more advanced and lightweight tracking devices, have allowed more precise determination of stopover duration and the discovery of new information about birds' behaviour during stopover periods (McKinnon and Love, 2018). Consequently, continued research into the selective pressures experienced during stopover and how birds respond to these are key to both advancing understanding of optimal migration theory and applying knowledge of this to conservation actions.

1.3 Determinants of migration strategy

According to optimal migration theory, the selective pressures birds experience during migration lead to different migration strategies developing depending on the criteria individuals are optimising (Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997;

Alerstam, 2011). These strategies govern the various decisions individuals make during migration, including how often to stopover and how long to spend at stopover sites, which affect the overall speed or energy expenditure of migration. Previous research (Hedenström and Alerstam, 1997) has consequently categorised these into time-minimising strategies and energy-minimising strategies (Table 1). Birds following a time-minimising strategy will aim to complete migration in as little time as possible. This typically involves accumulating large amounts of fat during stopover, which allows birds to make longer flights between stopover sites (Alerstam, 2001). In contrast, species aiming to minimise total energy expenditure during migration typically migrate at a slower pace, making longer and more frequent stopovers and accumulating fat at a slower rate during these periods (Hedenström and Alerstam, 1997). Predation risk also affects birds' decisions during stopover and birds will often adopt strategies to minimise mortality risk, which may take priority over time or energy minimisation during certain stages of their migration (Fransson and Weber, 1997; Lank et al., 2003; Hope et al., 2014)

Table 1. *Typical characteristics of time-minimising, energy-minimising, and mortality-minimising migration strategies.*

Migration strategy	*Key variable being optimised*	*Duration of stopover periods*	*Rate of fat accumulation during stopover*	*Frequency of stopover periods*	*Total distance travelled during migration*	*Intensity of competition at final migration destination*	*Season when strategy is more commonly adopted*
Time-minimising strategy	Overall migration speed	Short	Fast	Less frequent	Long distance	More intense	Pre-breeding (spring) migration
Energy-minimising strategy	Overall energy expenditure	Long	Slow	More frequent	Short distance	Less intense	Post-breeding (autumn) migration
Mortality-minimising strategy	Mortality risk (typically predation risk is minimised)	Variable	Variable	Variable	Variable	Less intense	Post-breeding (autumn) migration

A significant determinant of migration strategy is the level of competition species experience once they arrive at their migration destinations. Species experiencing more intense competition at breeding or non-breeding grounds are likely to adopt a time-minimising strategy to gain early access to limited resources at these locations (Alerstam, 2011). For this reason, migration strategy may also vary depending on the time of year; most species are time-constrained during spring migration, due to the need to establish breeding territories and rear young during limited periods of suitable environmental conditions (McKinnon et al., 2012). This makes early arrival advantageous since competition for breeding territories and mates will be less intense during this time. However, this time constraint is removed during the non-breeding season, meaning it may be more beneficial to adopt strategies that conserve energy or reduce the risk of mortality during autumn migration (Nilsson et al., 2014). Consequently, many species adopt a time-minimising strategy during the spring and an energy-minimising strategy during the autumn migration (McNamara et al., 1998; Karlsson et al., 2012; Nilsson et al., 2013). This has been observed in passerines (Karlsson et al., 2012; Nilsson et al., 2014), as well as non-passerines, including shorebirds (Zhao et al., 2017) and cranes (Mi et al., 2022).

Species migrating over shorter distances are likely to be less time-constrained during their migration. Especially during the post-breeding migration, short-distance migrants are often able to adopt an energy-minimising strategy, since they are not required to migrate at such fast speeds to reach their non-breeding grounds in time to carry out processes such as moult (La Sorte et al., 2013; Nilsson et al., 2014). A recent study on three passerine migrants stopping over at the island of Helgoland, Germany, found that the Northern Wheatear *Oenanthe oenanthe*, a long-distance migrant, made shorter stopovers in comparison to the shorter distance migrants European Robin *Erithacus rubecula* and Common Blackbird *Turdus merula* (Packmor et al., 2020). The shorter distance migrants' departure timings were also more dependent on weather conditions; due to being less time constrained, these birds can be more selective in the conditions they choose to depart in. In contrast, long-distance migrants may frequently migrate in nonoptimal flight conditions, such as strong crosswinds, since delaying migration may not be compatible with the time constraints they face (Nilsson et al., 2014; Packmor et al., 2020).

Both interspecific and intraspecific variation in morphology have been documented as additional factors affecting migration strategy. A recent study on shorebirds that migrate using the East Asian-Australasian Flyway found that the seasonal differences in migration speed often observed between pre-breeding and post-breeding migrations were less pronounced in species with larger body sizes (Zhao et al., 2017). The authors hypothesised that this was due to larger species, such as the Far Eastern Curlew *Numenius* *madagascariensis,* being more restricted by time-constraints. This is possibly due to the lower fuel deposition rates and longer moult times observed in larger species; moult is often completed on the non-breeding grounds to avoid coinciding with migration, since both have a high energetic cost (Remisiewicz, 2011). Certain morphological characteristics evolve as a consequence of a species' migration strategy; for instance, time-minimising species often evolve longer, more pointed wings in order to increase their flight speed (Lockwood et al., 1998; Minias et al., 2015). However, variation within these characteristics themselves may also influence strategies birds adopt during migration. This has been demonstrated in Common Snipe *Gallinago gallinago* migrating through central Poland (Minias et al., 2013). Birds with more pointed wing shapes showed greater rates of fat deposition and stayed for shorter durations at stopover sites than birds with more rounded wings. Birds with more rounded wing shapes were hypothesised to be at lower risk of predation due to faster takeoff times (Swaddle and Lockwood, 2003; Minias et al., 2013), meaning they could remain at stopover sites for longer periods.

Intraspecific variation in migration strategy may be observed between different sexes. This is commonly seen in differences in spring migration timing between males and females, with males often arriving earlier to establish breeding territories (Morbey and Ydenberg, 2001). This may be reflected in aspects of their stopover behaviour; Dierschke et al. (2005) found a positive relationship between departure fuel loads and fuel deposition rate in male Northern Wheatears, whereas this relationship was absent in females. This indicates that males were experiencing stronger selection for time-minimising migration strategies (Hedenstrom and Alerstam, 1997; Dierschke et al., 2005). Differential migration, a term used to describe differences in migration strategy, such as route, timing, or stopover behaviour, between distinct groups of a population (Briedis and Bauer, 2018), may be more likely to occur in species exhibiting greater sexual dimorphism (Rubolini et al., 2004). The Great Bustard *Otis tarda* shows the greatest level of sexual size dimorphism found in birds (Alonso et al., 2009). Since the larger males are more sensitive to high temperatures on breeding grounds and do not take part in parental care, a larger proportion of males are migratory and leave breeding grounds earlier than migratory females (Alonso et al., 2009; Palacín et al., 2009). Male and female birds may also spend the non-breeding season in different locations. This has been documented in a number of species, including Northern Flickers *Colaptes auratus* (Gow and Wiebe, 2014), where females migrate further than males as a consequence of sexual dimorphism in parental care. Segregation at non-breeding locations is likely to cause significant differences in migration strategy due to differences in migratory distance or competition experienced at non-breeding grounds (Catry et al., 2012; Briedis and Bauer, 2018).

Similarly, differential migration has been observed among different age classes of many bird groups, including birds of prey (Bai and Schmidt, 2012), shorebirds (Handel and Gill, 2010) and passerines (Spina et al., 1994). Juvenile birds typically lack the experience of older birds so may follow more direct migration routes driven by their endogenous navigation mechanisms (Gwinner, 1996), whilst adults often follow more optimal routes due to social learning and cues learned from previous migrations (Hake et al., 2003). This has been observed in European Honey Buzzards *Pernis aviporus* during their autumn migration (Hake et al., 2003); whilst juveniles flew straight across the central Mediterranean Sea, adult birds took a less direct route, crossing the sea at the strait of Gibraltar. Despite this, adult birds completed their migration faster than juveniles, possibly due to the weather conditions encountered en route (Alerstam, 2001; Hake et al., 2003). Differences in migration strategy between age classes are often reflected in stopover behaviour. Earlier migrating adult Western Sandpipiers *Calidris mauri* show decreased predator vigilance during stopover to increase refuelling rate and decrease stopover time, enabling them to depart before the arrival of migrating Peregrine Falcons *Falco peregrinus* (Lank et al., 2003; Hope et al., 2014). In contrast, juveniles, which migrate later since they do not have to complete a non-breeding moult of flight feathers (O’Hara et al., 2002), show longer stopover times as a consequence of increased predator vigilance due to the higher number of Peregrines present during this time (Lank et al., 2003; Hope et al., 2014). Consequently, the refuelling rates and stopover durations shown by birds following mortality-minimising strategies are variable depending on the nature of the mortality risk.

Variation in environmental conditions across space and time may influence a bird’s migration strategy. Demoiselle Cranes *Grus virgo* follow a loop migration route, crossing the higher plateaus of the Himalayas during their post-breeding migration to the Indian subcontinent but avoiding these by taking a more westerly route during the spring (Mi et al., 2022). The spring route covers a larger total distance but due to reduced snow and ice cover, offers sites containing more plentiful food resources, allowing the increased refuelling rates required for time-selected migration (Hedenström and Alerstam, 1997). Favourable weather conditions encountered along this route during spring allow birds to arrive at their breeding grounds at the required time (Mi et al., 2022). During their post-breeding migration, the cranes follow a more direct route across the Qinghai-Tibet plateau in order to minimise total energy cost due to decreased migration distance.

Whilst many bird species exhibit a high repeatability of migratory behaviour between years (Franklin et al., 2022; Kürten et al., 2022), some species may exhibit plasticity or flexibility in their migration strategies enabling them to vary their behaviour depending on environmental conditions (Piersma and Drent, 2003; Senner et al., 2020). Developmental plasticity may occur in some species during early life stages, with environmental conditions encountered during this time leading to individual changes in migratory behaviour which become fixed in later life stages (Gill et al., 2014; Senner et al., 2020). For instance, a change in staging site use by juvenile continental Black-tailed Godwits *Limosa limosa limosa* from Spain to Portugal has occurred in recent years, whereas adults still use traditional sites (Verhoeven et al., 2018). Since a parent's migration route was shown not to be inherited by its offspring, it is likely that changes in migratory behaviour by godwits occurred as a consequence of behaviour learned during early life stages (Verhoeven et al., 2018; Verhoeven et al., 2022).

Phenotypic flexibility in migratory strategy involves reversible changes in migratory behaviour and may be observed in adult individuals in some species as responses to variable environmental conditions (Piersma and Drent, 2003; Senner et al., 2020). These can include food availability, competition and both short and long-term weather events. Experimental manipulation of predator risk has shown that Blackcaps are able to increase their refuelling rates and depart from stopover sites more quickly when there is an increased risk of predation (Fransson and Weber, 1997). Plastic responses to short-term weather events are frequently recorded in migrating birds and can include increased stopover duration, increased focus on refuelling and reverse migratory flights to avoid extreme weather (Senner et al., 2015). Recent studies have shown that the advancements of spring arrival times in many migratory birds may be partly due to plastic behavioural responses (Pulido, 2007; Haest et al., 2018). However, despite recent knowledge advances, the relative importance of plasticity, when compared with evolutionary processes, in changes to migratory behaviour is difficult to determine and requires further research (Gienapp et al., 2007; Buskirk et al., 2012; Charmantier and Gienapp, 2014).

Such plasticity in migration strategy may increase a species' resilience to unpredictable changes along their migration route (Gilroy et al., 2016). Species that show little flexibility in stopover site choice are likely to show high site fidelity and reliance on a low number of stopover sites during migration. This may increase their vulnerability to future climatic or anthropogenic changes at these sites. Red-necked Stints *Calidris ruficollis* and Curlew Sandpipers *Calidris ferruginea* migrate between very similar breeding and non-breeding sites via the East Asian-Australasian Flyway, although whilst Curlew Sandpipers show high reliance on a few stopover sites, concentrated around the Yellow Sea region, Red-necked Stints use a more varied selection of sites (Lisovski et al., 2021). Since the Yellow Sea region has experienced rapid environmental change due to anthropogenic development, Curlew Sandpipers are experiencing a fast population decline in this region, whereas the Red-necked Stint population is stable (Studds et al., 2017; Lisovski et al., 2021). Plasticity may also increase resilience to climate change; phenotypic flexibility in spring arrival timing may allow species to time their arrivals with temporal changes in prey availability (Gienapp et al., 2007; Pulido, 2007; Charmantier and Gienapp, 2014). Therefore, understanding the degree of plasticity and flexibility in species' migration strategies and stopover behaviour is key to predicting future population changes and informing conservation actions (Gilroy et al., 2014; Senner et al., 2020).

To conclude, migration strategies govern the decisions birds make during migration, including stopover behaviour and the timing and speed of migratory flights. Competition birds experience during and after their migration has a large impact on migration strategy, which may also vary depending on the time of year, age and sex. Environmental conditions may also be important factors and some birds may exhibit plasticity or flexibility in their migration strategy in response to these. Predicting future changes to migratory bird populations caused by climate change requires further understanding of the factors affecting migration strategies and flexibility within these.

1.4 Flexibility of migratory behaviour in inland wetland species

Migration strategies may be affected by the distribution of suitable habitat across a species' migration route. Inland wetland habitats naturally occur in a patchy distribution as a result of the distribution and movement of water (Hu et al., 2017; Reis et al., 2017), which are determined by climatic, geological and topographical factors, including rainfall, relief, and soil permeability (Merot et al., 2003). Additionally, wetland habitat distribution may show temporal variation due to fluctuations in climate, as well as seasonal changes and more short-term weather events. During periods of drought, wetlands may decrease in size due to the lowering water table, whereas during periods of cold weather, surface water may temporarily freeze over, making these areas of habitat unsuitable for wetland birds (Gehrold et al., 2014). Additionally, whilst many inland wetlands hold water year-round, a significant proportion of inland wetlands are more ephemeral and only form during periods of high rainfall (Jonhson and Rogers, 2003; Brooks, 2005). As a result, migratory wetland birds are required to adopt strategies that enable them to withstand limited and unpredictable stopover habitat availability across spatial and temporal scales throughout their migration route.

Whilst the migration strategies of coastal wetland birds have been well studied, with particular focus on shorebirds (Warnock and Takekawa, 2003), less is known about the behaviour of inland wetland birds during migration (Minias et al., 2010). Coastal wetland birds often show high site fidelity in their use of migration stopover sites (Coleman and Milton, 2012; Pakanen et al., 2019); for instance, a study in 2009 fitted Red Knots of the subspecies *roselaari* with leg flags in coastal Washington and resighted 47% of birds migrating through the same site in 2010 (Buchanan et al., 2012). However, several studies have shown some inland wetland species to be less site faithful. A recent study on Whooping Cranes *Grus americana* migrating through central North America showed that whilst birds remained consistent in their timing of migration and use of a general “migration corridor”, they were less faithful to specific stopover sites (Pearse et al., 2020). Similarly low stopover site fidelity has been observed in Black Storks *Ciconia nigra*, which are also a soaring migratory wetland species (Chevallier et al., 2011). Whilst these studies did not directly investigate the reasons for low stopover site fidelity exhibited by these species, they speculate that being flexible in stopover site choice may allow birds to respond to temporal variations in site quality caused by changes in food availability or surface water distribution (Chevalier et al., 2011; Pearse et al., 2020). Another study investigating site fidelity in two inland wader species, the Wood Sandpiper *Tringa glareola* and the Common Snipe *Gallinago gallinago* (Minias et al., 2010), found a positive relationship between refuelling rates and stopover site fidelity in Wood Sandpipers, a time-minimising migrant, but not in the energy-minimising Common Snipe, which do not require as high refuelling rates during stopover. These studies indicate that variability in food and other resource availability may be important determinants of stopover site fidelity and plasticity in migration strategy.

Less is known about the variation and plasticity of other aspects of migration strategies in inland wetland species. However, there are indications that flexibility in migratory strategy may be reflected in stopover duration and timing. Studies have shown Great Reed Warblers *Acrocephalus arundinaceus* to exhibit repeatability in stopover site choice but flexibility in the timing of migratory flights and stopovers in response to the high temporal variation in resource availability and weather conditions (Hasselquist et al., 2017; Malmiga et al., 2020). Wood Sandpipers migrating through wetlands in northeastern Austria during the autumn in 2004 and 2005 showed considerable variation in stopover duration with some birds passing through quickly (transients) and others remaining for longer periods (Muraoka et al., 2009). Birds arriving later in the season showed higher fat deposits indicating that they may have used earlier sites for refuelling. Studies on waterfowl, such as Mallards *Anas platyrhynchos* breeding in north-east Europe, suggest even greater flexibility in migration strategy within these taxa, with birds showing widespread variation in migration distance, timing and direction depending on environmental conditions (Gehrold et al., 2013; van Toor et al., 2013). The degree of plasticity in migration strategies adopted by wetland birds and the factors contributing to this are still uncertain for many species and require further research.

Anthropogenic changes to wetlands over the past century have been extensive and have significantly affected both the distribution and quality of these habitats. Some studies estimate that, on average, over half of the world's wetlands have been lost since 1900 (Junk et al., 2013), largely due to draining for agriculture and development projects (Reis et al., 2017). These have further fragmented the distribution of inland wetlands beyond their already patchy natural distribution. Loss of wetland habitats may affect migratory birds through the removal of crucial stopover sites for certain species, as well as overall reduced stopover habitat connectivity (Merken et al., 2015). The latter of these may be of particular importance for inland wetland species, which despite not generally showing high fidelity to certain sites, may depend on a network of habitats across their migration route (de Elgea and Arizaga, 2016). Smaller, more temporary wetlands are often not given as high levels of protection, despite a number of inland species depending on these during migration (Skagen and Knopf, 1994; de Elgea and Arizaga, 2016). Whilst wetlands have been heavily targeted by conservation efforts in recent decades, human development is likely to continue to affect these habitats in the future. Therefore, understanding how anthropogenic changes to wetlands affect birds with different migration strategies will be key to identifying species at greater risk.

