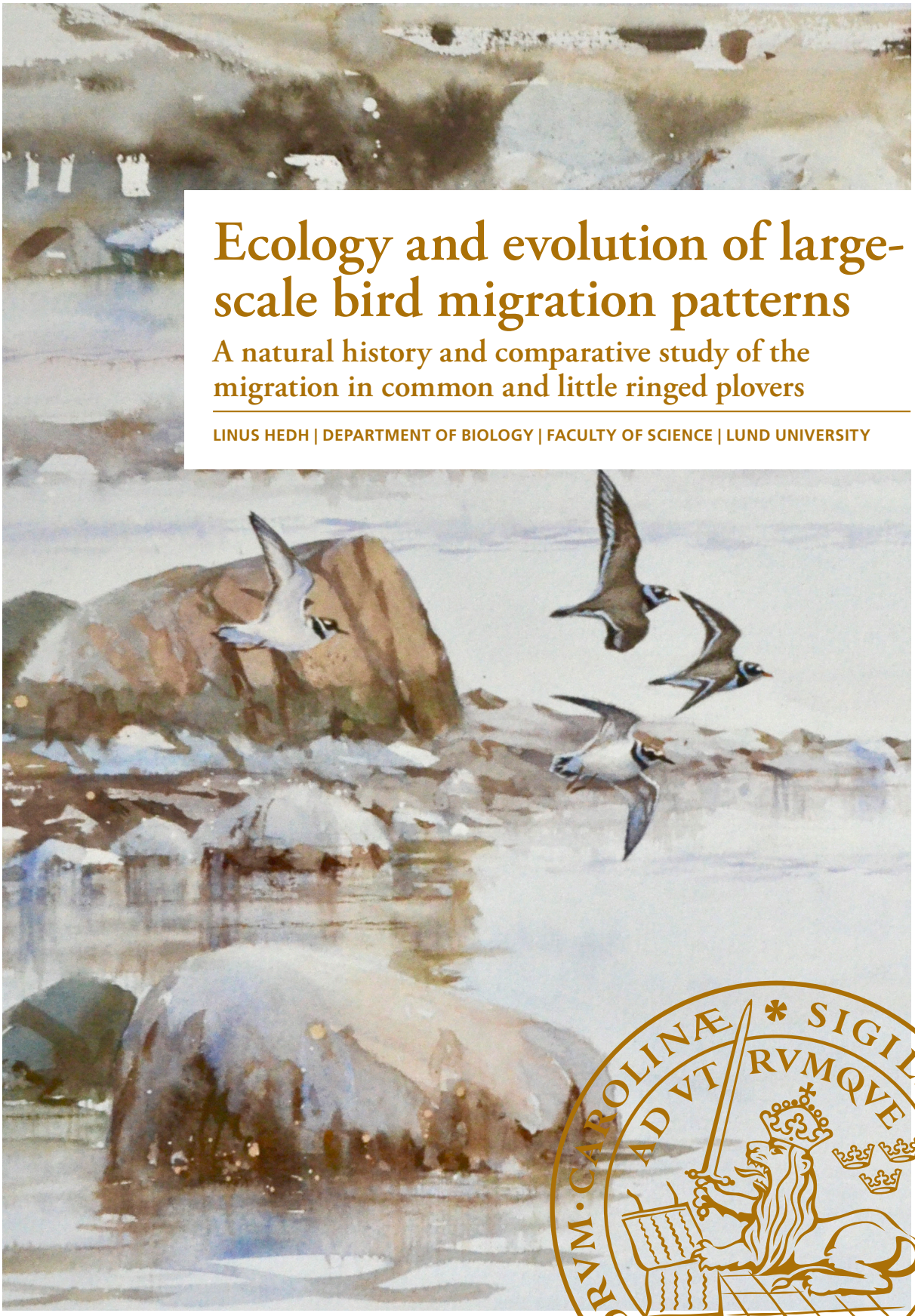
Ecology and evolution of large-scale bird migration patterns

A natural history and comparative study of the migration in common and little ringed plovers