Inland wetland birds face a number of challenges during their migration due to limited habitat availability across their migration route and high spatial and temporal variability in resources. Consequently, many species have been found to exhibit relatively high degrees of plasticity and flexibility in their migration strategies regarding stopover site fidelity and timing of migratory flights. Whilst this may give species a greater capacity to adapt to future anthropogenic changes to wetlands, this is still uncertain (Senner et al., 2020; Conklin et al., 2021) and the degree of plasticity and variability in migratory behaviour shown by many species requires further research.

1.5 The function of small island stopover sites

During migration, many species encounter extensive areas containing no suitable habitat for stopover, meaning they must cross these in a single flight. Such ecological barriers may include deserts, mountain ranges or the sea (Schmaljohann et al., 2007; Gill et al., 2009). Crossing these regions involves a high level of energy expenditure, due to the distance covered, as well as the inhospitable conditions often encountered, meaning birds must accumulate relatively large amounts of fat and undergo significant physiological preparations beforehand (Weber, 2009; Skrip et al., 2015). Research often focuses on the behaviour of birds at ‘staging sites’ prior to crossing ecological barriers; studies have shown these sites to be of disproportionate importance to the overall success of a bird’s migration, due to their role in allowing birds to prepare for long migratory flights (Myers et al., 1983; Baker et al., 2004; Warnock, 2010). However, whilst birds’ stopover behaviour prior to crossing ecological barriers has been well studied, there is less understanding about how migrants behave immediately after these crossings. Despite the relative lack of knowledge on this, understanding stopover strategies after crossing ecological barriers is key to gaining a full picture of a species' overall migration strategy.

Many species which normally exclusively inhabit inland regions, are forced to make sea crossings during their migrations. Following these sea crossings, small offshore islands are often used as stopover sites due to their positioning as the first point of landfall. This has been documented for a number of terrestrial species from a wide range of ecological settings (Moore et al., 1990; Ferretti et al., 2021). A range of passerine species have been recorded making forced stopovers on the islands of Antikythira, Strofades and Gavdos, Greece, arriving in highly fat-depleted states (Barboutis et al., 2022); notably, over 50% of captured Collared Flycatchers *Ficedula albicollis* were estimated to have insufficient flight ranges to travel onwards to more suitable refuelling locations. This suggests that the geographical location of many islands makes them important stopover sites for individuals in poor physical condition following sea crossings.

However, many birds stopping at small islands during migration arrive in less fat-depleted states, indicating they are not forced to stop at these locations due to insufficient flight ranges (Barboutis et al., 2022). Additionally, despite the wide range of species recorded stopping over, such islands often contain a limited diversity of habitats and relatively scarce food resources, meaning from a refuelling perspective, they may be far from optimal sites for most species (Maggini et al., 2020; Ferretti et al., 2021). This creates uncertainty over the relative role of refuelling in birds' decisions to stop at these sites. There are indications that some birds may spend relatively short periods of time at small islands before moving on to habitats with greater foraging opportunities. 10 out of 12 migrant passerine species captured on the island of Ponza, Italy, showed negative fuel deposition rates and generally stayed for no longer than one day on the island (Maggini et al., 2020). An experimental study on temporarily caged birds, also caught during migration stopover at Ponza, showed that birds exposed to lower food availability showed increased diurnal locomotor activity (Ferretti et al., 2019). Similar experimental fasting studies have shown that nocturnal migratory restlessness is also increased by low food availability (Eikenaar and Bairlein, 2014), suggesting that birds are likely to leave stopover sites when refuelling opportunities are low.

Most studies on stopover ecology on small islands focus on small passerines, often at sites located in the Mediterranean or Gulf of Mexico (Moore et al., 1990; Maggini et al., 2020; Barboutis et al., 2022); in contrast, non-passerine species with potentially more restricted habitat requirements are underrepresented, despite being frequently recorded using these sites (Prys-Jones et al., 1992; Nur et al., 2019; Barboutis et al., 2022). Further research should continue to develop understanding of the relative role refuelling opportunities have in the decision to stopover on islands and whether species habitat requirements affect this.

Recent research investigating functions of stopover other than refuelling may shed light on how birds use islands following sea crossings. Factors such as physiological recovery and catching up on sleep may explain the use of these sites by species with habitat requirements different to those present. There are frequent observations of birds sleeping immediately after sea crossings (Schwilch et al., 2002; Covino and Cooney, 2015; Ferretti et al., 2020), as well as at stopover sites following flights across other ecological barriers, such as at oases in the Sahara Desert (Jenni-Eiermann et al., 2011). However, since birds with high energy stores still stop to sleep and recover at such islands suggests that the physiological stress of long sea crossings requires them to recover at the first point of landfall (Ferretti et al., 2021; Barboutis et al., 2022). Weather-related factors may also explain use of islands by migrating birds; raptors, such as the Grey-faced Buzzard *Butastur indicus*, may use islands to minimise the length of sea crossings, since thermal uplift is not as strong over sea (Nourani et al., 2018). Islands may also allow birds to avoid adverse weather conditions that may occur en route (Agostini et al., 2005; Nourani et al., 2018). Therefore, it is important to consider all aspects of stopover function when assessing the value of small islands as stopover sites.

The use of small islands by birds during migration represents an intriguing yet understudied aspect of the study of migration strategies. Further research in this area may reveal further insights into the decision-making process involved in stopover site selection and departure by migrating birds, especially in the context of crossing ecological barriers. Recently, increased attention has been given to characterising the relative roles of different stopover sites throughout birds' migrations (Warnock, 2010) and determining the role these islands have in allowing birds to complete their migration is important to understand their conservation value.

1.6 Fine scale habitat use and movement activity in birds during stopover

The development of telemetry-based methods to study stopover behaviour of migratory birds has allowed researchers to explore less well-known aspects of stopover periods (Flack et al., 2022). Traditional mark and recapture methods are often of limited use, particularly in species with cryptic habits, since birds can often be difficult to relocate or recapture, leading to insufficient data being collected. In comparison, telemetry-based methods allow more precise locations of individuals to be obtained and allow individuals to be distinguished from each other with ease. Not only does this allow more accurate estimates of stopover duration to be obtained, but also allows finer scale behaviours to be studied, such as local scale habitat use and movement activity patterns (Schofield et al., 2018; Kuang et al., 2019).

Studying fine scale habitat use and movement activity can improve understanding of how individuals optimise their behaviour during stopover periods (Alerstam, 2011; Smith et al., 2014). Choosing appropriate habitats is essential for birds during stopover periods, since this will ensure refuelling rates are optimised, and consequently birds often show greater movement activity at the beginning of stopover periods, as they search for the most profitable habitats (Chernetsov, 2006; Seewagen et al., 2010; Cohen et al., 2012). Research suggests that spatial behaviour in birds during stopover is largely determined by food distribution (Chernetsov, 2006), although it may also be affected by predation risk. For example, a study on Western Sandpipers stopping over at Boundary Bay, Canada, found that both predation risk and food availability were highest in areas closest to the shoreline, meaning birds foraged in areas at a medium distance from the shore where this tradeoff could be optimised (Pomeroy, 2006). The scale of movement during stopover varies considerably between species, with some species remaining within temporarily established territories (Dierschke and Delingat, 2001) and others moving relatively large distances.

Spatial behaviour during stopover can also vary considerably between individuals of the same species, although this is relatively understudied (Kuang et al., 2019). For instance, sexual dimorphism may lead to differing habitat choices between sexes; a study in the Tagus Estuary, Portugal found that male Black-tailed Godwits foraged in areas with more exposed mud than females, which have longer bills (Catry et al., 2012). Differences in personality traits between individuals, such as boldness, can also affect habitat choice decisions and the level of movement activity during stopover (Spiegel et al., 2017; Baert et al., 2018). Additionally, birds in poor body condition generally exhibit greater movement activity during stopover periods in attempts to locate more food resources (Moore and Aborn, 2000; Ktitorov et al., 2010).

Habitat selection during stopover periods is often relatively understudied for many species in comparison to their requirements during non-migratory periods (Kuang et al., 2019). This poses a conservation issue since understanding habitat requirements of birds at stopover sites is essential for optimal management of these sites. Consequently, further research is required into habitat selection during stopover and fine scale behaviour of birds within these sites.

1.7 Introduction to project and study species: the Common Snipe *Gallinago gallinago*

The Common Snipe (hereafter “snipe”) is a species of wader with a widespread distribution across the Palearctic region. Snipe breed in inland wetlands or moorlands and several distinct flyways, in which different populations of snipe migrate, have been identified (Svasas and Paulauskas, 2006; Minias et al., 2011); populations breeding in Russia and Northern Europe migrate in a southwest direction to wintering grounds in Southern Europe, the British Isles and Africa, whereas birds from Iceland migrate southeast to wintering locations in Ireland and the United Kingdom.

Past studies conclude that snipe are energy-minimising migrants, spending relatively long periods at stopover sites and making short journeys between these (Meissner, 2003; Wlodarczyk et al., 2007). However, these studies focus solely on stopover sites in continental Europe, with the stopover ecology of snipe migrating through other regions remaining relatively understudied. Snipe migrating from Scandinavia or Iceland to the United Kingdom and Ireland have to complete considerable sea crossings during their migrations (Svasas and Paulauskas, 2006), meaning these populations experience vastly different conditions to birds which follow continental migration routes.

North Ronaldsay is a low-lying island located in the northeast extremity of the Orkney archipelago (Haswell-Smith, 2008). The island is primarily used for grazing livestock, although it also contains areas of wetland habitat, including lochs surrounded by extensive iris beds (Pennington, 1988). Due to its isolated location (Figure 1), North Ronaldsay is often the first point of landfall for birds migrating across the sea from Scandinavia or Iceland and the island is well known among both ornithologists and amateur birdwatchers, owing to the large diversity of migrant birds which have been recorded there (Butcher, 2021). The island’s bird life has been continuously monitored by the island’s bird observatory since the 1980s, with snipe recorded in relatively large numbers (Butcher, 2021). This makes them a useful study species for investigating variability in stopover behaviour at this location.

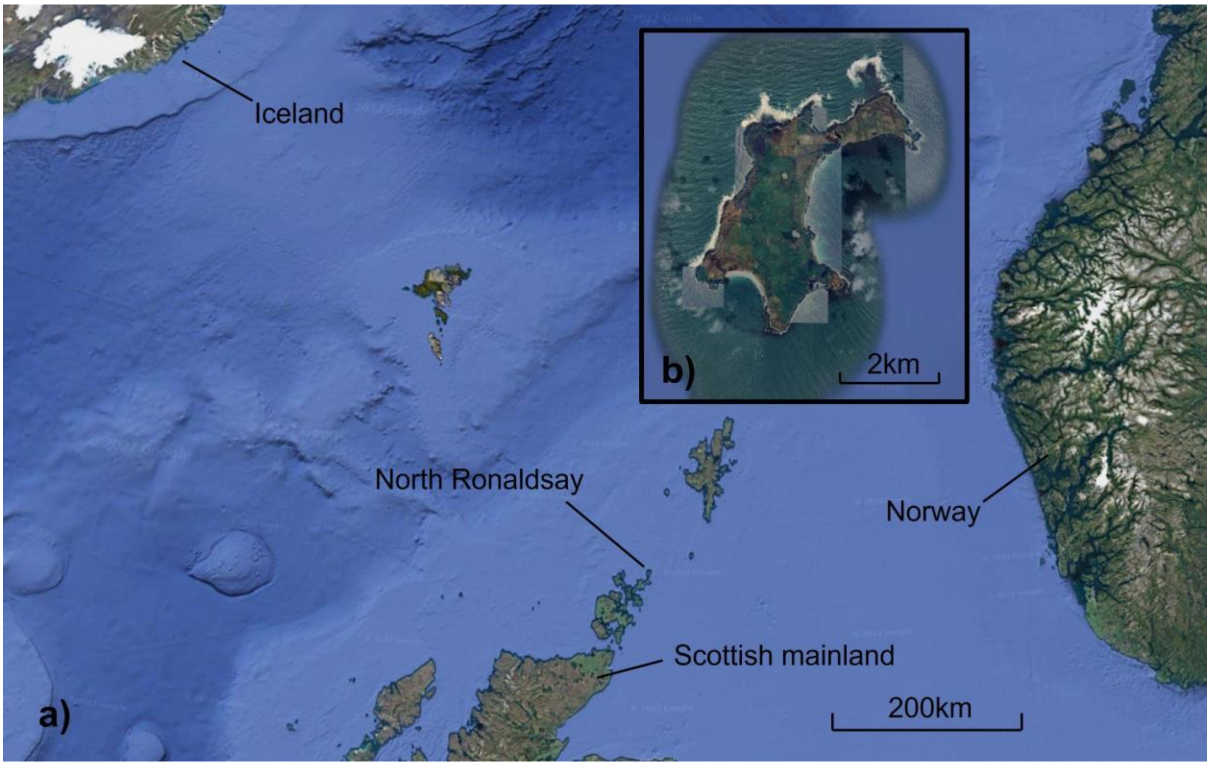

Figure 1. *a) Satellite image of North Sea and GIUK gap (Google Earth, 2022) with locations of North Ronaldsay, Iceland, Norway and the Scottish mainland labelled. b) Satellite image of North Ronaldsay, Orkney (Google Earth, 2022).*

In the following chapter, I investigate the effects of weather and time of year on the number of snipe present on North Ronaldsay over the annual period using migrant bird census data collected by North Ronaldsay Bird Observatory. This will allow me to determine the conditions in which snipe use North Ronaldsay as a stopover site and suggest how they respond to variation in weather conditions during migration. This chapter also demonstrates how research can make use of migrant bird census data collected by bird observatories and similar organisations in the context of migration strategies and stopover behaviour, since few studies currently make use of this resource (Knudsen et al., 2007; Dunn, 2016).

In Chapter 3, I investigate the effects of body condition, age and arrival date on the stopover duration of snipe on North Ronaldsay during the autumn migration period through a radio telemetry study. This will provide suggestions about the type of stopover strategy used by snipe on North Ronaldsay (time vs. energy minimising) and how variable this is between different individuals. I also investigate habitat use of migrating snipe on North Ronaldsay and determine how movement activity changes over the course of their stopover and how this is influenced by arrival date and body condition.

Combined, these chapters aim to investigate factors affecting migration strategy and stopover behaviour exhibited by snipe following more northerly migration routes. This may provide further insights into the flexibility of migratory behaviour in inland waders and wetland species in general, as well as the function of small island stopover sites and how birds behave immediately following sea crossings.

2.0 Using long-term migrant bird census data to investigate the effects of weather conditions and seasonality on the abundance of Common Snipe *Gallinago gallinago* at a stopover site in Orkney, Scotland

2.1 Abstract

Understanding how factors such as weather and time of year affect stopover site use by migratory birds can reveal the role that stopover sites play during migration, which has important implications for conservation. Long-term migrant bird census data collected by bird observatories and similar organisations are a valuable and currently underused resource for investigating these issues. This study uses migrant bird census data collected by North Ronaldsay Bird Observatory combined with past weather data to demonstrate this by modelling the effects of weather conditions and seasonality on the numbers of Common Snipe on North Ronaldsay, Orkney. We show that snipe numbers varied considerably over the annual period, reaching a small peak during the spring migration period and a much larger peak during the autumn migration period. Increases in precipitation led to increases in snipe numbers, whereas increasing wind speed caused the number of snipe to decrease. Whilst the inclusion of wind direction parameters significantly improved model AIC values, we found wind direction to be less important than expected when modelling snipe numbers. The large numbers of Common Snipe recorded on North Ronaldsay during the autumn add to previous evidence that the Northern Isles are significant stopover sites for this species. We suggest that future studies make use of the availability of long-term census data collected by bird observatories for understanding migratory timings and stopover site use by birds and build upon the methods used in this study.

2.2 Introduction

Migration is exhibited across many animal taxa and has important ecological consequences, such as effects on community structure, biomass and energy transfer, and infectious disease spread (Wilcove and Wikelski, 2008; Altizer et al., 2011; Hu et al., 2016; Hansen et al., 2020). Migratory species face a variety of different threats at each stage of their annual cycle due to dependence on different sites throughout the year (Vickery et al., 2014, Gilroy et al., 2016). Often termed as a “multiple jeopardy” (Newton, 2004), this makes migratory species highly sensitive to anthropogenic change, since threats have the potential to occur at a greater range of spatiotemporal points in their annual cycle (Sergio et al., 2019). Migratory periods may be particularly risky, with many species exhibiting lower survival rates during these periods in comparison to resident phases of their annual cycles (Sillett and Holmes, 2002; Rushing et al., 2017; Sergio et al., 2019). Climate change has already led to significant impacts on populations of migratory species and recent research has highlighted the increased vulnerability of such species to current and future climatic changes (Møller et al., 2008, Kubelka et al., 2018; Mallory and Boyce, 2018; Zurrel et al., 2018; Kubelka et al., 2022). Therefore, it is of great importance to understand how current and future climate change may continue to affect species during migratory periods in order to reduce further population declines (Zurrel et al., 2018).

The timing of migratory flights and stopover periods can have significant effects on the survival probabilities of birds during migration, as well as subsequent impacts on fitness at their destinations. Consequently, many species have been shown to optimise the timings of migratory flights (Alerstam, 2011), with many species’ arrival and departure timings from stopover sites exhibiting high repeatability each year (Franklin et al., 2022). However, the environmental conditions that birds experience en route may also significantly impact birds’ survival during migration (Briedis et al., 2017; Loonstra et al., 2019) and consequently, many species may exhibit flexibility in stopover site use in response to changes in conditions (Morganti et al., 2011). Therefore, it is important to understand the environmental factors that affect the use of stopover sites by migrating birds, as this can provide indications of the function of these locations and their importance for conservation.

Previous research has highlighted the importance of weather conditions in influencing stopover decisions by migrating birds. This can occur through a number of mechanisms. Firstly, weather conditions may increase or decrease the energy required to complete migratory flights, which in turn affects stopover decisions by migrating birds (Richardson, 1990; Shamoun-Baranes et al., 2010a). Wind direction and speed has been shown to be particularly important in this aspect. In general, tailwinds will facilitate migratory flights due to reduced energy expenditure, whereas strong headwinds or crosswinds may prevent certain species from leaving a stopover site (Shamoun-Baranes et al., 2017). Temperature may also affect birds' flight capabilities, especially for soaring species, due to its effects on thermal uplift (Richardson, 1990; Shamoun-Baranes et al., 2003). Rainfall and other precipitation events can cause individuals to land and halt their migratory flight in certain situations (Overdijk and Navdeo, 2012).

Similarly, some locations can act as 'emergency stopover sites', which are only used by birds in unfavourable weather conditions. For instance, during periods of poor wind assistance, Red Knots *Calidris canutus* migrating between Mauritania and the German Wadden Sea will make an additional stopover at an area of wetlands on the French Atlantic Coast, often arriving in poor energetic condition (Shamoun-Baranes et al., 2010b). Emergency stopovers are often associated with periods of severe weather, such as storms or high rainfall events (Overdijk and Navedo, 2012), which can also lead to significant mortality in some cases (Newton, 2007). Weather conditions may also have indirect effects on a bird's migration by affecting resource availability at stopover sites (Jensen et al., 2016; Halupka et al., 2017). Consequently, the effects weather may have on bird's migration are complex and require ongoing research given the risks many migratory species face from current and future climate change (Zurell et al., 2018).

Birds may exhibit flexibility in migratory behaviour in response to different weather conditions. The effect of weather on food availability at stopover sites may cause birds to alter their stopover site choice and departure timings (Bauer et al., 2008). Additionally, following long periods of severe weather conditions, birds may sometimes choose to depart in subsequent suboptimal conditions due to increased migratory restlessness resulting from having to delay their stopover departure (Shamoun-Baranes et al., 2017). The migration strategy of a species is also likely to affect how flexible a species is in its migratory response to weather (Packmor et al., 2020). Similarly, birds' responses to weather conditions may vary depending on the time of year (Morganti et al., 2011). However, for many species, the degree of flexibility in migratory responses to weather is uncertain and requires further research.

Small islands often represent the first point of landfall for birds following sea crossings during migration, which represent a significant ecological barrier for the majority of landbirds (Moore et al., 1990; Ferretti et al., 2021). Whilst there has been significant research into the effects of weather conditions on stopover departure decisions by birds prior to making sea crossings (Sjöberg et al., 2015; Bradarić et al., 2020), less research attempts to determine the effects of weather on stopover decisions following such crossings. Birds may experience highly variable conditions whilst at sea, which will have a significant impact on their ability to complete their flight, as well as their subsequent body condition upon its completion. Additionally, whilst many species have been recorded stopping over on small islands in highly fat-depleted states, many studies have shown birds arriving with good body conditions, which creates uncertainty over the function of such islands for migrating land birds (Maggini et al., 2020; Barboutis et al., 2022). Therefore, understanding the effects of weather conditions on stopover decisions of birds on islands may be useful in revealing the ways in which species use these stopover sites. This will improve understanding of the stopover decisions of birds following the crossing of ecological barriers and will also allow the conservation value of such islands to be determined more accurately (Maggini et al., 2020).

The Northern Isles in Scotland, made up of the Shetland and Orkney archipelagos, are well established as stopover sites for a wide range of migratory birds (da Prato et al., 1980; Corse and Summers, 1999; Delingat et al., 2008; Miles et al., 2017). Due to their location, the Northern Isles are often the first, or last depending on the season, point of landfall for migratory land birds crossing the North Sea or Northern Atlantic from or to Scandinavia or Iceland. This makes these islands a useful location to study birds’ stopover behaviour following or before the crossing of relatively large ecological barriers. Despite this, there are few studies that attempt to investigate the environmental factors affecting birds’ stopover behaviour on these islands. North Ronaldsay Bird Observatory was set up in 1987 and provides valuable data on bird migration in the Northern Isles. North Ronaldsay is a hotspot for bird migration within the Northern Isles, due to its optimal positioning and relative isolation. The observatory has used a combination of bird ringing and collection of migrant bird census data to provide continuous monitoring of its bird life since it was established (Archer et al., 2010; Butcher, 2021). Methods to standardise census counts, along with the size of this dataset, make it a valuable and comprehensive resource of long-term data on bird migration and similar data have been collected by other bird observatories and similar organisations at a number of important stopover sites across the world (Miles et al., 2017). Despite this, there are still relatively few studies that make use of these data to investigate stopover behaviour of migratory birds.

The Common Snipe *Gallinago gallinago* is a species of wader that breeds in Northern Europe, Iceland and Russia, favouring inland areas of wetland or moorland. Previous research has demonstrated distinct differences in migration route between populations of this species, depending upon their breeding and wintering locations (Svazas and Paulauskas, 2006, Minias et al., 2011). The stopover behaviour of birds migrating southwest through central Europe during the autumn has been relatively well documented; ringing studies have shown that individuals migrating through these regions are energy-minimising migrants, migrating relatively slowly with short flights between stopover sites (Wlodarczyk et al., 2007; Meissner, 2003; Minias et al., 2011). However, the stopover ecology of populations of snipe migrating through more north westerly regions of their range has received relatively little research attention. Individuals from Iceland and many birds from Scandinavian populations carry out significant sea crossings during their southward autumn migration to the United Kingdom and Ireland (Svazas and Paulauskas, 2006; Gunnarsson and Tómasson, 2011), so consequently experience vastly different conditions en route to their wintering grounds. Therefore, studying these populations may reveal further variation in migratory strategy and stopover behaviour within this species. Additionally, this presents a relatively understudied situation, where an energy-minimising migrant is forced to carry out a relatively large migratory flight before reaching a stopover site. Snipe are recorded in relatively large numbers using the Northern Isles as stopover sites during migration periods (Boyd and Petersen, 2006; Andrews and Nightingale, 2021; Butcher, 2021), so consequently are a suitable study species, for which arrival numbers can be correlated with weather conditions across the entirety of both migratory seasons using a long-term dataset.

This project aimed to investigate the effects of weather conditions and seasonality on the number of Common Snipe present on North Ronaldsay using long-term migrant bird census data. We hypothesised that there would be greater numbers of snipe present on the island during the following weather conditions:

- Increased wind speeds (more birds forced to stopover due to unfavourable flight conditions)
- Increased tailwind assistance (for example, easterly or north-westerly wind directions during the autumn allowing birds to cross the sea from Scandinavia or Iceland respectively to the Northern Isles)
- Increased rainfall (more birds forced to stopover due to unfavourable flight conditions)

2.3 Methods

Using long-term migrant bird census data provided by NRBO, combined with historical weather data, we modelled the effects of weather and seasonality on the number of Snipe present on North Ronaldsay each day.

2.3.1 Methods of data collection

Bird census data was collected between the years of 1985 and 2020 as part of NRBO's continuous monitoring of the bird life on the island. NRBO staff members carried out the census daily, which involved walking a route through a section of the island (census area), which each member of staff was allocated for that particular day. Each participant counted the number of each bird species they saw and recorded this, along with the hours they spent on the route, in the observatory log at the end of the day. The census areas were rotated between each staff member each day to reduce bias. Total coverage (observation hours) was calculated for each day, since the number of available staff varied between and within years. The observatory aimed to cover as many census areas as possible each day, although sometimes full island coverage was not possible.

We obtained historical weather data from the Met Office MIDAS Open database, located in the Centre for Environmental Data Analysis archive (Met Office, 2019). We used data for the following weather variables, recorded hourly from the Kirkwall and Fair Isle weather stations: wind speed; wind direction; rain accumulation; and maximum temperature. Due to the timings of data collection during NRBO census counts and the likely effects of the previous night's weather on a given day's bird counts, we considered weather conditions during the 24-hour period between 21:00 (on the previous day) and 21:00 (on the given date), which we defined as an 'effective day'.

For each effective day, we calculated the following statistics (summarised in Table S1) using data from the Kirkwall weather station: mean wind speed; mean maximum temperature; and total daily rain accumulation. Some rainfall accumulation observations were collected after periods considerably greater than 24 hours. We replaced these, along with any other additional missing data, with observations from the Fair Isle weather station, ensuring that these were collected within the correct time interval. Additionally, we calculated two groups of summary statistics for wind direction. The first of these included the mean north westerly and mean easterly wind components, calculated using $\cos(x+45°)$ or $\sin(x)$ respectively, where x was the wind direction measured as an angle relative to true north. The second group included the proportion of hours where the wind direction fell between 270° and 0°, defined as "ICOUNT", and the proportion of hours where the wind direction fell between 45° and 135°, defined as "SCOUNT".

2.3.2 Modelling of census data

Data analysis was carried out in R version 4.2.0 (R Core Team, 2022). Using the "mgcv" package version 1.8.40 (Wood, 2017), we produced generalised additive mixed models

(GAMM) to predict seasonal changes in the number of snipe present on North Ronaldsay across the annual period using snipe counts from the NRBO migrant bird census dataset.

The models considered the effects of the following covariates on snipe numbers as smooth functions: Julian date; total number of observation hours each day, so that changes in observer coverage were accounted for; and each of the calculated weather variables discussed previously. We were unsure whether using mean north westerly/easterly wind components or using SCOUNT/ICOUNT would be more appropriate for determining the effect of wind direction on snipe numbers, so produced two full models, one of which included SCOUNT and ICOUNT as wind direction variables (full model 1) and another which included mean north westerly and mean easterly wind components instead (full model 2). We also included an additional categorical variable, defined as “SEASON”, which classified observations as occurring during either spring (Julian date <180) or autumn (Julian date >= 180) to consider the fact that snipe should be migrating in opposite directions during these periods. This was included as an interaction with either ICOUNT (full model 1) or the mean north westerly wind component (full model 2). The models also included a temporal autoregressive component to consider the effect that the number of birds present during the two days prior to the focal day had on the number of snipe present during the focal day.

For each of the full models, we tested whether inclusion of covariates caused a significant improvement on the model fit by comparing Akaike Information Criterion (AIC) values between the full model and models with one specified covariate or interaction removed. If a model with a particular covariate removed had an AIC value of more than 2 units greater than the full model, then we considered this covariate to have caused a significant improvement to the full model fit. We then determined the nature of the relationships between covariates and snipe numbers using the full model output summary and by plotting each covariate against its partial residuals. We also compared AIC values between the two full models to determine which method of measuring wind direction produced a better model fit.

2.4 Results

Modelled and observed snipe census counts on North Ronaldsay show clear seasonal changes, rising and falling twice over the annual period (Figure 2). The first of these reaches a peak during early April (Julian date = 108) and is relatively weak, with modelled snipe numbers reaching 40.9 birds (when using median values for all other model covariates). After this, modelled snipe numbers decrease until mid-July (Julian date = 206) when they reach their lowest number at 4.6 birds. Following this, the number of snipe rises at an increasing rate before reaching a strong peak during October (Julian day = 295), with the model output peaking at 257.9 birds. Following this, snipe census counts decrease relatively quickly, with modelled numbers falling to 16.6 birds by the end of the year. There is large variation in the observed census counts, especially during the spring and autumn peak periods; snipe census counts varied between 0 and 297 birds during the spring peak, and between 0 and 850 birds during the October peak. Modelled snipe numbers generally increase with increasing levels of observer coverage.

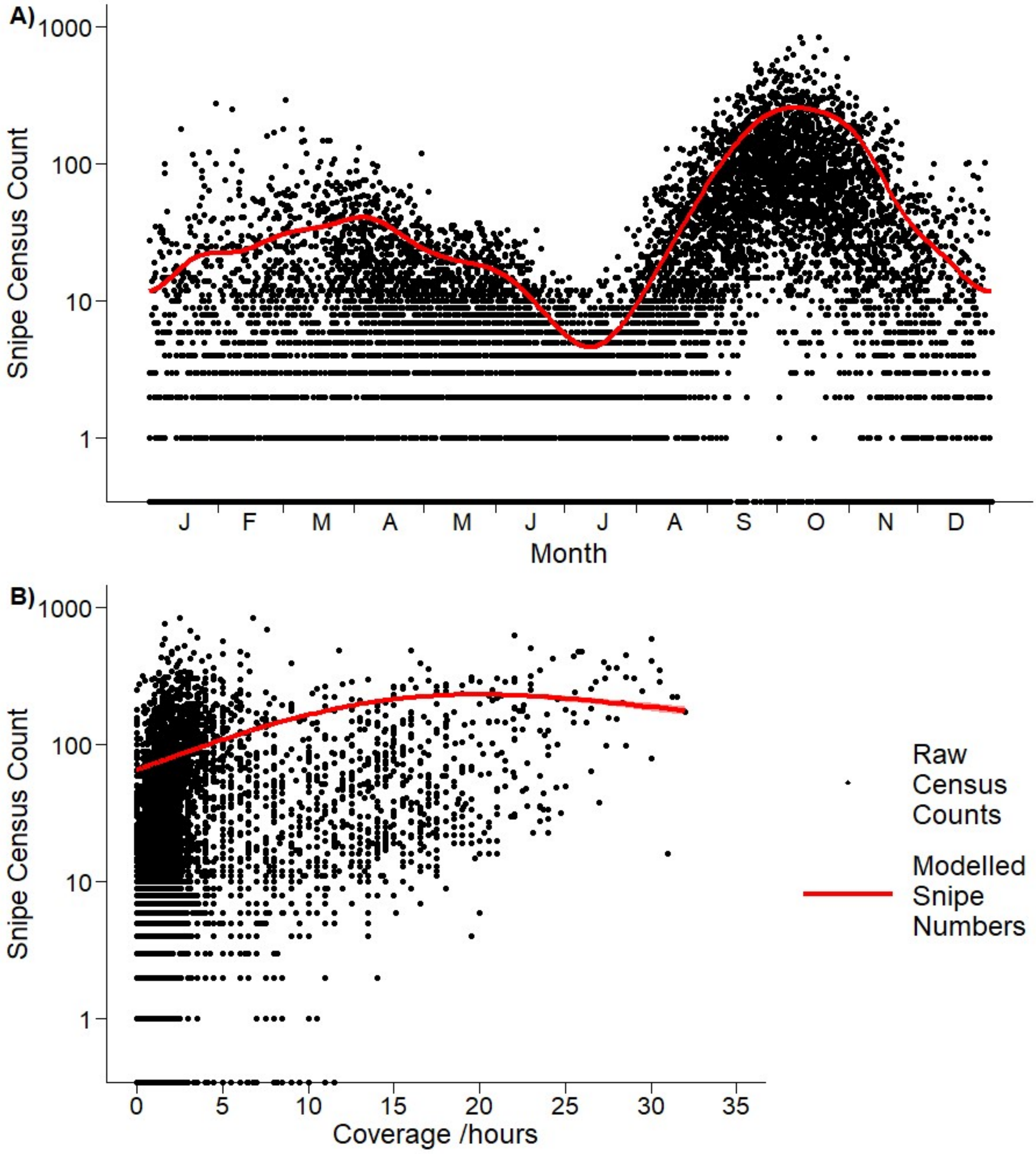

Figure 2. *Observed census counts and modelled numbers of Common Snipe Gallinago gallinago on North Ronaldsay, Orkney over A) the annual period and B) varying levels of observer coverage. Snipe census counts were carried out by North Ronaldsay Bird Observatory between the years of 1985 and 2020. The fitted generalised additive mixed model (full model 2) considers Julian Date (although figure axis shows months for ease of interpretation), the number of observation hours and weather variables as covariates and includes a temporal autoregressive component to consider the effects of the number of snipe*

present during the two days prior to the focal day on each snipe count. 95% confidence intervals for the predicted model estimate are shown by the shaded area.

Removal of any of the weather covariates included in the full models caused significant reductions in model fit for both full model 1 and full model 2 (Table 1). Removal of the interaction between "SEASON" and northerly wind component also led to this effect. Partial residual plots (Figure 3; Figure S1; Figure S2) show that increasing mean hourly precipitation led to increases in snipe numbers counted on North Ronaldsay, whereas increases in mean wind speed led to decreases in the number of snipe counted. Overall, increases in temperature were associated with increases in snipe numbers. However, this relationship is not linear (Figure 3), with a marginal decrease in snipe numbers between -2°C and 7°C, before a more noticeable increase at higher temperatures. Effects of wind direction on the variation in snipe numbers were very marginal for all wind direction variables considered by the models (Figure S1; Figure S2), despite inclusion of these variables causing significant improvements to model fit (Table 1).