Hedh, Linus

2022



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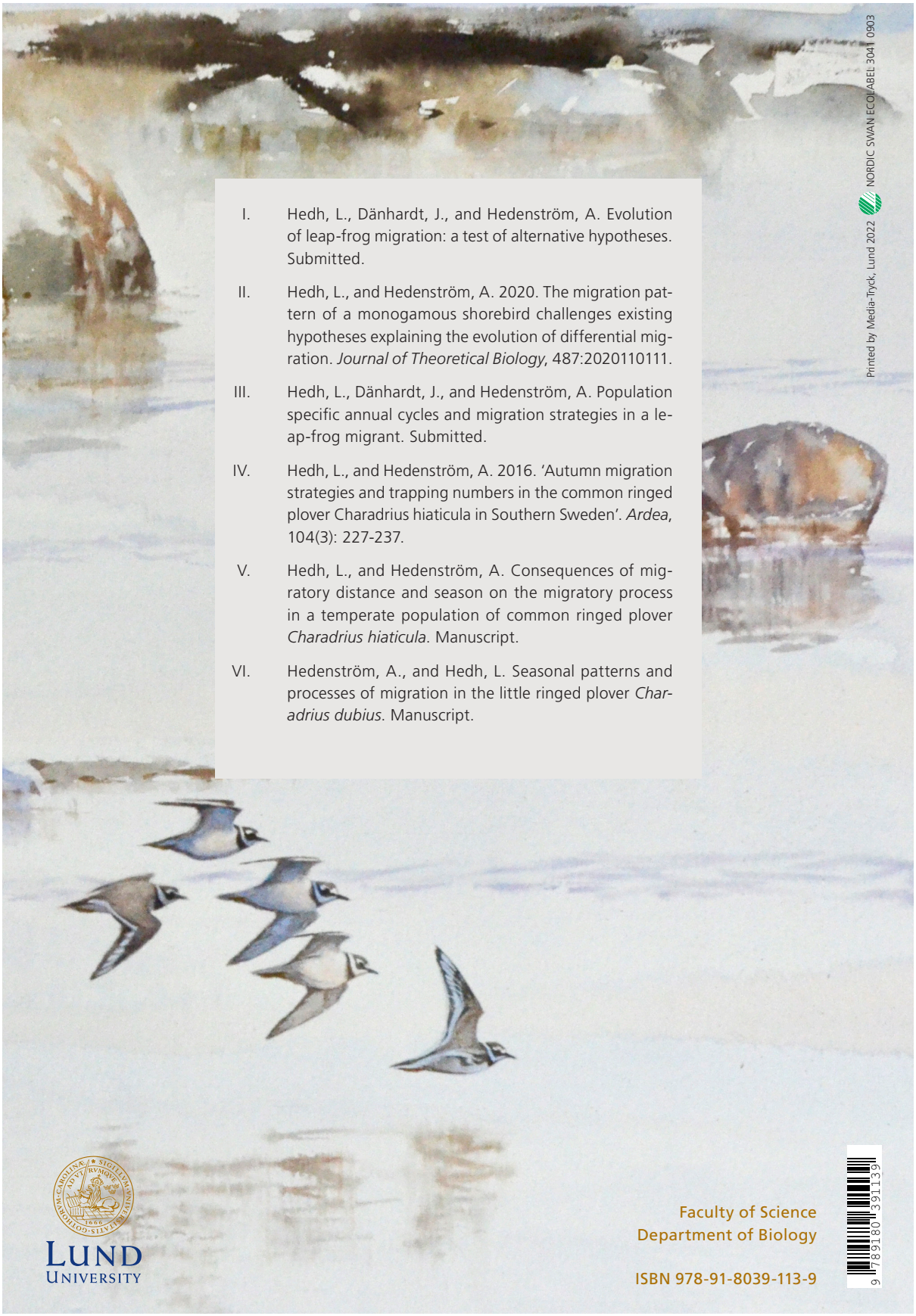

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Linus Hedh

LUND UNIVERSITY

DOCTORAL DISSERTATION

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Abstract

Migration distance and seasonal redistribution patterns may vary between and within bird populations. A common pattern is leap-frog migration, in which northerly breeding populations migrate farther and winter south of more southerly breeding populations. Another common pattern is difference in migration distances between males and females within the same population. Evidently different populations and sexes may experience different environmental conditions and selection pressures throughout the annual cycle. Such systems are interesting from an evolutionary perspective, since it allows researchers to identify and study cost-benefit trade-offs, ecological drivers and constraints to better understand species distributions and behavioral adaptations, such as migration. The aim of this thesis was to study the migration patterns and processes in the common ringed plover *Charadrius hiaticula* and little ringed plover *Charadrius dubius* to test predictions and assumptions in the underpinning hypotheses regarding the evolution of between and within population migration patterns, and behavioral adaptations associated with the migratory journey.

By studying different populations of common ringed plovers, a textbook example of leap-frog migration, the general leap-frog pattern was confirmed. However, two populations breeding on the same sub-Arctic latitude separated in the winter. Relative winter distribution, body size patterns and autumn departure/arrival patterns between four populations suggest that neither body size nor spring predictability could explain leap-frog migration. Thus, two hypotheses explaining leap-frog migration could be rejected. Individuals from a temperate population spread out over the whole known (subspecies-specific) wintering distribution area. Interestingly, on average, males were found to migrate farther (~ 800 km) compared to females. This pattern is rare among birds. Neither of the proposed hypotheses set out to explain differential migration could satisfactorily explain the observed pattern. A new hypothesis was formulated (but not tested), which proposes that sex specific energetic needs upon spring arrival and winter site-specific fueling rates may sometimes benefit one sex - in this case males - to migrate farther.

Migration distance alone did not seem to have an effect on migration speed in the common and little ringed plover. Contrary to the general predictions and observations, lower migration speeds were found in spring compared to autumn in little ringed plovers and in a temperate breeding population of common ringed plover. Interestingly, the Arctic population of common ringed plovers realized a higher spring migration speed compared to the temperate population, suggesting that high fueling rates may be attained on European spring stopover sites, well timed in relation to the onset of the northern breeding season. Temperate populations of common ringed plovers arrive in spring with a higher inter-annual variation compared to Arctic populations, indicating a more flexible migratory schedule. Migration distance and season influenced the number, organization and duration of migratory flights in the common ringed plover. In autumn, there was no difference in number of migratory flights between individuals migrating different distances. However, individuals migrating longer distances initially made 2-4 short flights followed by a longer flight. This is indicative of a time minimizing strategy, which was unexpected given previous assumptions of autumn migration being more relaxed. In spring however, the number of flights increased with distance and there is no clear way to distinguish between strategies without knowledge of fueling conditions.

Key words: ringed plover, leap-frog migration, migration speed, migration process, light level geolocator, migration

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List of papers

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Additional published papers not included in the thesis

Hedh, L., Guglielmo, C.G., Johansson, L.C., Deakin, J., Voight, C. and Hedenström, A. 2020. Measuring power input, power output and energy conversion efficiency in un-instrumented flying birds. *Journal of Experimental Biology*, 223:jeb223545.

Author contributions

I. L.H. conceived the idea of the study; L.H., J.D. and A.H. collected the data; L.H. analyzed and visualized the data; L.H. wrote the first draft with support from A.H.; L.H., J.D. and A.H. edited and revised the manuscript; L.H., J.D. and A.H. acquired the funding.

II. L.H and A.H. conceived the idea of the study; L.H. and A.H. collected the data; L.H. analyzed and visualized the data; L.H. wrote the first draft with support from A.H.; L.H. and A.H. edited and revised the manuscript; L.H. and A.H. received funding.

III. L.H., J.D. and A.H. conceived the idea of the study; L.H., J.D. and A.H. collected the data; L.H. did the formal analysis of the data and drafted the manuscript with input from J.D. and A.H. All authors contributed critically to the drafts and edited the manuscript. L.H., J.D. and A.H acquired the funding.

IV. A.H conceived the idea of the study; L.H. collected and analyzed the historical ringing data and made visualizations; L.H. wrote the first draft with support from A.H.; L.H. and A.H. edited and revised the manuscript; A.H. received funding.

V. L.H. and A.H. conceived the idea of the study; L.H. collected the data; L.H. analyzed and visualized the data; L.H. wrote the first draft; L.H. and A.H edited and revised the manuscript; L.H. and A.H. received funding.

VI. A.H. conceived the idea of the study; L.H. and A.H. collected the data; L.H. and A.H. analyzed and visualized the data; A.H. wrote the first draft; L.H. and A.H edited and revised the manuscript; L.H. and A.H. received funding.