Table 2. *Akaike information criterion (AIC) values calculated for generalised additive mixed models (GAMM) used to predict numbers of Common Snipe Gallinago gallinago on North Ronaldsay recorded during daily census counts. Full models consider Julian date, the number of observation hours and weather variables as covariates and include a temporal autoregressive component to consider the effects of the number of snipe present during the two days prior to the focal day on each snipe count. We present AIC values for these models, along with models with one specified weather-related covariate or interaction removed. AIC values which show a significant reduction in model fit compared to the full model are highlighted in bold.*

Model	Akaike Information Criterion value	AIC Difference to full model
Full model 1	383088.9	NA
Full model 1 - "TEMP"	387162.2	**4073.3**

Model	Akaike Information Criterion value	AIC Difference to full model
“Full model 1 - “PRECIP”	387374.2	**4285.3**
Full model 1 with no interaction between “NWCOMP” and “SEASON”	383586.9	**498.0**
Full model 1 - “NWCOMP”	384034.9	**946.0**
Full model 1 - “ECOMP”	383635.5	**546.6**
Full model 1 - “WINDSP”	391503.0	**8414.1**
Full model 1 - “SEASON”	384168.9	**1080.0**
Full model 2	382586.5	0
Full model 2 - “TEMP”	386509.1	**3922.6**
“Full model 2 - “PRECIP”	387160.7	**4574.2**
Full model 2 with no interaction between	382674.6	**88.1**

Model	Akaike Information Criterion value	AIC Difference to full model
“ICOUNT” and “SEASON”		
Full model 2 - “ICOUNT”	383874.4	**1287.9**
Full model 2 - “SCOUNT”	383342.6	**756.1**
Full model 2 - “WINDSP”	394629.5	**12043**
Full model 2 - “SEASON”	383292.8	**706.3**

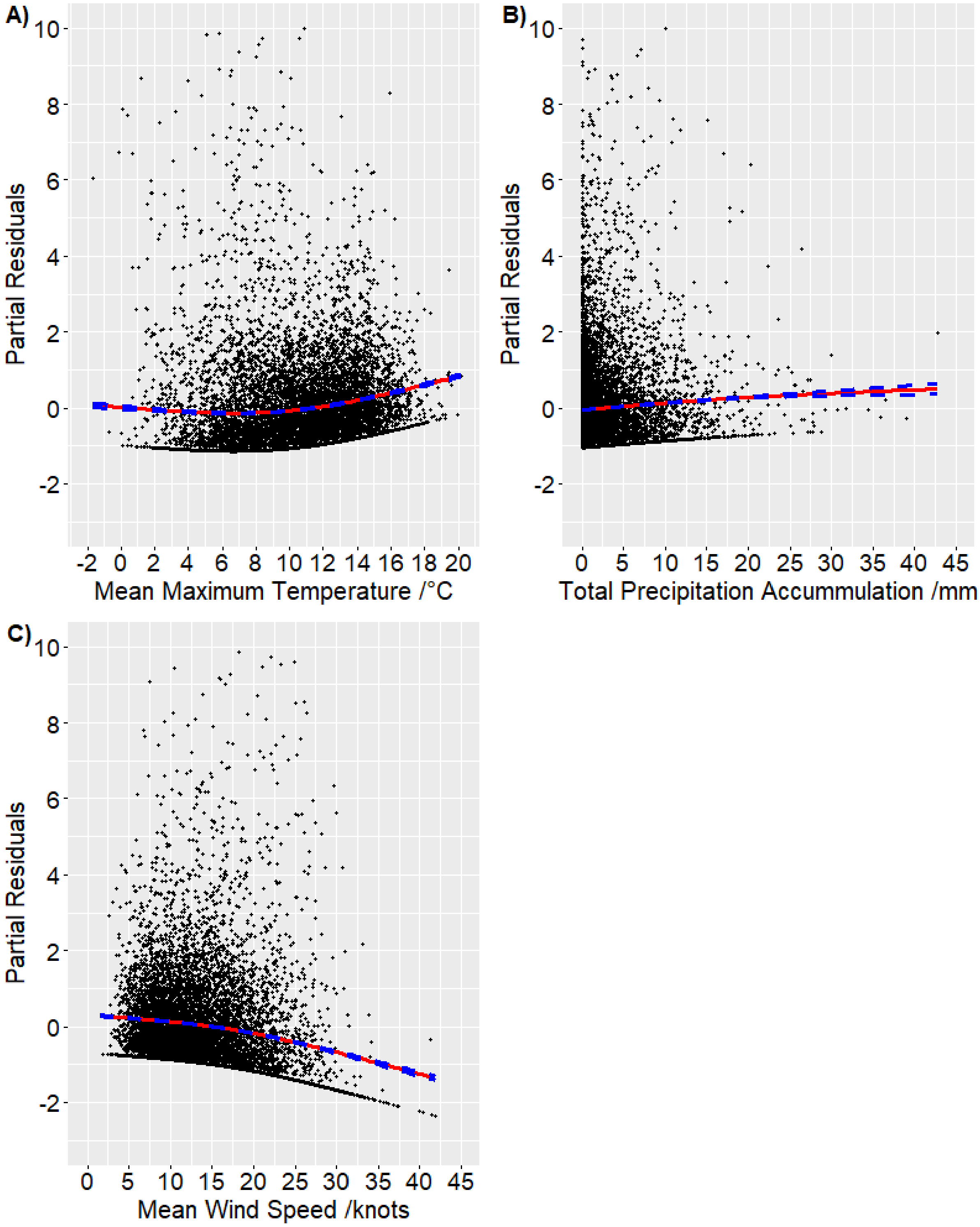

Figure 3. *Partial effects plots showing the effects of: A) mean maximum temperature; B) total precipitation accumulation; and C) mean wind speed on modelled numbers (full model 2) of Common Snipe on North Ronaldsay. In each plot, the red line shows the partial effect, with blue dashes indicating 95% confidence intervals and black dots indicating plotted partial residuals. Despite a slight decrease in modelled snipe numbers as temperature increases from -2 ℃ to 6 ℃, snipe numbers appear to increase overall as mean maximum temperature*

increases. Snipe numbers increase with increasing mean precipitation accumulation but decrease with higher mean wind speeds.

2.5 Discussion

As expected, we found that the number of snipe present on North Ronaldsay exhibits a clear seasonal pattern, with a small peak during the spring and a much larger peak during the autumn. The autumn migration period appears to start rapidly in late August, continuing into October, with the seasonal model peaking at about 260 birds. After this peak, snipe numbers fall rather quickly to around 15 birds by the end of the year. Increasing precipitation caused a significant increase in the number of snipe counted on North Ronaldsay, whereas increasing wind speed caused snipe counts to decrease. Whilst we predicted snipe numbers to increase with increasing precipitation, the decrease in numbers with increasing wind speed does not align with our hypothesis. Overall, snipe numbers appear to increase with increasing temperature. Despite its inclusion leading to significant improvements in model fit, wind direction only had marginal effects on snipe numbers. Increases in easterly and north westerly wind components and increases in the proportion of hours with easterly or north westerly winds recorded all appear to have little noticeable effect on snipe numbers. This was unexpected, since we predicted wind directions providing tailwinds from Scandinavia or Iceland to increase the number of snipe counted due to either more birds choosing to make these sea crossings or a higher proportion of birds successfully completing these.

This study confirms previous findings and accounts that Common Snipe migrate in relatively large numbers through the Northern Isles, particularly during the autumn (Boyd and Petersen, 2006; Andrews and Nightingale, 2021; Butcher, 2021). The timing of peak autumn migration intensity of Common Snipe through North Ronaldsay in October appears to be later than the timings observed in birds following different routes through stopover sites in continental Europe; the median date for captures of migrating snipe through ringing stations in Poland was during mid-August (Minias et al., 2011). However, this may be due to North Ronaldsay being situated closer to wintering locations than these sites, meaning we cannot be certain that this confirms a difference in migration timing between different snipe populations. There is a lack of previous research on Common Snipe migration timings during the spring to compare our results to. However, the small increase in snipe during the spring appears to mirror the historical departure dates of snipe from Great Britain, suggesting that many of the additional birds counted on North Ronaldsay during this time are northbound or eastbound migrants (BTO/RSPB/BirdWatch Ireland/SOC/WOS, 2023).

The large differences in snipe numbers present during spring and autumn may be due to contrasting migration strategies of this species during spring and autumn. Previous research into Common Snipe migration behaviour indicates that this species takes an energy-minimising approach during the autumn migration periods (Meissner, 2003; Wlodarczyk et al., 2007). Therefore, snipe migrating through North Ronaldsay during the autumn may spend relatively long periods of time at this stopover site, causing numbers to accumulate as more birds arrive throughout the season. However, these studies solely focussed on the autumn migration period and the spring migration strategy of Common Snipe is understudied. Multiple studies have shown that birds are often more time constrained during the spring, due to increasing competition for breeding resources at their destinations as the season progresses (Karlsson et al., 2012; Nilsson et al., 2013). This may cause birds to stopover for much shorter periods, meaning snipe numbers do not have the chance to accumulate in the same way during the spring.

Alternatively, Common Snipe may often avoid using North Ronaldsay as a stopover site during the spring or use it under a more specific set of conditions. Due to North Ronaldsay’s relative proximity to other islands and the Scottish mainland, snipe flying over North Ronaldsay during the spring may have less of a need to stop on the island. Since these birds are likely to have only just begun their sea crossing at this stage, they may have sufficient energy reserves to continue flying in most instances. During the autumn, however, snipe flying the opposite direction over North Ronaldsay are likely to have been flying for a considerable distance (potentially several hundred kilometres for many individuals), so may be experiencing significantly depleted energy stores or elevated physiological stress as a consequence of uninterrupted migratory flight (Linscott and Senner, 2021; Schmaljohann et al., 2022). This will increase their need to find a stopover site to refuel and recover from physiological stress, so they may stop at the first available opportunity. Raw census counts in Figure 2 indicate that snipe counts may occasionally reach large numbers during the spring, indicating North Ronaldsay may become more important as a stopover site under certain conditions during the spring.

It is difficult to be certain of the extent that differing migration strategies between spring and autumn might have on snipe numbers, since census counts are likely to be higher during the autumn due to the addition of juvenile birds. Juvenile birds often show increased mortality rates during winter due to weather events or predation, meaning many of these fledged birds may not survive until the following spring: there are simply more birds available to be counted in the autumn (Clark, 2004; Cresswell and Whitfield, 2008). It is also unknown how much the fledging of juvenile birds from both the breeding population on North Ronaldsay and neighbouring regions, such as Shetland, may contribute to snipe counts on North

Ronaldsay during the autumn compared to migrant birds which have travelled longer distances. However, ringing recoveries demonstrate that Common Snipe wintering in the British Isles originate from a number of locations in Scandinavia, Russia and Iceland (Robinson et al., 2022). Additionally, the wintering population is estimated at around 1 million birds, which is around 10 times larger than the breeding population (Musgrove et al., 2011; Musgrove et al., 2013), meaning migrant birds from other regions form the majority of the population during this time.

We interpret the observed increase in numbers of snipe on North Ronaldsay associated with precipitation as likely due to the deterioration of flight conditions, forcing birds to halt their migratory flights and land on the island. Additionally, birds already present on the island may decide to delay their departure until the weather conditions improve (Schaub et al., 2004). This has notably been recorded as a feature of short and medium distance migrants which are not as time-constrained during migration (Packmor et al., 2020). Snipe have been previously shown to adopt an energy-minimising strategy during migration and the lack of time constraints here may allow them to select more favourable weather conditions for departure (Meissner, 2003; Wlodarczyk et al., 2007; Minias et al., 2011).

A significant limitation of using observation data to determine the effects of weather on the numbers of migrating snipe is that birds are likely to be harder to see in certain weather conditions. This is likely to be due to a combination of the effects of weather on viewing conditions as well as its effect on birds' behaviour. Therefore, it is possible that not all relationships between weather variables and census counts shown by our results reflect a true change in the number of snipe present at the stopover site. We suggest that the observed decrease in the number of snipe counted during periods of high wind speeds may be due to birds being more reluctant to fly, instead remaining in cover low to the ground making them more difficult to see. Additionally, viewing conditions are likely to be significantly more challenging during periods of strong winds, which may also reduce the number of birds counted. Other weather conditions are also likely to influence birds' behaviour; for instance, during periods of heavy rain or colder temperatures, birds may move to different areas due to changes in the distribution of available feeding habitat. These may be in areas where birds are more difficult to locate, therefore influencing the number counted during the day's census. Other weather conditions likely to influence viewing conditions include fog and heavy rain, which would both make birds more challenging to locate.

Similarly, whilst staff at North Ronaldsay Bird Observatory are competent field ornithologists, our models do not account for inevitable minor differences between observers in their likelihood of locating birds which are difficult to see, such as those concealed among vegetation or that remain low to the ground. Another limitation of the method of data collection used in the NRBO census is that some birds may be counted more than once if they pass between census areas during the same day. Discussion amongst staff may resolve this in more notable cases; for example, it will be noted if a large flock is seen moving into another census area. However, without marking birds it is inevitable that this will happen occasionally. Also, whilst our models consider the total number of hours of coverage per day, they do not consider the number of hours of coverage in each census area. Since habitats differ slightly between census areas, it is likely that some areas will hold larger numbers of snipe, meaning increased coverage in these areas will lead to a greater increase in the census count than in others.

The lack of a strong relationship between wind direction and snipe numbers was unexpected, given the findings of previous research (Liechti and Bruderer, 1998; Liechti, 2006). In particular, the lack of a clear effect of easterly winds on snipe numbers could be considered surprising, since easterlies are associated with facilitating migration of birds across the North Sea and the arrival of migrant birds of many species along the east coast of Britain during autumn (Bradarić et al., 2020; Manola et al., 2020). Additionally, studies have shown wader species often base stopover departure decisions on wind direction, selecting periods of tailwinds, which facilitate onward migration (Ma et al., 2011, Anderson et al., 2019). It may be that Common Snipe are not as selective as other species in their choice of wind directions for stopover site departure.

Future research is required to confirm the migration strategies of Common Snipe using northerly migration routes which cross the sea from Scandinavia and Iceland to the United Kingdom. Radio telemetry or ringing field studies could allow the study of stopover behaviour of individual birds on the Northern Isles and may reveal contrasting results to previous studies focussing on sites further south in continental Europe (Wlodarczyk et al., 2007, Minias et al., 2011). Ultimately, GPS tags could be used to track the migration routes of individuals migrating from Iceland and coastal stopover sites in Scandinavia where birds are likely to make a sea crossing in their next migratory flight. This would confirm the stopover site choice of these populations and allow precise determination of stopover timings. In the context of snipe migrating through the Northern Isles, this may assist with determining the relative origins of snipe present at these stopover sites during the autumn, indicating the importance of these sites to different populations. In a wider context, this may reveal further variability in migratory strategies of different populations of Common Snipe, which experience different conditions and habitats across their migration routes (Svazas and Paulauskas, 2006).

There are a number of organisations and institutions which collect long-term census data on migratory bird numbers, including bird observatories in the United Kingdom, as well as other regions of the world (Dunn, 2016; Andrews and Nightingale, 2021; Butcher, 2021). Using the Common Snipe as a case study, this study demonstrates that these data can be used to investigate stopover timings of migrating birds and make inferences about their migration strategies, using a model which corrects for changes in observer coverage. We also highlight the value of combining these resources with environmental datasets, such as the MIDAS Open database (Met Office, 2019) to correlate migratory behaviour with changes in environmental conditions. These long-term datasets are valuable, due to the length of time the projects have been running and due to the standardisation methods often adopted by such organisations.

However, there are relatively few examples of research that make use of this resource (Knudsen et al., 2007; Dunn, 2016; Miles et al., 2017) and this study represents one of the few attempts to investigate migratory behaviour of a species using such data. We suggest that future research should continue to build on this to create a more detailed picture of stopover timings for species at other stopover sites where long-term migrant bird censuses are carried out. Using a similar model to the GAMM we use here, studies could investigate migration timings for a large number of species with relatively little additional effort. Future models should consider weather conditions across a larger spatial area, in addition to local scale weather, to gain a more complete picture of how weather conditions affect stopover site use. Such studies would be useful from both a theoretical perspective, by improving knowledge of species migratory patterns, and for conservation purposes by improving knowledge of species' reliance on different stopover sites.

To conclude, relatively large numbers of snipe stopover on North Ronaldsay during the autumn, indicating that this site functions as a significant stopover site for this species during this period. Smaller numbers of snipe stopover on the island during the spring, although high counts still occasionally occur during this period. Variation in weather conditions led to significant changes in the number of snipe stopping over on the island, implying that changes in weather conditions alter either the proportion of snipe deciding to stopover on North Ronaldsay or the number of birds successfully completing sea crossings. This suggests that future climate change may alter the dependency of migratory species on small island stopover sites, such as North Ronaldsay, as weather regimes become increasingly altered.

3.0 Using radio telemetry to investigate factors affecting Common Snipe *Gallinago gallinago* stopover duration, movement activity and habitat use on North Ronaldsay, Orkney

3.1 Abstract

Understanding how long birds spend at stopover sites during migration, as well as their habitat selection and movement activity during these periods, is important for understanding the decisions birds make to optimise time and energy use during migration. This study used manual radio telemetry to study the stopover behaviour of Common Snipe *Gallinago gallinago* on North Ronaldsay, Orkney during their autumn migration. We found considerable variation in the stopover durations of snipe, with some birds remaining at the site for over a month, although found no significant relationships between body condition, arrival date or age on stopover duration. We found that snipe often remained faithful to relatively small areas of the island during stopover, using patches of rough grassland or wetland during the day, often moving to more exposed areas such as beaches or patches of short grass during the night. Whilst we found no significant effects of body condition, arrival date or stage of stopover on snipe movement activity, we suggest studies with increased sample sizes and improved tag attachment methods may reveal negative correlations for the latter two variables. This study adds to previous evidence of high variability and flexibility in migration strategies in inland waders and shows how a diverse range of habitats on a small island allow a migratory species to remain at a stopover site for extended periods.

3.2 Introduction

Migratory species across a range of taxa have been documented to pause their migrations at particular sites, during a process known as stopover (Sawyer and Kauffman, 2011; Taylor et al., 2011; Grove et al., 2023). This is particularly well documented in birds, which primarily use stopover periods to replenish fat stores used to fuel migratory flight, recover from physiological stress and avoid periods of adverse weather conditions (Linscott and Senner, 2021; Schmaljohann et al., 2022). Research has shown that the majority of energy and time expenditure during migration occurs during stopover periods (Hedenström and Alerstam, 1997; Wikelski et al., 2003), meaning optimal use of these periods is critical to the success of a bird's migration. Therefore, it is important that key stopover sites are identified and that we understand how birds use these areas during migration in order to prioritise future conservation actions.

The decisions birds make at stopover sites form part of their overall migration strategy (Hedenström and Alerstam, 1997; Alerstam, 2011). Optimal migration theory predicts that birds will follow decisions that allow them to optimise time or energy expenditure during migration. Birds following time-minimising strategies generally stopover for shorter periods and accumulate fat at a greater rate, attempting to complete their migration in as few flights as fast as possible. Species following an energy-minimising strategy will stopover more frequently and for longer periods, accumulating fat at a relatively slow rate, aiming to minimise energy expenditure during migration (Hedenström and Alerstam, 1997). Therefore, studying stopover durations can provide indications of the type of strategy birds follow during migration, which may impact their response to climate change (Both and Visser, 2001; Rivalan et al., 2007).

Whilst being governed by their overall migration strategy, birds' stopover durations may be variable depending on other factors. Generally, birds will depart stopover sites during periods when weather conditions facilitate migratory flight. These include reduced precipitation, lower wind speeds, increased tailwind assistance and reduced cloud cover (Dänhardt and Lindström, 2001; O'Neal et al., 2018). Studies have shown that long distance migrants that follow a time minimising strategy often depart in less optimal weather conditions compared to shorter distance, energy-minimising migrants (Packmor et al., 2020), due to the increased pressure they face to complete migration within a certain timeframe. Birds that arrive at stopover sites in fat depleted states will usually remain at stopover sites for longer in order to restore fat reserves which enable them to achieve sufficient flight ranges to reach their next stopover destination (Schaub et al., 2008; Schmaljohann and Klinner, 2020). Studying stopover durations can also reveal the relative quality of stopover sites; in low quality stopover sites, birds with fuel loads allowing sufficient flight ranges usually depart quickly, although birds which are fat depleted may be forced to stay for longer periods (Domer et al., 2021).