Abstract

Migration distance and seasonal redistribution patterns may vary between and within bird populations. A common pattern is leap-frog migration, in which northerly breeding populations migrate farther and winter south of more southerly breeding populations. Another common pattern is difference in migration distances between males and females within the same population. Evidently different populations and sexes may experience different environmental conditions and selection pressures throughout the annual cycle. Such systems are interesting from an evolutionary perspective, since it allows researchers to identify and study cost-benefit trade-offs, ecological drivers and constraints to better understand species distributions and behavioral adaptations, such as migration. The aim of this thesis was to study the migration patterns and processes in the common ringed plover *Charadrius hiaticula* and little ringed plover *Charadrius dubius* to test predictions and assumptions in the underpinning hypotheses regarding the evolution of between and within population migration patterns, and behavioral adaptations associated with the migratory journey.

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Introduction

Animals living in a seasonal environment need to adapt to the continuously fluctuating environmental conditions (Fretwell 1972). One behavioral adaptation to mitigate potentially negative effects or exploit opportunities presented by the environment - and which has fascinated humans for centuries - is to migrate (Alerstam 1990, Dingle 2014). Migration can be found in almost all major animal groups (Hansson and Åkesson 2014). However, most notable - and perhaps most studied - are these journeys in birds, in which some species have been shown to travel thousands of kilometers encompassing hemispheric scales, within a single year (Salomonsen 1967, Gill et al. 2005, Egevang et al. 2010, Klaassen et al. 2011, Bairlein et al. 2012, Sokolovskis et al. 2018). These journeys allow migratory birds to track seasonal pulses of food resources, which are separated in time and space (Thorup et al. 2017, Norevik et al. 2019), and to find suitable environmental conditions for both reproduction and survival (Lack 1968, Alerstam et al. 2003).

Migration is found in a variety of bird species, across phylogenetic origins (Helbig 2003, O'Connor et al. 2018), and migratory behavior is expressed to various degrees in terms of migration distance and strategies (Alerstam 1990, Newton 2008). As with partial migrants, when only a subset of a populations is leaving their breeding grounds in the non-breeding season (Lack 1943, Chapman et al. 2011), between and within population patterns can also be found among fully migrating populations. Already in the mid 19th century, Nilsson (1858) noted that migratory populations breeding at more northerly latitudes (I will adopt a north hemispheric perspective throughout this text) may also maintain more northerly wintering grounds as compared with populations breeding at latitudes farther south. Later, Palmén (1874) discovered that the relative sequential order of wintering latitudes of many species, and populations, was reversed relative to the breeding latitude. Hence, populations breeding farther north winter south of more southerly breeding populations. Almost a century later, Salomonsen (1955) - using ringing data, which by then had been systematically collected for little over half a century (Newton 2008) - compiled further accounts of these patterns, which are referred to as "chain" and "leap-frog" migration, respectively (Fig. 1). Early students of ornithology also noted that males often migrate shorter distances than females and that they usually return earlier in spring (e.g., Linné 1758). The "differential migration" pattern between males and females within populations, in which males usually migrate a shorter distance, has

now been established as a rule rather than an exception (Fig. 1) (Ketterson and Nolan 1983, Cristol et al. 1999).

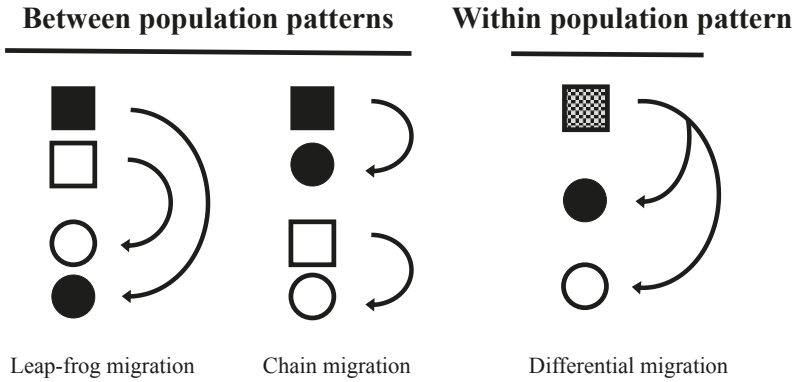

Figure 1. Graphical examples of the different between and within population migration patterns described in the main text (above). Squares represents a breeding areas and circles respresents wintering areas. Colors (black and white) represents different populations or sexes. Note that more latitudinal patterns exists and excelnt reviews of these can be found in Salomonsen (1955) and Newtoon (2008).

With these migration patterns in mind, it becomes evident that different populations or individuals may experience different environmental conditions throughout the annual cycle. To illustrate, just imagine the widely diverse conditions two willow warblers *Phylloscopus throchilus* may encounter when arriving to a temperate breeding area in southern Sweden and to the sub-alpine birch forest, in the Arctic part of the species' distribution range, where snow and sub-zero degrees are not uncommon in spring. Thus, timing of migration in relation to resource pulses along the migratory routes, and at the departure and destination sites, are likely to be under strong selection and may differ between populations (Conklin et al. 2010, Bauer et al. 2016, 2020, Briedis et al. 2016). Moreover, the ecological context that a migrating bird is facing may affects the employed migration strategy (Alerstam and Lindström 1990, Hedenström and Alerstam 1997). For example, in spring, when fierce competition for breeding resources is taking place and rank order of arrival is predicted to be crucial (Kokko 1999), birds are expected to maximize the speed of migration to outcompete potential opponents (Hedenström and Alerstam 1997). Such selective forces should, in combination with the current environment, physiological constraints and migration distance, result in different behavioral outcomes to complete the migratory journey in an optimal way (Alerstam and

Lindström 1990, Ens et al. 1994, Weber et al. 1998, Alerstam and Hedenström 1998).

What is hopefully clear is that migration is, to paraphrase Alerstam (1990), "the 'cement' with which birds put together several different temporary detached niches to form a complete and adequate living niche". A growing number of studies are confirming that different events of the annual cycle are inter-linked, so that the consequences of one event occurring in one part of the year may have carryover effects on another (Harrison et al. 2011). In the case of migratory birds, such effects may come into play in a spatially distant location relative to the source. Thus, to be put in an evolutionary perspective, patterns and behaviours of migration must be analyzed in a cost-benefit framework in relation to ecological conditions and life-history strategies, for each stage of the annual cycle (Greenberg 1980, Myers et al. 1985, Alerstam et al. 2003, García-Peña et al. 2009, Newton 2011, Marra et al. 2015, Grist et al. 2017, Lok et al. 2017). Fortunately, we are living in an exciting time, when technological advancements make it possible to use novel tracking techniques to observe even the smallest birds, sometimes over large parts of the annual cycle and even entire life cycles in larger birds (e.g. Sergio et al. 2014; Sokolovskis et al. 2018; Williamson and Witt 2021)

Aims

The aim of this thesis is to address a set of questions regarding the evolution and ecology of migration patterns, which can be generalized to

i) why do different migratory patterns evolve, resulting in variation in migratory distances and redistribution patterns within and between populations, and

ii) what are the behavioral adaptations, such as migration speed, timing, and the process of migration, associated with these differences?

The question of <u>why</u> a pattern evolves and <u>how</u> to carry out the migration accordingly, are evolutionary and mechanistic questions, respectively. But they are certainly not unrelated. By asking the question <u>how,</u> one may through careful observations of nature, pinpoint important selective forces that enable us to find answers to the question <u>why</u> (Lundberg and Alerstam 1986, Piersma 2007). By extension, the aim is to contribute to our general understanding of the evolution of migration.

To address these questions, I have mainly used individual tracking techniques to comparatively study the migration of two species in the genus of plovers, *Charadrius*. Plovers exhibit highly variable migratory patterns and behaviors, both inter- and intraspecifically, which provides an exciting study system to test theory

about the evolution and ecology of migration (Conklin 2019). I have mainly focused my work on the common ringed plover *Charadrius hiaticula*, which is a textbook example of a ”leap-frog” migrant (Fig. 1) (Salomonsen 1955, Hale 1980, Newton 2008). I have also studied the little ringed plover *Charadrius dubius*, in which individuals breeding just next to each other have been shown to be separated up to 7000 km in the non-breeding season (Hedenström et al. 2013).

The aims are largely motivated by the wide base of previous theoretical work concerning the evolution of differential migration patterns and behavioral adaptations related to migration (reviewed in Gauthreaux Jr. 1982; Ketterson and Nolan 1983; Alerstam and Hedenström 1998; Cristol et al. 1999; Somveille et al. 2015). However, with the technological advancement of miniaturized tracking devices, new opportunities to revisit and analyze patterns and behaviours from a different perspective is now possible (Bäckman et al. 2017, McKinnon and Love 2018). Individual tracking may provide critical data that have previously been lacking or hard to obtain. Firstly, although previous comparative studies on the evolution of different migration patterns and behaviours have focused on intraspecific variation, details of population/group-specific origins and wintering sites (i.e., migratory connectivity [Webster et al. 2002]) have remained largely unknown except for a few study systems (e.g., red knot *Calidris canutus* [Piersma and Davidson 1992]). Secondly, complete annual timing, with regard to arrival and departure times from breeding and non-breeding areas, has similarly been lacking. Finally, year around tracking aids the possibility to observe and understand potential interrelationships between different parts of the annual cycle (Marra et al. 2015).