Species with specific habitat requirements, such as wetland species, may exhibit greater plasticity in some aspects of their migratory strategies to enable them to cope with temporal and spatial variation in habitat and food resources along their migration route (Muraoka et al., 2009; Chevallier et al., 2011; Pearse et al., 2020). This has been demonstrated in a variety of taxa, including warblers, cranes, and waders, and may be reflected in stopover site choice, stopover durations or the timings of migratory flights (Muraoka et al., 2009; Hasselquist et al., 2017; Verhoeven et al., 2018; Malmiga et al., 2020; Pearse et al., 2020). Plasticity or flexibility in migratory strategy may allow birds to better adapt to future changes along their migration route (Gilroy et al., 2016), such as climate change or habitat loss due to anthropogenic development. However, the degree of flexibility in stopover behaviour is uncertain for many species and requires further research.

Over the past few decades, there has been rapid development in the technologies used to study birds' stopover behaviour. Telemetry-based studies have significant advantages over other traditional mark and recapture methods, such as ringing, due to the ability to readily distinguish between individuals and obtain precise estimates of their locations with relative ease. This allows more accurate determination of stopover duration and also allows determination of finer scale habitat use at stopover sites, including during nocturnal periods, which is difficult to assess using more traditional methods (Schofield et al., 2018; Kuang et al., 2019).

Understanding local scale habitat use and movement activity within stopover sites is important as it can reveal further insights into decisions individuals make to ensure that stopover periods are used in the most effective way, which impacts whether their migrations are successful or not (Alerstam, 2011; Smith et al., 2014). For instance, birds often exhibit increased movement during the first stages of stopover periods to assess the availability of habitats in the area (Chernetsov, 2006; Cohen et al., 2012). Birds arriving in more fat depleted states often exhibit greater movement activity during this period and may use a greater range of habitats, due to the increased need to forage (Moore and Aborn, 2000; Ktitorov et al., 2010). Similarly, birds may move around more in poor quality stopover habitats due to sparsely distributed food resources (Ferretti et al., 2019). Birds may depart such sites and move on to areas of more suitable foraging habitat in many cases (Maggini et al., 2020). Habitat use may vary between individuals of the same species due to differences in age or sex, along with differences in exploratory or boldness personality traits between individuals (Spiegel et al., 2017; van den Hout et al., 2017; Baert et al., 2018; Kuang et al., 2019). Studying the habitats birds use during stopover allows prioritisation of conservation actions by improving understanding of birds' requirements at stopover sites. Despite this, habitat use during migration stopover is understudied for many species and current knowledge is often based on studies at breeding or wintering locations (Kuang et al., 2019).

During migration, birds are often required to complete long flights across ecological barriers, such as the sea (Gill et al., 2009). These flights come with increased mortality risk due to the inability to stop at any point during their duration, along with the higher potential of encountering severe weather conditions and the lack of food availability (Strandberg et al., 2010; Lok et al., 2015). Stopover sites located before or after these crossings may be particularly important to birds' survival and consequently may have a high conservation value, despite often having relatively little foraging opportunities (Ferretti et al., 2021). Offshore islands are important examples of this, with birds often arriving at these sites in poor condition having completed significant sea crossings (Barboutis et al., 2022). Immediately following the crossing of ecological barriers, birds may be less selective in their habitat use, due to the primary need to rest and recover from the physiological impacts of long distance flights (Buler and Moore, 2011; Ferretti et al., 2021). Therefore, determining the relative functions of stopover sites situated at the boundaries of ecological barriers for migratory birds is important, since these sites may provide alternative or additional functions in comparison to other sites.

The Common Snipe *Gallinago gallinago* (from hereafter "snipe") is a species of wading bird with a widespread distribution across the Palearctic region, which breeds in areas of inland wetlands and moorlands. During the autumn, the populations which breed in northern Europe, Iceland and Russia migrate in an overall south westerly (or south easterly in the case of Icelandic populations) direction to wintering locations in southern Europe, Africa and the British Isles. Research has revealed distinct differences in migration routes between different populations of snipe (Svazas and Paulauskas, 2006; Minias et al., 2011), with the stopover behaviour of snipe migrating through central Europe being relatively well documented by ringing studies (Wlodarczyk et al., 2007; Meissner, 2003; Minias et al., 2011). These studies suggest that snipe migrating through these regions are energy-minimising migrants.

The stopover ecology of snipe populations migrating through north westerly regions of Europe has received comparatively little attention. Snipe from Iceland and Scandinavia undertake significant sea crossings as part of their southward migration to the United Kingdom and Ireland, meaning they encounter very different conditions to birds migrating through continental Europe (Svazas and Paulauskas, 2006; Gunnarsson and Tómasson, 2011). Studying these populations may reveal further variation in migratory strategy and stopover behaviour. Large numbers of snipe use the Northern Isles as stopover sites during migration (Boyd and Petersen, 2006; Andrews and Nightingale, 2021; Butcher, 2021), which may present an understudied situation where an energy-minimising migrant has been forced to complete a relatively long migratory flight.

This study used radio telemetry to investigate factors affecting individual variation in stopover behaviour in snipe on North Ronaldsay during the autumn of 2022. We aimed to determine the effects of weather conditions and arrival body condition on snipe stopover durations and additionally investigate snipe habitat use and movement activity during stopover. We hypothesised that stopover duration would be higher for birds that arrived in poorer body condition or during periods of adverse weather conditions, including increased rainfall and higher wind speeds. We also predicted that snipe would show increased movement during the earlier periods of stopover, due to initial searches for favoured habitats. Additionally, we expected birds in poorer body condition to exhibit increased activity due to the increased need to refuel.

3.3 Methods

3.3.1 Study site

Fieldwork was carried out on North Ronaldsay, a 6.9km^2 island located at the north-east extremity of the Orkney islands. The island has a rocky coastline interspersed with a few large sandy bays, with the interior of the island mostly used for agricultural purposes such as grazing livestock. There are also areas of rough grassland and several lochs, some of which are surrounded by extensive areas of irises (Pennington, 1988). The island is well-known as a hotspot for bird migration among birdwatchers and ornithologists, due to its remote location and relative positioning, which mean that birds migrating across the sea from regions such as Scandinavia and Iceland often make their first landfall there (Butcher, 2021).

3.3.2 Snipe capture methods and attachment of transmitters

Snipe were captured using one of three methods. The first of these involved capturing birds at dusk using mist nets positioned at known roost sites. The second method involved using walk-in “Ottenby style” traps, which were constructed from synthetic netting attached to metal frames using fishing line (see Figure S3 for trap design). We used the trap designs and advice detailed by Busse and Meissner (2015) as guides when designing our own traps. Guiding fences were created from wire mesh and metal frames, which were positioned to passively funnel birds into the traps (Figure S3). For both of these methods, snipe were lured to the trapping sites using playback of Common Snipe calls and drumming display sounds. Birds were also captured at night using the dazzling technique, which involved shining a torch at the birds, allowing them to be approached and caught with a hand net. After recording the date and time of capture, along with the capture method used, we fitted birds with a BTO ring, before determining their age and sex using standard methods. Wing length was measured using a ruler and body weight was recorded using scales. We estimated each bird's body fat by calculating the weight to wing ratio, dividing its weight (g) by its wing length (mm).

We then fitted birds with 1.95g radio transmitters (model: Holohil BD-2, average battery life: 14 weeks, battery life range: 10-20 weeks), which were attached to the birds' lower back feathers using cyanoacrylate glue (Loctite Superglue). To allow for comparison of early- and late-migrating individuals, we tagged birds over a range of dates through the autumn (Table S2). In total, we fitted tags to 11 birds (using nine transmitters, reusing two of the tags which became detached from birds and were refound). Tags weighed no more than 2.2g including applied glue. To adhere to the recommendation that tags should not exceed 3% of the bird's total bodyweight, we did not tag birds weighing under 85g. Following the attachment of tags, we held birds until the glue had dried and the tag was securely attached to feathers (approximately three to five minutes) and then released them either at the site of capture or at a designated safe release location at NRBO. NRBO staff and volunteers holding appropriate BTO ringing permits assisted with the capture and ringing of Snipe, although the fitting of radio tags and subsequent tracking was only carried out by persons holding the relevant BTO special methods endorsement specific to this project.

Following release, we located birds daily using a handheld radio receiver (model: Biotrack Sika) and a Yagi antenna during daylight hours. We also located birds at night at less regular intervals. We aimed not to flush birds when locating them to minimise disturbance. Upon locating a bird, we recorded its GPS coordinates and the type of habitat it was using. We continued to record the bird's location until the loss of detectable radio signal; at this point, we assumed that the bird had departed the island and resumed its migration. We recorded minimum stopover duration as the time between capture and assumed departure from the island. If a tag became detached from the bird before it had departed the island, we retrieved the tag and reused it where possible. In these cases, minimum stopover duration was recorded at the last date when we could be sure the tag was still attached to the bird. For each bird, we recorded whether the tag remained attached until departure or whether it fell off prior to this.

3.3.3 Analysis

We carried out data analysis using R version 4.2.0 (R Core Team, 2022). Using a generalised linear model, we tested for significant effects of wing length-corrected body mass, age and Julian date of capture on the minimum stopover durations of radio-tagged snipe. Additionally, we mapped use of the island by radio-tagged snipe using the leaflet package version 2.1.1 in R (Cheng et al., 2022) to visually assess habitat use during both day and night. We then predicted the effects of the number of days elapsed since capture (from hereafter ‘day of stay’), Julian date of capture and wing-corrected body mass on the distance travelled per hour between consecutive location fixes by tagged birds using a linear mixed-effects model, which included variation between individual birds as a random effect. We used the distance travelled per hour between each successful fix (as opposed to simply the distance between these) because birds were located at irregular time intervals. We calculated this by dividing the straight-line distance between consecutive fixes by the time elapsed between these.

3.4 Results

3.4.1 Stopover durations

The minimum length of stay of radio-tagged birds varied from 0.9 days to 33.9 days, with a mean of 14.2 days (dates of capture, assumed departure/tag detachment dates and biometrics for each radio-tagged bird are summarised in Table S2). Of the 11 birds tagged, five birds departed with the radio tag still attached, with five tags becoming detached before departure and one tagged bird remaining on the island at the end of the study period. The mean minimum length of stay of birds that departed with tags still attached was 12.0 days compared to 15.4 days for instances where an actual departure was not recorded (either the tag became detached, or the bird was still present at the end of the study). There were no significant effects of Julian date of capture, wing-corrected body mass or age on snipe stopover duration (Table S3).

3.4.2 Spatial use of the island

Birds used areas across the entire island during stopover, including both coastal and inland locations (Figure 4, Figure S4). Many birds appeared faithful to certain areas, often using the same areas repeatedly over several days. These birds also usually exhibited a separation between daytime and nighttime locations, which were located in distinct clusters. However, not all birds showed a clear separation between preferred nighttime and daytime locations, using the same locations during both day and night. Additionally, some birds moved more widely around the island than others, although no individual ranged over more than half of the island’s total area. The ranges of individual birds appear to form distinct largely non-overlapping clusters (Figure 4), which fieldwork observations suggest may correspond to different flocks, sometimes numbering well over 100 birds, which were found in the same locations consistently throughout the autumn in areas of suitable habitat.

Daytime locations included areas of rough grassland, areas of marshland (particularly in areas of irises surrounding lochs or pools) and less frequently grazed areas of short grass. Birds were often situated along the edges of ditches or streams or in patches of grass tussocks or irises. In larger areas of habitat, birds were often associated in loose flocks during the day. We did not usually see the birds when locating them with the radio receiver, with birds usually remaining tight to the ground and reluctant to fly. However, if we approached within 10-20m of the birds, they usually flushed, especially when associated in a flock. Night-time locations were often more exposed, including open areas of grazed short grass and coastal areas, such as beaches with patches of seaweed and rocky areas. However, some birds also used areas of rough grass and iris beds during the night, similar to the locations used during the day.

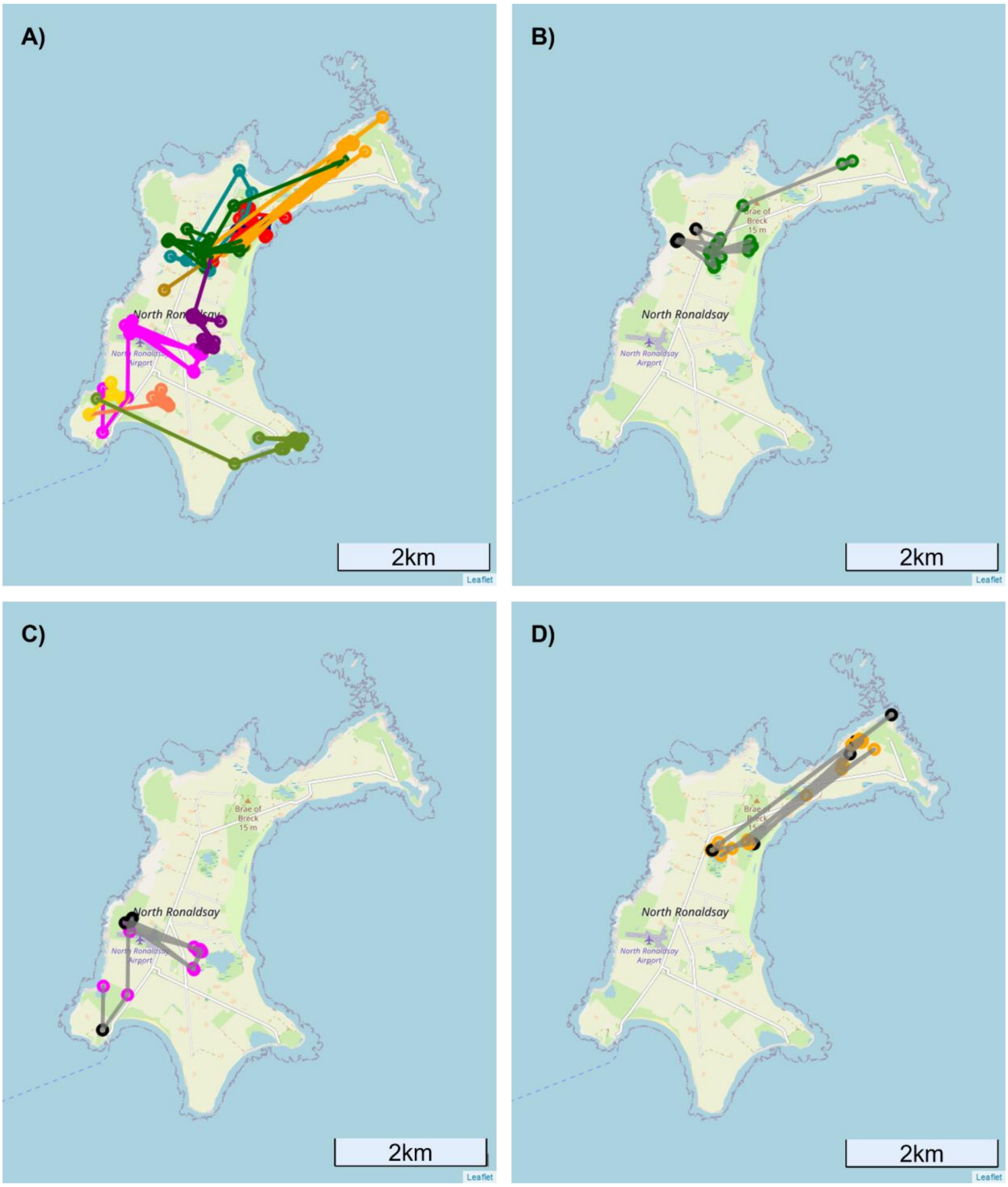

Figure 4. *Map of North Ronaldsay showing movements of radio-tagged Common Snipe Gallinago gallinago during migration stopover periods in autumn 2022.* ***A)*** *shows movements of all birds which were tagged during the study period, with each bird's indicated by a different colour. Circle markers indicate positions where birds were located and lines between these indicate the path between successive fixes.* ***B)*** *and* ***C)*** *show movements of two individual birds which exhibited the typical behaviour of birds observed in this study, favouring one location during the day (coloured circle markers) and another location during the night (black circle markers).* ***D)*** *shows an individual which exhibited a different behaviour,*

moving regularly over larger distances between two different areas, with no clear distinction between daytime (coloured circle markers) and nighttime (black circle markers) locations. For ***B)****,* ***C)*** *and* ***D)****, grey lines indicate paths between consecutive fixes.*

The mean distance travelled between successful fixes by each bird was 409m, with mean distances of 44.3m travelled per hour by each bird between successful fixes. We found no significant relationships between day of stay, Julian date of capture or wing-corrected body mass on the distance travelled per hour (Table S4). There was considerable variation in the distance travelled per hour between different birds (Figure 5), with some travelling less than others. Several birds, such as Snipe 1 and Snipe 3, travelled further distances during the first few days following capture, although this was not always the case, with other birds moving similar distances throughout their stopover duration. There appears to be a clear distinction between periods when birds were relatively stationary and periods when they suddenly moved further distances (Figure 5), with the distance travelled per hour for some birds fluctuating quite dramatically. Some birds travelled little for periods of up to 10 days (e.g., Snipe 4). Whilst the relationship between Julian date of capture and distance travelled per hour was not significant, there are indications that birds caught earlier in the autumn made the largest recorded movements and had the highest values for mean distance travelled per hour (Figure 5).

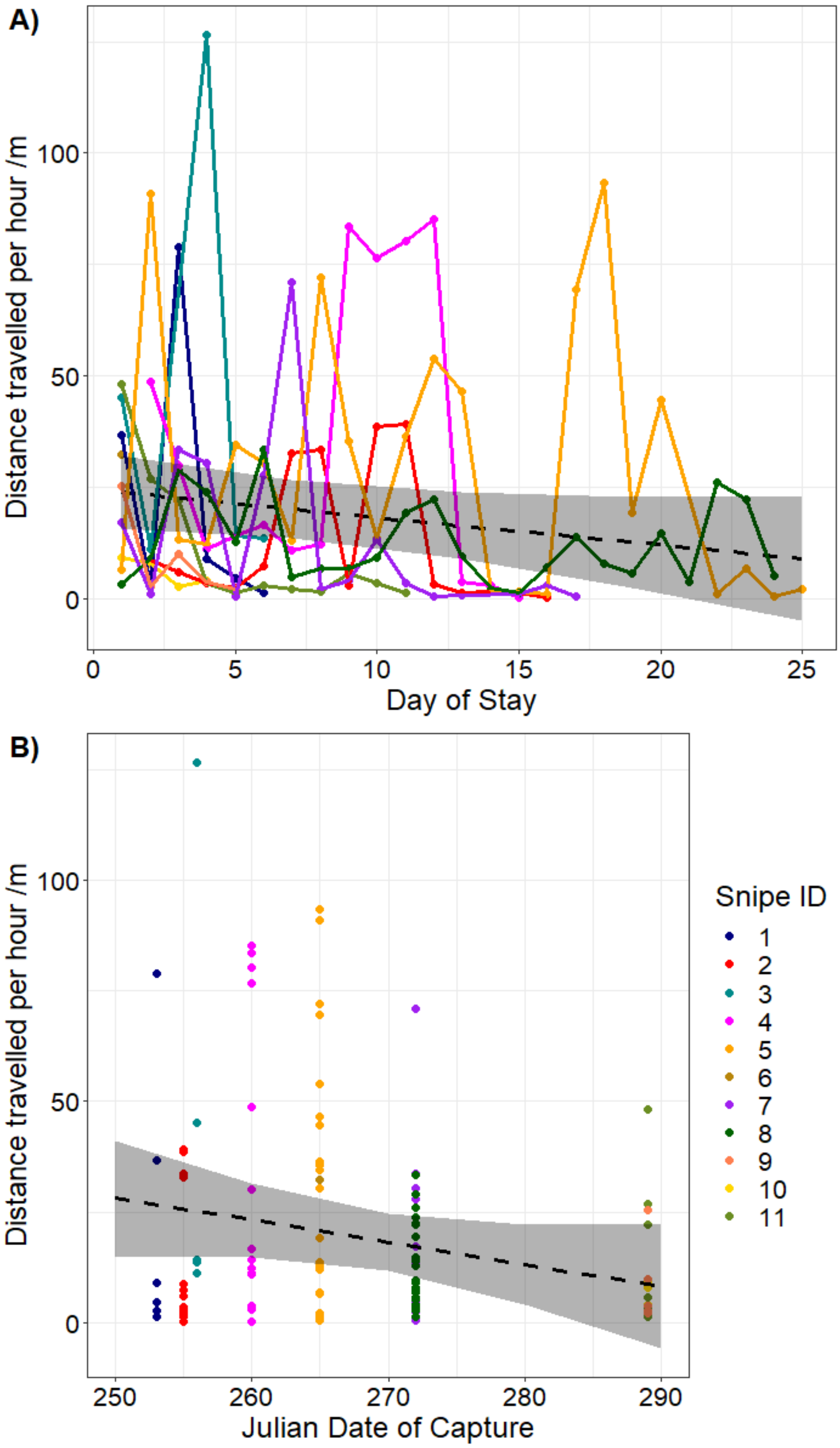

Figure 5. *Effects of A) day of stay (where the first day of stay is assumed to be the capture date) and B) Julian date of capture on the distance travelled per hour of radio-tagged Common Snipe Gallinago gallinago during stopover on North Ronaldsay. Dashed lines indicate the estimates for a linear mixed effects model of the effects of each variable on distance travelled per hour, with 95% confidence intervals indicated by shaded areas. Both*

day of stay and Julian date of capture have non-significant effects on the distance travelled per hour by snipe, although the plots hint a possible negative correlation exists for both variables.

3.5 Discussion

We found considerable variation in the minimum stopover durations of Common Snipe migrating through North Ronaldsay, with some birds departing after less than 5 days and some birds exhibiting unexpected patterns of residency, remaining at the site for over a month. Since we only recorded confirmed departures for five birds, it is likely that the small sample size of this study and the premature detachment of tags from birds were the most significant factors affecting the discovery of any statistically significant relationships. We found no significant relationships between wing-corrected body mass, Julian date of capture or age on birds' minimum stopover durations, in contrast to our original hypotheses. Snipe used habitats across the entire island, although they usually remained faithful to relatively small areas, with no individual ranging over more than half of the island's total area. Favoured areas during the day included patches of rough grassland and iris beds, whereas during the night, birds often used more exposed areas, such as beaches or patches of short grass. We found no significant effects of day of stay, Julian date of capture or wing-corrected body mass on the distance travelled per hour by snipe between consecutive fixes, which also did not align with our hypotheses.

The median length of stay of snipe recorded in this study is between five to eight days longer than the median stay recorded by studies of snipe in central Europe (Meissner, 2003; Wlodarczyk et al., 2007). The true value for median stopover duration of birds on North Ronaldsay is likely to be higher still due to tags falling off before birds departed. Along with the finding that some birds remained on the island for over a month, this suggests that snipe migrate through North Ronaldsay slowly, supporting previous findings that they exhibit behaviour of energy-minimising migrants (Meissner, 2003; Wlodarczyk et al., 2007) and suggesting similarities in migration strategy between snipe migrating through North Ronaldsay and populations that follow continental migration routes (Minias et al., 2011).

The fact that some birds remained on North Ronaldsay for longer periods suggests that the island contains relatively good quality refuelling habitat for migrating snipe, since birds did not move on after a short period. Studies on songbirds stopping over on coastal islands in the Mediterranean show that birds usually move on from these sites after short periods if sufficient foraging resources are not present (Maggini et al., 2022). Additionally, it is likely that snipe may have remained at the stopover site for longer periods than usual due to the need to recover from the physiological stress of sea crossings, which birds migrating through continental Europe do not have to endure (Minias et al., 2011). Common Snipe are relatively unusual among shorebirds since they carry out an extensive post-juvenile moult during migration and the extra energy requirements of moult may require juvenile snipe to spend more time refuelling at stopover sites than other species (Podlaszczuk et al., 2017). Extended periods of residency at stopover sites, which exceed the time periods required to carry out typical stopover functions, have been described in several migrant species and are hypothesised to be due to birds taking advantage of favourable conditions at a stopover site or populations following seasonal changes in resource availability throughout the non-breeding season (Stach et al., 2012; Tøttrup et al., 2012; McKinnon et al., 2013; Arlt et al., 2015; Roques et al., 2021). A long-term study may confirm whether the residency patterns in snipe observed in this study occur regularly and potentially uncover the drivers behind these.

Whilst many birds remained on the island for extended periods, there was considerable variation in the stopover durations of snipe, with some birds departing after just a few days. Similar variation in stopover duration has been found before in wetland species, such as Wood Sandpipers (Muraoka et al., 2009), and, along with variation in stopover site choice and migration timing, may be an indication of plasticity in migratory strategy in these species. Inland wetlands are ephemeral habitats and resource availability in these areas is often unpredictable due to fluctuations in weather conditions (Kingsford et al., 2004; Sergio et al., 2011). Therefore, this plasticity in migratory strategy may allow wetland birds to cope with the variable quality of stopover sites along their migration route (Muraoka et al., 2009; Pearse et al., 2020). Previous research shows that snipe may exhibit significant variation in migration timing and choice of non-breeding locations between different years (Glutz von Blotzheim et al., 1977; Meissner, 2000; Meissner 2003) in addition to the distinct differences in migratory route described between different populations (Svazas and Paulauskas, 2006; Minias et al., 2011). Plasticity in migratory strategy in snipe and other wetland species merits further study and may explain the large variation in stopover durations recorded by this study.

The lack of a significant relationship between wing-corrected body mass and stopover duration could be considered surprising as birds in poor condition might be expected to remain at the stopover site for longer periods. However, a previous study on snipe migrating through central Poland found that birds departed from the stopover site regardless of their refuelling rates (Wlodarczyk et al., 2007), suggesting that fuel reserves may not play such an important role in determining stopover durations in this species, which is typical of energy-minimising species (Alerstam and Lindström, 1990). Additionally, the lack of a significant relationship between Julian capture date and stopover duration in this study may be considered unexpected under optimal migration theory, since birds migrating later in the migration season may be under greater time pressure to reach their breeding or wintering grounds (Lyons and Haig, 1995). It is possible that unexpectedly warm weather experienced on North Ronaldsay during late autumn 2022 was responsible for this (Met Office, 2022), meaning late-migrating birds did not have to depart the stopover site as early as they would have under more typical conditions. Whilst these factors are all potential explanations for our results, the small sample size of this study introduces a significant caveat affecting the power of statistical tests. Therefore, further studies using greater sample sizes and improved tag attachment designs are required to determine the factors affecting stopover duration and migratory strategy in snipe using more northerly migratory routes.

A significant proportion of snipe appeared to exhibit a distinct daily routine in their spatial use of the island, using areas with more cover during the day and moving to more exposed locations during the night. It is likely that snipe chose areas of more dense cover, such as iris beds, ditches and rough grass during the day in order to evade predation. We propose that these sites were likely often daytime roost locations where birds slept or remained largely stationary. Previous research also shows that snipe spend long periods of time resting during stopover (Wlodarczyk et al., 2007) and this may be of increased importance for birds which have just completed a sea crossing. The more exposed locations chosen during the night were likely areas where birds went to feed and included patches of seaweed or short grass, which may have contained improved feeding opportunities due to either higher concentrations of invertebrates present or increased detectability of prey (Devereux et al., 2004; Aldabe et al., 2019). The cover of darkness may have allowed birds to feed in these more exposed locations by providing protection from predation. Nocturnal foraging habits have been recorded numerous times in Common Snipe (Davies, 1977; McNeil et al.,1992), although they may be equally likely to feed during the day also (Thomas et al., 2006). Waterbirds have been shown to increase nocturnal foraging during migration due to not being able to meet their increased energy requirements during this period with solely diurnal foraging (Santiago-Quesada et al., 2014). Combined with the exposed nature of the habitats on North Ronaldsay and birds' increased need to rest after completing sea crossings, this may cause snipe to spend significantly more time foraging during the night.

It is unclear why some birds did not follow this activity pattern and showed no distinction between daytime and nighttime locations. Potential explanations for this could be differences in personality between individuals, with bolder individuals opting to forage during both day and night (Spiegel et al., 2017). Morphological differences between individuals may also explain this; wing shape has been previously shown to be associated with different snipe stopover strategies (Minias et al., 2013) and in this instance it may be that birds with wing shapes more well adapted for predator evasion were able to forage during the day as well as the night. Individuals in poorer body condition may be forced to increase foraging activity during the day in addition to nocturnal foraging, although we cannot confirm this using our data due to the low sample size. A simpler explanation could be that the habitats these individuals used functioned well at providing both protection from predation and foraging opportunities, so birds did not need to move to different locations at night.

Whilst we found no significant relationships between day of stay or Julian date of capture on the movement activity of snipe during our study, our results hint that a negative correlation may exist between these variables (Figure 5), which could be revealed by a study using increased sample sizes. This would align with previous research which concludes that birds often exhibit increased movement activity during the earlier stages of their stopover (Chernetsov, 2006; Cohen et al., 2012; Smith and McWilliams, 2014). A significant limitation of investigating the effect of day of stay on movement activity of snipe in this study was that we could not be sure of birds' true arrival date to the stopover site, forcing us to use the date of capture as the assumed arrival date. Relationships between Julian date and movement activity in birds during stopover have also been found in a previous study (Schofield et al., 2018), which suggested seasonal changes in weather conditions and food resources as likely explanations. However, most studies into movement activity during stopover periods focus on songbirds, meaning further research is required for other groups. Research into the factors causing variation in habitat choice at the individual level during stopover remains relatively scarce so we encourage future studies to focus on this (Kuang et al., 2019).

A large proportion of the transmitters used in this study fell off before birds departed the island, which introduces several limitations. One of the most notable of these is that the true stopover durations of birds whose tags fell off prematurely may have been considerably longer than recorded, especially when one considers that the birds may have also been present on North Ronaldsay for some time before capture. This may have affected the finding that there were no significant effects of Julian date of capture, wing-corrected body mass or age on snipe stopover duration (Table S3). Also, the potential negative relationship between day of stay and movement activity of snipe (Figure 5A) may have been a consequence of more mobile birds exhibiting a higher chance of tag detachment, assuming tag detachment is more likely during the sudden movements of take-off and landing. Another explanation for this could be that more mobile birds departed the stopover site earlier. Additionally, we did not have sufficient data to analyse the conditions affecting departure decisions of snipe from North Ronaldsay. Future studies using a greater sample size and refined tag attachment method may wish to focus on this, since this may reveal further insights into the stopover behaviour of snipe, specifically following the crossing of ecological barriers. Recent studies have used a survival analysis approach, using Cox Proportional Hazards models, to analyse this type of data, with this being successfully used in the study of songbirds (Dossman et al., 2016; Morbey et al., 2018) and shorebirds (Herbert et al., 2022).

The tag retention time range recorded by our study is similar to previous studies fitting glue-mounted radio tags to Common Snipe, with Green (1998) achieving a retention time of between 4 and 44 days. This suggests that this method produces unreliable retention times when used on snipe and we therefore encourage further comparisons of tag attachment methods for snipe and similar species (Mong and Sandercock, 2007) in order to determine the most appropriate method for this type of study. This would help to address the issue of tags falling off prior to departure. Addressing the issue of determining the exact arrival date of snipe is more problematic when using a method where birds are tagged at the stopover site. One way to reduce this issue would be to only tag birds during days when there are sudden increases in the number of snipe present, meaning there would be a higher chance of tagging a freshly arrived bird. Fitting GPS tags to birds at breeding grounds would theoretically allow their entire migration to be followed, meaning exact arrival dates at stopover sites could be determined. However, in most cases it would be impossible to know which stopover sites a bird would use, meaning this method would not be appropriate for studies focussing on a specific stopover site.

A limitation of using manual radio telemetry to assess habitat use and movement activity of snipe was that we could only locate birds a limited number of times per day. This may have caused our results not to be representative of birds' behaviour over the entire day, since birds may have moved to other locations undetected. Additionally, some birds may have moved greater distances per day than our results suggest, since we could only calculate the straight-line distance between consecutive fixes. It is also difficult to make more detailed inferences about birds' behaviour from simple single location fixes, meaning we can only speculate whether snipe were using areas for roosting, feeding or other purposes. Using automated radio telemetry or other recently developed technologies that allow birds to be located more frequently, such as GPS transmitters, would allow a greater quantity of data to be collected and improve its accuracy compared to the methods used in this study (Schofield et al., 2018).

Overall, snipe migrating through North Ronaldsay likely use an energy-minimising strategy, similar to snipe populations which migrate using other routes (Minias et al., 2011). We found large variation in snipe stopover durations, providing further suggestions that the species exhibits considerable flexibility in its migratory strategy. However, the detachment of tags and small sample size of this study mean that further research is required to accurately determine the factors affecting departure decisions and movement activity in more northerly snipe populations. Birds arriving on the island are likely to have completed significant sea crossings and this, along with the range of foraging opportunities and roosting habitats, may explain why birds remain at the site for extended periods, as opposed to relocating to other sites. The variation in habitat choice between different individuals and during different times of day highlights the importance of maintaining habitat diversity at stopover sites for migratory birds.

4.0 General Conclusions and Discussion

4.1 Summary of findings

This thesis aimed to investigate the factors affecting stopover behaviour of Common Snipe migrating through North Ronaldsay. I addressed prior knowledge gaps in snipe migratory behaviour by focusing on snipe following understudied migration routes in the northerly part of their range. Through this, I also aimed to contribute to understanding of plasticity in bird migration strategies and the function of small island stopover sites, both of which have received relatively little research attention.

Chapter 2 investigated the effects of weather and time of year on the number of snipe present on North Ronaldsay over the annual period. The study demonstrated how migrant bird observation data collected by bird observatories and similar organisations can be used to model daily changes in numbers of migrant bird species present at stopover sites. The results show that snipe numbers increase during the expected spring and autumn migration periods, although the autumn peak involved a much greater number of birds. This suggests that either snipe migrate through North Ronaldsay in a much greater intensity during this time or a greater proportion of birds choose to stopover on the island. Whilst it is likely that the addition of juvenile birds during the autumn is partially responsible for this, it may be that snipe adopt different migration strategies during spring and autumn. This could involve following different migration routes or alternatively adopting a time-minimising strategy during spring, where the number of stopover sites is reduced, leading to fewer birds stopping on North Ronaldsay or using it under a more specific set of conditions. Alternatively, this may be due to the close proximity of North Ronaldsay to the Scottish mainland in comparison to its location in relation to Scandinavia or Iceland. During the autumn, southwards migrating snipe are likely to have been travelling for considerably longer distances over the sea than northwards migrating snipe during the spring, meaning they have a greater need to locate a stopover site. This would suggest that the location of small islands in relation to larger land masses affects their role as a stopover site and that birds are more likely to use these sites following longer sea crossings.

The results in Chapter 2 showed that increasing precipitation led to increases in snipe numbers on North Ronaldsay, which could likely be due to the deterioration of flight conditions. However, this explanation is not consistent with the trends shown by other weather conditions; for instance, the decrease in snipe numbers with increasing wind speeds contradicts this explanation. It is likely that observation effects had a greater influence on snipe counts in this case, with increasing wind speeds making it harder to accurately locate and count birds. Contrary to our predictions, wind direction appeared to have a minimal effect on snipe numbers. This suggests that either snipe are not particularly selective in their choice of local wind directions for stopover site departure or that snipe do not require significant tailwind assistance when completing sea crossings to or from Scandinavia or Iceland. Whilst radar studies show that overall migration intensity across the North Sea is often dependent on wind assistance (Manola et al., 2020; Bradarić et al., 2020), the results here suggest this may not be the case for all species. I conclude that the effect of weather on suitability of flight conditions likely plays a part in snipe stopover decisions, although this does not appear to apply to all weather conditions.