Paper specific aims

In **Paper I**, we first described the between population patters of common ringed plovers by tracking four different populations breeding in a in a climate/latitudinal gradient. Second, we test assumptions and predictions in some of the hypotheses trying to explain leap-frog migration.

In **Paper II**, we describe the within population migration pattern in a temperate breeding population of common ringed plover. Because males winters farther from the breeding area compared to females we evaluate hypotheses trying to explain differential migration and propose a new one.

In **Paper III**, we describe the migration and annual cycle of two populations of common ringed plovers (one Arctic and one temperate), with the aim to test predictions regarding migration timing, speed and time allocations, in relation to the leap-frog migration pattern (i.e. with respect to differences in migration distance and contrasting environments in winter/breeding).

In **Paper IV**, we studied stopover behaviour and migration timing of common ringed plovers at a stopover site by using ringing data obtained by Ottenby Bird

Observatory. Our aim was to contrast the behaviour of two subspecies (*C. hiaticula* and *C. tundrae*, i.e. temperate and sub-Arctic/Arctic breeding populations) and test predictions obtained from optimal bird migration theory.

In **Paper V**, we studied the migratory process in one population of common ringed plover breeding in southern Sweden, in which individuals have been shown to vary in migration distance. We further tested the effect of season and migration distance on the number of migratory flights, duration initial fueling period, duration of total stopover time, total flight duration and maximum individual flight duration. We discuss the result in relation to different adaptive values.

In **Paper VI**, we studied the migratory process and migration strategies in a population of little ringed plovers. We specifically evaluated the effect of season and migration distance on migratory behaviour.

In the following sections I will describe the general methodology, study system and study sites. But before I do that, I will briefly highlight some of the ecological drivers, adaptive values and physiological constraints, which are all generally related to different hypotheses trying to explain the evolution of differential migration patterns (such as leap-frog migration and differential migration by sex) and may act on selective forces, influencing behaviour during migration and organization of the annual cycle

Ecological and physiological drivers and constraints of migration

Seasonality (food availability and thermoregulation)

While the geographical origin of bird migration is still debated (Winger et al. 2014, O'Connor et al. 2018), seasonality, with variation in food resource availability in time and space, is recognized to be one of the ultimate factors for the evolution of seasonal migration in birds (Berthold 1999, Bell et al. 2000, Zink 2002, Salewski and Bruderer 2007, Somveille et al. 2015). Increased seasonality in a given geographical area results in decreased food resources when conditions deteriorate, which in turn increase mortality and consequently reduce fitness (Lack 1954, 1968). Under these circumstances, moving to another area when the climatic conditions deteriorate may be a viable option (Bell 2000). This is elegantly illustrated by the general pattern of an increasing proportion in migratory bird species when moving from lower to higher latitudes, where the amplitude and severity of seasonality increases (Newton and Dale 1996, Somveille et al. 2015). Seen from another perspective, increased seasonality also promotes a surge of food in other parts of the year, which may increase reproductive output and consequently increase fitness in

temperate and Arctic areas (Cox 1968, Berthold 1999, Salewski and Bruderer 2007). Therefore it is worthwhile moving towards seasonal areas during the breeding season (Cox 1968).

It is easy to see that amplitude and severity of a seasonal environment not only have a direct effect on the food resource itself, but also on the physiological ability for the birds to thermoregulate (Angilletta 2009). The daily maximal metabolizable energy a bird can attain needs to cover all daily energetic costs, such as the basal metabolic rate, locomotion, other activities (e.g., moult, breeding, mate attraction) and on top of that thermoregulation (Wiersma and Piersma 1994). When lower temperature forces animals to divert more energy in to thermoregulation, other parts of the energy budget may not be covered sufficiently. This will eventually lead to death if adaptations to even out the deficiency are absent. Migration is such an adaptation, which allows birds to lower the thermoregulatory costs (Somveille et al. 2018).

The thermal environment may also generate different conditions during winter depending on wintering site. In temperate wintering areas the cost of thermoregulation is generally much higher compared with those experienced in the tropics or lower latitudes (e.g., Castro et al. 1992). Furthermore, apart from the shorter summer season in Arctic environments, the thermal environment may shorten the window of breeding even more due to higher energy requirements compared to temperate breeding sites (Piersma et al. 2003).