Chapter 3 investigated individual variation in stopover behaviour in snipe migrating through North Ronaldsay in autumn. Whilst there were no significant effects of body condition, Julian date of capture or age on stopover durations, it is likely that premature tag detachment and the low sample size of this study reduced the power of statistical tests carried out. Therefore, I am cautious to accept these results as conclusive and suggest that further research is required. However, the median stopover durations recorded by this study are similar in length to those recorded by previous studies into snipe stopover behaviour (Meissner, 2003; Minias et al. 2011), indicating that snipe following more northerly migration routes also adopt an energy-minimising migration strategy. The results also suggest that snipe exhibit high variability in some aspects of their stopover behaviour, with some birds remaining for long periods and others leaving within a couple of days. This provides further indications that inland wetland birds exhibit considerable flexibility in their migration strategies (Muraoka et al., 2009; Malmiga et al., 2020; Pearse et al., 2020), which may suggest that the distribution of a species' preferred habitat and predictability of resources within this have an influence on birds' migration strategies.

Chapter 3 also shows that small islands can provide sufficient resources for migrating birds to stopover for extended periods, as opposed to moving on to more profitable areas once they have recovered from the previous sea crossing. Recent research into passerine stopover behaviour on Mediterranean islands suggest that these sites are often characterised by limited foraging opportunities and mainly used for short periods by exhausted birds which are unable to fly any further (Maggini et al., 2020; Barboutis et al., 2022). However, the results presented in Chapter 3 suggest that this may not always be the case, especially for non-passerine species with different habitat requirements to songbirds. This suggests that small islands may be used by migrating birds for a greater range of functions than just rest and physiological recovery. Additionally, this adds to previous research indicating that the occurrence of short-term residency periods during migration is more frequent than previously thought and suggests that stopover sites are not always used solely for traditional refuelling and recovery purposes (Stach et al., 2012; Tøttrup et al., 2012; McKinnon et al., 2013; Arlt et al., 2015; Roques et al., 2021).

Studies assessing stopover habitat use during both day and night are valuable, since, as demonstrated in Chapter 3, birds may select distinctly different habitats during the nighttime. Snipe exhibited a distinct routine in their movement and habitat use on North Ronaldsay, with assessment of their nighttime activity made possible through the use of radio telemetry. This shows that studying habitat use using purely observational methods during the day may cause key areas of habitat to be neglected by conservation planning. Whilst the results do not show a significant change in birds' movement activity over the course of their stopover periods or depending on the time of year, this may be a consequence of the low sample size, since previous research has found clear relationships between these variables (Chernetsov, 2006; Cohen et al., 2012; Schofield et al., 2018).

Chapter 2 allowed me to estimate the timing and frequency of sightings of snipe on North Ronaldsay, whereas Chapter 3 allowed me to estimate the distribution of stopover lengths of individual snipe passing through North Ronaldsay. Combined, these two datasets should allow an estimate of the true numbers of individual snipe that make use of the island during the autumn season. The easiest way to estimate total snipe numbers would be to parameterise a simple mixture model of N individuals with arrival dates assumed to follow a log-normal distribution and individual stopover durations following an exponential model fitted to the observed stopover durations of tagged individuals. Since the sample size used in the collection of stopover durations in Chapter 3 was too small to justify a detailed analysis, I developed a toy model to demonstrate how this approach could be used in future studies with more detailed stopover duration information. Using an estimate of 1500 snipe and a mean arrival Julian date of 280 and standard deviation of 30 for the log normal arrival date, I found a plausible looking estimate (when comparing this to arrival timings shown by the model output in Figure 2 from Chapter 2) of the number of birds that use the island as a stopover site over the entire autumn migration period each year (Figure 6). During some years, this must be significantly higher, since census counts recorded by NRBO occasionally reach over 800 birds on peak days during some years. It is likely that coinciding of optimal weather conditions (e.g., high precipitation causing more birds to land and lower wind speeds leading to improved observation conditions) with the peak timing of snipe migration led to higher counts in these years. Whilst this number is relatively small compared to the total wintering population of snipe in the United Kingdom (Musgrove et al. 2011, Musgrove et al. 2013), when considering the small size of North Ronaldsay (6.9km^2) and the number of surrounding islands with the potential to host similar numbers of snipe, this suggests that the Northern Isles are an important group of stopover sites for this species.

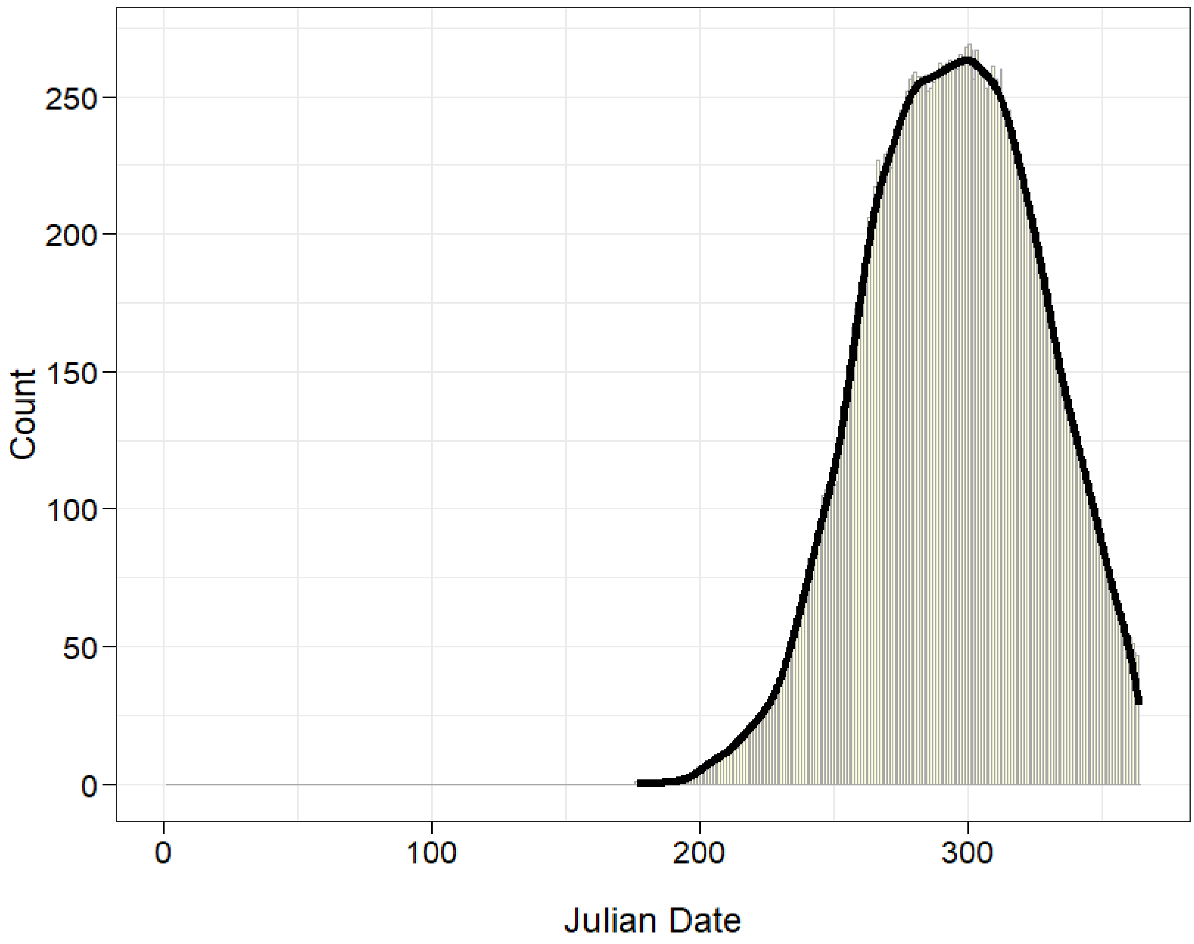

Figure 6. *Theoretical snipe counts during autumn migration on North Ronaldsay produced using a simple mixture model produced using estimates of snipe arrival timings and stopover durations. The model assumes a total of 1500 individuals were present throughout the migration period, with arrival dates assumed to follow a log-normal distribution (mean: 280, s.d.: 30) and individual stopover durations following an exponential model fitted to the observed stopover durations of tagged individuals (mean of lognormal distribution for stopover durations: 2.28, s.d.: 1.06).*

Understanding the causes, timing, and mechanisms of species movements, such as migration, are key topics in movement ecology research (Nathan et al., 2008; Mandel et al., 2011). Recently there has been a rapid increase in the number of studies using tracking devices to study movements of species at the individual level, which allows a greater understanding of how and why organisms move (Wilmers et al., 2015; Joo et al., 2022). Chapter 3 exemplified how telemetry-based methods can reveal insights into the timing of migratory movements by a species and the level of variation shown between individuals. It also detailed some of the issues researchers may face when using tracking devices in movement ecology studies, such as premature tag detachment, and those wishing to carry out future tracking studies on related species may benefit from reading about the specific issues encountered here. The conservation importance of movement ecology research is increasingly being recognised (Fraser et al., 2018; Katzner and Arlettaz, 2020) and this chapter added further evidence to this, showing how studying fine scale movements by individuals can reveal important habitats used by species during migration. This could inform conservation actions by allowing identification of key areas to protect, as well as determining appropriate habitat management strategies for target species. Moving away from the individual level, Chapter 2 demonstrated how a combination of observation and meteorological data can be used to understand the timing of movements of species over the annual period and how this varies with changes in environmental conditions. This is an essential consideration when predicting how species movements will be affected by climate change and the methods used in this chapter could easily be applied to other species and locations.

4.2 Future directions

Due to the premature detachment of tags and the small sample size used, Chapter 3 did not investigate the effects of weather on stopover departure probabilities in snipe on North Ronaldsay. This would have provided information about how snipe adjust their stopover behaviour in response to variation in weather conditions. I encourage future research to investigate this in both snipe and other inland wetland species, since this may reveal further insights into the stopover strategies in these taxa. Understanding if birds can adjust their migration strategies in response to variation in environmental conditions is an important consideration when predicting their response to future climate change (Gilroy et al., 2016). Further studies with increased sample size may also reveal if the potential relationships between the stage of stopover and time of year on snipe movement activity that we suggest in chapter 3 exist. Similar findings have been demonstrated in studies focusing on passerine species (Chernetsov, 2006; Cohen et al., 2012; Schofield et al., 2018), although few studies have investigated individual variation in movement activity during stopover in non-passerines, despite this being an important aspect of how birds optimise their stopover behaviour.

Since manual radio telemetry remains one of the more cost-effective telemetry-based methods of studying stopover behaviour, I encourage further studies investigating optimal transmitter attachment methods in snipe and similar species. Whilst glue-based attachment methods have been successfully used to study stopover behaviour in many species, this method provided insufficient retention times for our study. Harness-based methods may merit further investigation, although these often produce retention times which far exceed the time required for studies of stopover behaviour (Mong and Sandercock, 2007) and can pose health risks to long-billed species in some cases; for example, backpack loop harnesses have been shown to cause mortality in Woodcock due to birds' bills being caught in the harness loops (Duriez et al., 2006). A refined tag attachment method that achieves appropriate retention times for studies of stopover behaviour but does not significantly increase mortality risk is therefore required.

Using GPS tracking to study snipe stopover behaviour over the entire migratory period and across entire flyways would provide significant advances in understanding of snipe migratory behaviour. The majority of current research into snipe stopover behaviour, including this project, focuses on behaviour at a single stopover site or region, which limits the ability to understand how individuals vary their stopover responses across different conditions. Long term studies would likely be more suited for this, since birds would be subjected to a greater range of conditions. Long term telemetry studies are currently relatively scarce, although as technologies such as automated radio telemetry and GPS transmitters continue to advance such studies will become increasingly feasible (Flack et al., 2022). Further aspects of snipe migration strategies could be studied using this method, such as migration route and stopover site fidelity between years and factors affecting the timing of migration.

Since current research suggests that inland waders may exhibit increased flexibility in aspects of their migration strategy compared to coastal waders (Muraoka et al., 2009), further research into how habitat choice affects migratory behaviour may generate some useful insights. This could be done by comparing factors affecting stopover durations or stopover site choice in closely related species with contrasting habitat requirements. Similarly, I suggest that establishing habitat choice preferences during stopover for species in which this currently remains unknown may provide useful information from a conservation perspective, since this may differ from typical habitat requirements during non-migratory periods (Kuang et al., 2019).

I encourage future research to make use of data collected by bird observatories and similar organisations for the study of migration timings and stopover responses to weather. The model approach in Chapter 2 could readily be applied to any species recorded migrating through North Ronaldsay or other stopover sites where similar data are recorded. Future studies may wish to build upon this model by including a greater number of study species or comparing species which specialise in different habitats. Using mixture models to estimate the number of birds passing through stopover sites through combinations of telemetry data and count data (e.g., bird census counts), as in the toy example I presented in the previous section, could be another useful future direction. Such studies could allow direct comparisons of migration intensity between different stopover sites and how this varies across the annual period. This may help to identify key stopover sites for different species, which will help to establish which areas to focus conservation efforts.

Impacts of climate change have already been documented in migratory bird populations, which may be particularly vulnerable to this due to their reliance on multiple locations throughout the year (Newton 2004; Vickery *et al.* 2014; Zurrel *et al*. 2018; Sergio *et al.* 2019; Kubelka *et al.* 2022). Consequently, it is critical that future research continues to document how migratory species respond to environmental change, as well as investigate the mechanisms that govern birds' migration strategies. This will help to establish appropriate conservation priorities so that further population declines in these species are minimised.

Appendices

Table S1. *Summary of covariates used in generalised additive models to model effects of Julian date, observation hours and weather variables on snipe census counts on North Ronaldsay. Definitions are given for covariates where appropriate.*

Covariate	Definition
Julian Date	-
Coverage	Number of observations hours each day
TEMP	Mean maximum temperature recorded each day
PRECIP	Total daily rainfall accumulation
WINDSP	Mean wind speed recorded each day
ICOUNT	Proportion of hours each day where wind direction was recorded between 270° and 0°
SCOUNT	Proportion of hours each day where wind direction was recorded between 45° and 135°
NWCOMP	Mean north-westerly wind component calculated using cos(x+45°)
ECOMP	Mean easterly wind component calculated using sin(x°)

Covariate	Definition
SEASON	Classifies observations as either “spring” (Julian date <180) or “autumn” (Julian date >= 180)

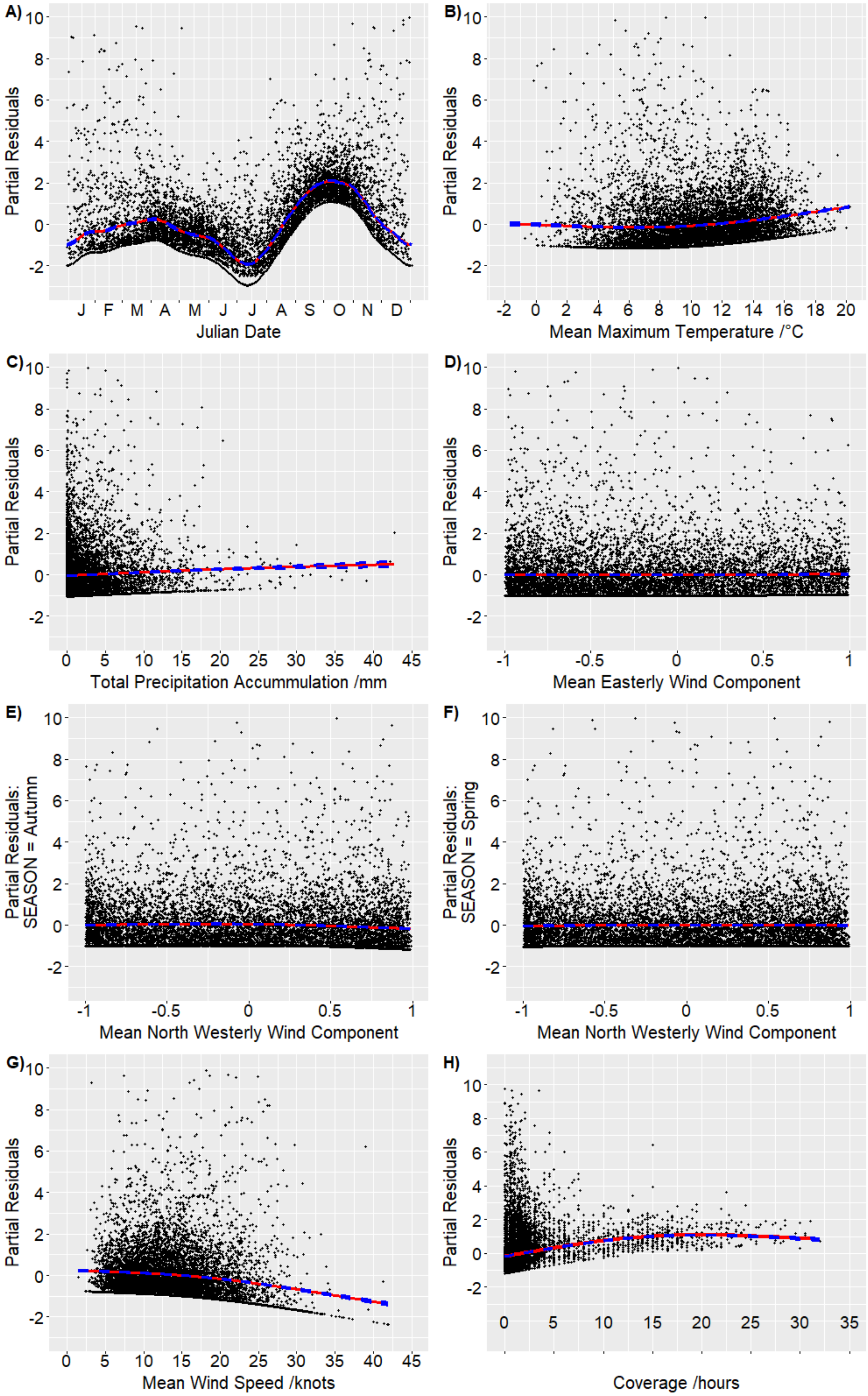
A)
Partial Residuals
Julian Date
J F M A M J J A S O N D
B)
Partial Residuals
Mean Maximum Temperature /°C
C)
Partial Residuals
Total Precipitation Accummulation /mm
D)
Partial Residuals
Mean Easterly Wind Component
E)
Partial Residuals: SEASON = Autumn
Mean North Westerly Wind Component
F)
Partial Residuals: SEASON = Spring
Mean North Westerly Wind Component
G)
Partial Residuals
Mean Wind Speed /knots
H)
Partial Residuals
Coverage /hours

***Figure S1.** Plots showing partial effects of generalised additive model (full model 1) covariates on daily Common Snipe Gallinago gallinago numbers on North Ronaldsay, Orkney. The fitted generalised additive mixed model considers Julian Date (A), weather variables (B-G) and the number of observation hours (H) as covariates and includes a temporal autoregressive component to consider the effects of the number of snipe present during the two days prior to the focal day on each snipe count. In each plot, the red line shows the partial effect, with blue dashes indicating 95% confidence intervals and black dots indicating plotted partial residuals.*

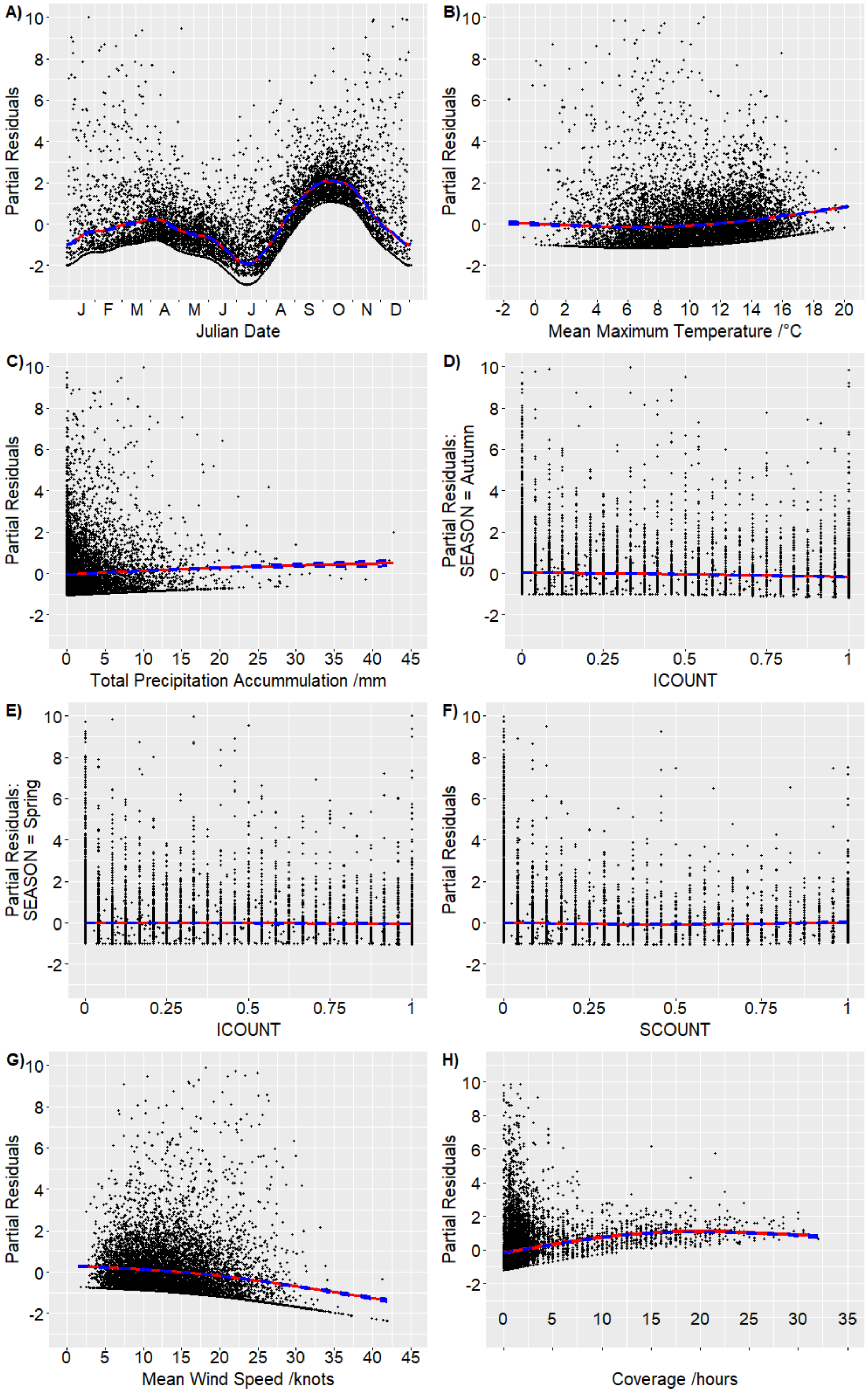
A)
Partial Residuals
-2
0
2
4
6
8
10
J F M A M J J A S O N D
Julian Date
B)
Partial Residuals
-2 0 2 4 6 8 10 12 14 16 18 20
Mean Maximum Temperature /°C
C)
Partial Residuals
0 5 10 15 20 25 30 35 40 45
Total Precipitation Accummulation /mm
D)
Partial Residuals:
SEASON = Autumn
0 0.25 0.5 0.75 1
ICOUNT
E)
Partial Residuals:
SEASON = Spring
0 0.25 0.5 0.75 1
ICOUNT
F)
Partial Residuals
0 0.25 0.5 0.75 1
SCOUNT
G)
Partial Residuals
0 5 10 15 20 25 30 35 40 45
Mean Wind Speed /knots
H)
Partial Residuals
0 5 10 15 20 25 30 35
Coverage /hours

Figure S2. *Plots showing partial effects of generalised additive model (full model 2) covariates on daily Common Snipe Gallinago gallinago numbers on North Ronaldsay, Orkney. The fitted generalised additive mixed model considers Julian Date (A), weather variables (B-G) and the number of observation hours (H) as covariates and includes a temporal autoregressive component to consider the effects of the number of snipe present during the two days prior to the focal day on each snipe count. In each plot, the red line shows the partial effect, with blue dashes indicating 95% confidence intervals and black dots indicating plotted partial residuals.*

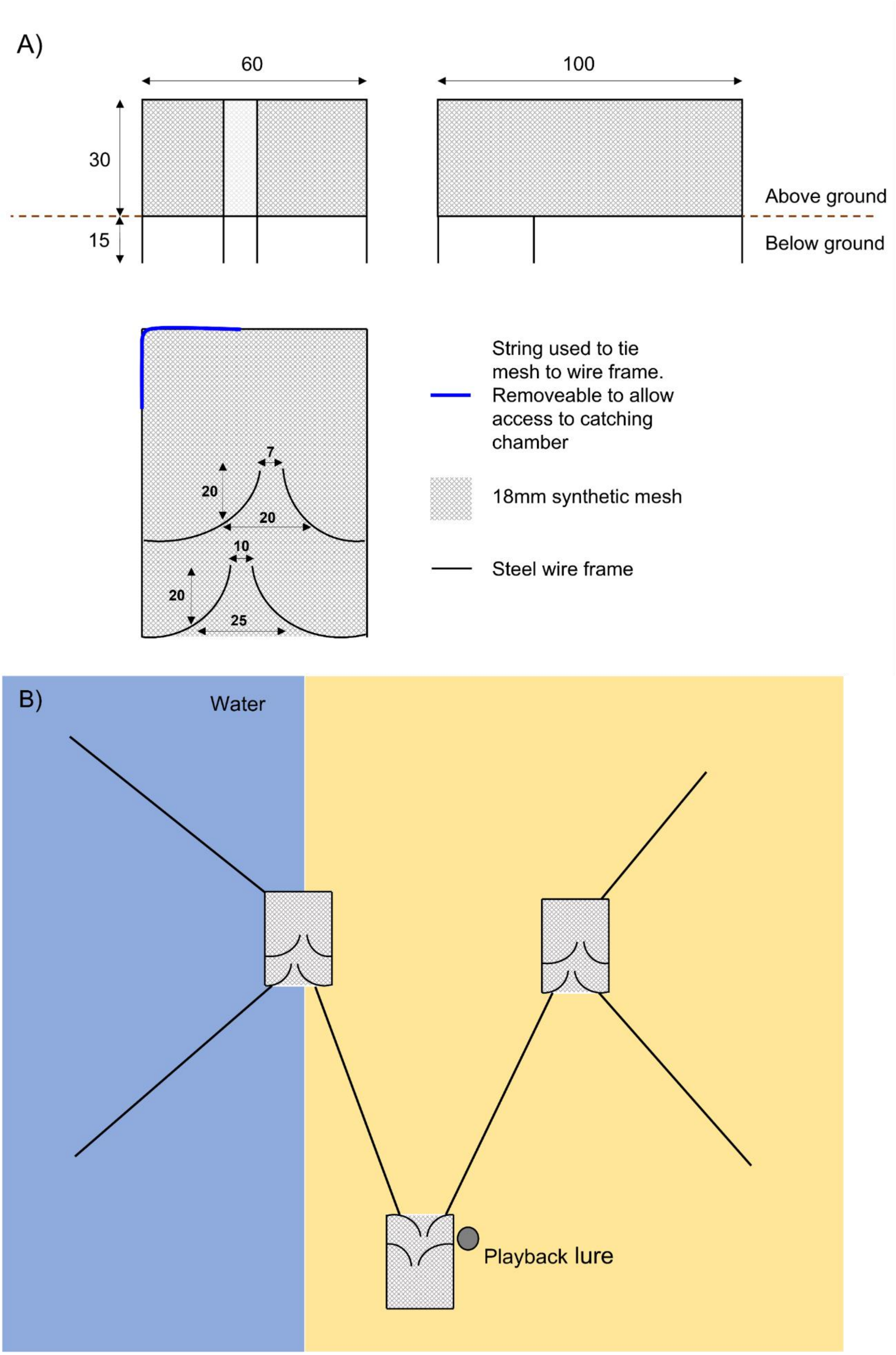

Figure S3. *A) Design of walk-in traps used to capture Common Snipe Gallinago gallinago on North Ronaldsay during autumn 2022. Trap dimensions are given in centimetres. Traps were* *created using 18mm synthetic mesh and frames created using steel wire. Mesh was attached to the wire frames using fishing line.* ***B)*** *Optimal placement of walk-in traps, hexagonal wire mesh baffles and a playback lure to maximise catches of Common Snipe. Wire baffles are represented by black lines between traps. Baffles had an average length of 2m. For traps placed on the water's edge or in damp areas, rocks and grass were placed inside the catching chambers to prevent birds from getting wet.*

Table S2. *Dates of radio tag attachment, capture methods, biometrics and assumed departure or tag detachment dates for radio-tagged Common Snipe Gallinago gallinago caught on North Ronaldsay during autumn 2022.*

Ring number	Date-time of tag attachment	Capture Method	BTO age code	Body mass /g	Wing length /mm	Weight to wing ratio	Assumed departure or tag detachment date-time
LN79253	10/09/2022 14:25	mist net	4	94.9	139	0.68	15/09/2022 10:00
LN79255	12/09/2022 14:55	mist net	3	108.7	140	0.77	27/09/2022 12:40
LN79256	13/09/2022 18:50	walk in	3	101.1	135	0.75	17/09/2022 22:00
LN12279	17/09/2022 18:50	walk in	4	110	140	0.79	01/10/2022 08:45
LN79262	22/09/2022 15:51	walk in	3	102.6	138	0.74	22/10/2022 09:30
LN79263	22/09/2022 17:36	walk in	3	100.6	141	0.71	23/09/2022 15:50

Ring number	Date-time of tag attachment	Capture Method	BTO age code	Body mass /g	Wing length /mm	Weight to wing ratio	Assumed departure or tag detachment date-time
LN79282	29/09/2022 13:35	walk in	3	102.5	130	0.79	19/10/2022 21:00
LN79283	29/09/2022 13:40	walk in	3	118.3	131	0.90	02/11/2022 12:00
LN12292	16/10/2022 20:30	dazzle	2	114.2	136	0.84	25/10/2022 20:40
LN12291	16/10/2022 20:45	dazzle	4	124.1	137	0.91	22/10/2022 09:30
LN12290	16/10/2022 20:00	dazzle	3	105	140	0.75	05/11/2022 11:30

Table S3. *Analysis of deviance table for generalised linear model testing the significance of weight to wing ratio, Julian date of capture, age and whether tags fell off prematurely on the stopover durations of Common Snipe Gallinago gallinago on North Ronaldsay.*

Explanatory Variable	*Df*	*Deviance Resid.*	*Df*	*Resid. Dev.*	*Pr(>Chi)*
NULL	-	-	10	1166.22	-
Weight to wing ratio	1	116.602	9	1049.62	0.3592
Julian date of capture	1	8.035	8	1041.59	0.8098
Age	2	304.493	6	737.10	0.3337

Explanatory Variable	*Df*	*Deviance Resid.*	*Df*	*Resid. Dev.*	*Pr(>Chi)*
Fell off?	1	43.462	5	693.63	0.5757

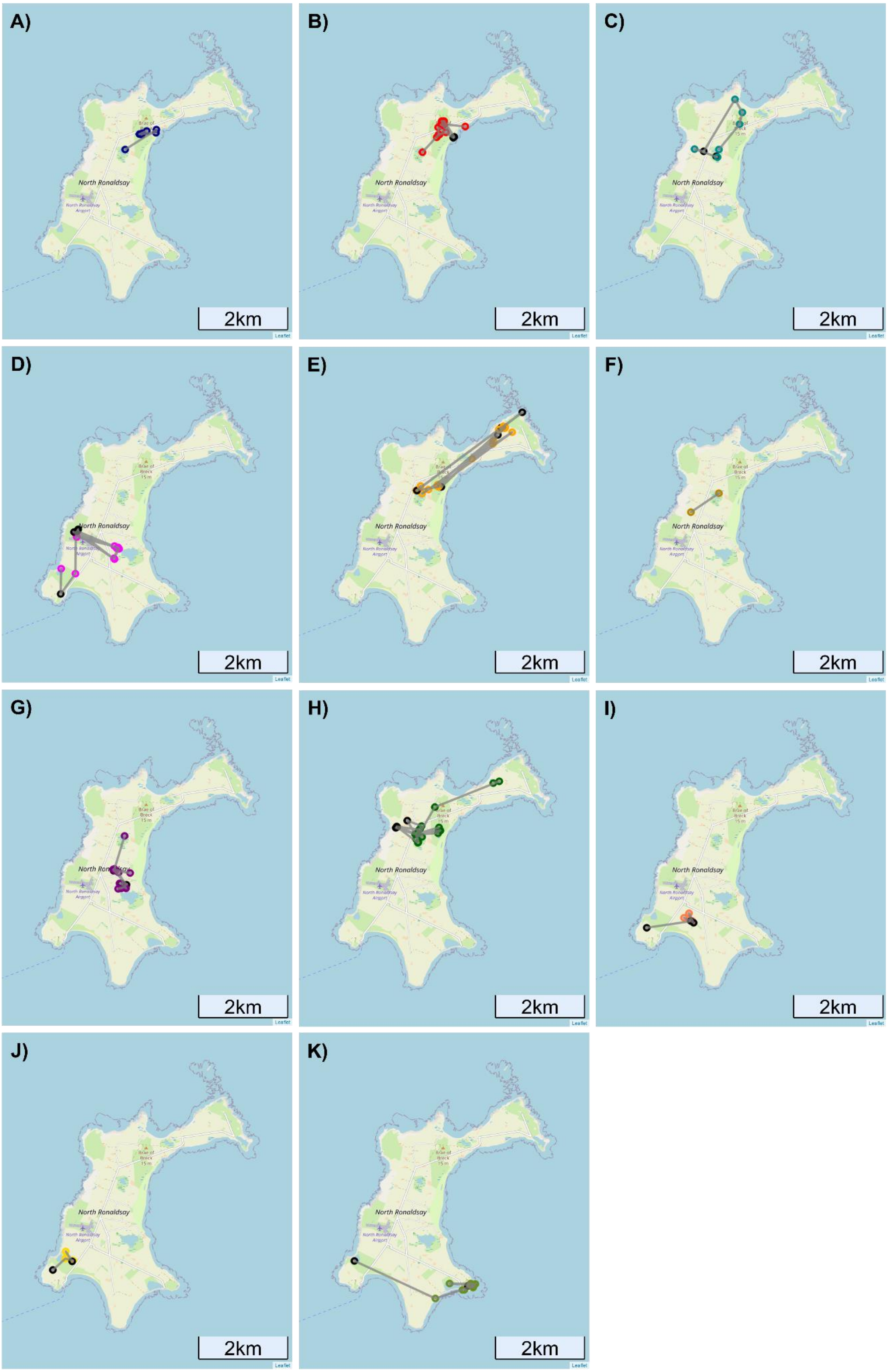
A)
B)
C)
D)
E)
F)
G)
H)
I)
J)
K)
North Ronaldsay
North Ronaldsay Airport
Brae of Breck 15 m
2km
Leaflet

Figure S4. *Movements of radio-tagged Common Snipe Gallinago gallinago on North Ronaldsay during stopover in autumn 2022. Each map A-K) represents a different individual. For each bird, daytime fixes are shown by coloured circle markers and nighttime fixes are shown by black circle markers, with the paths between successive fixes indicated by grey lines.*

Table S4. *Effects of day of stay, weight to wing ratio and Julian date of capture on the distance travelled per hour by Common Snipe Gallinago gallinago during stopover on North Ronaldsay, tested using a linear mixed effects model. Significance is indicated in bold. Random effects are also given.*

Explanatory Variable	*Estimates*	*CI*	*p*
(Intercept)	183.13	42.48 – 323.78	**0.011**
Day of stay	-0.62	-1.34 – 0.09	0.088
Weight to wing ratio	-30.73	-144.54 – 83.07	0.594
Julian date of capture	-0.50	-1.09 – 0.09	0.096
Random Effects			
σ^2	525.17		
$\tau_{00\ \text{Snipe}}$	56.39		
ICC	0.10		
N_{Snipe}	11		
Observations	125		
Marginal R^2 / Conditional R^2	0.088 / 0.177		

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