Competition

In many cases the environment in a particular area will allow for year-around residency, despite reduced resources and low temperatures during the winter months, but with a lower upper limit compared to other parts of the year (Fretwell 1972). If the limit is reached, density dependent processes, such as competition, will act so that birds that are unable to compete for resources have to give way and move somewhere else. On a population level competition can lead to obligate migratory behaviour (Cox 1968, Fretwell 1980), or partial migration (Lack 1943, Lundberg 1987). The same reasoning can be applied to a given wintering area: the suitability of the site will decrease with increasing bird numbers to a point in which birds, that for some reason are not able to compete, will have to move to another site (Fretwell 1972, Alerstam 1990). Competition has been identified as an important factor in most models and hypotheses trying to between and within population patterns of migration (Gauthreaux 1982, Ketterson and Nolan 1983, Lundberg and Alerstam 1986, Holmgren and Lundberg 1993). However, the importance of competition for the migratory behaviours and patterns may vary between seasons, sexes, populations and ecological context (Ketterson 1979, Ketterson and Nolan 1983, Cristol et al. 1999). Numerous ecological contexts have been pointed out, such as competition for breeding resources, mates and nest sites (von Haartman 1968,

Myers 1981b, Bensch and Hasselquist 1991, Martin and Martin 2001) food resources on stopover sites (Lindström et al. 2011, Minias et al. 2014) and favourable non-breeding sites (Ketterson and Nolan 1976, Pienkowski et al. 1985).

Several proximate mechanisms on how competitive interactions may be resolved, and how they are linked to differential migration patterns, have correspondingly been suggested. Competitions leading to spatial displacement can either be resolved based on rank order in arrival (prior occupancy), offering individuals that are familiar with an area competitive advantage over newcomers (Fretwell and Lucas 1969, Rutten et al. 2010), or unequal competitive ability between individuals (Sutherland and Parker 1985). The latter is in most cases attributed to trait related dominance (Gauthreaux 1978, Sutherland and Parker 1985). Dominance can be achieved either by phenotypic traits such as size (Ketterson 1979, Sutherland and Parker 1985) and sex (Ketterson 1979, Piper 1997), but also on state dependent factors such as motivation (Piper 1997). Sex as a determinant of dominance is a complicated case since body size and sex are often correlated. But sex is also correlated with testosterone levels, which may facilitate aggressive responses (Wingfield et al. 1987). In that respect, sex can be seen as a state dependent mechanism, since hormone levels may vary with season (Piper 1997). But, in most cases, males have been found dominant compared to females regardless of body size (Whitfield 1985, Piper 1997).

Cost of migration

Birds face three fundamental costs while migrating. First, all types of self-powered locomotion requires energy, which directly increases the energetic demands (Alexander 2003). An important implication for migrating birds, which are making long flights, is that sufficient fuel stores are required to meet these demands. These fuel stores mostly consist of adipose fat, stored at different locations on the body, and protein (King and Farner 1965, Lindström and Piersma 1993, Jenni and Jenni-Eiermann 1998). Adding fuel will increase the energetic cost of working, because the flight cost is dependent on body mass (Pennycuick 1969). Higher mass will not only increase the direct energetic cost, but also the potential flight range. However, the relationship between flight range and fuel load attain a negatively accelerating curve (Alerstam and Lindström 1990, Pennycuick 2008). Thus, longer flights require disproportionally more energy (fuel) than shorter flights. This leads over to the second cost - time. Fuel required to cover a certain distance usually needs to be accumulated during stopover periods (although a fly-and-forage strategy is used by some avian migrants, e.g. Strandberg and Alerstam 2007). Because fuel is consumed at a higher rate compared to fuel accumulation, which is much due to physiological constraints (Kirkwood 1983, Lindström 1991), birds need to spend more time on fueling (Hedenström and Alerstam 1997). Depending on the ecological context (e.g. spring versus autumn migration) and the time window to perform the next step in

the annual cycle (e.g. breeding or moult), time constraints due to fueling becomes an important ecological factor, especially for long distance migrants and larger sized birds (Hedenström 2006, Newton 2011). It should also be noted that because more time is diverted into fueling than flight during migration, a larger proportion of the total energy expenditure is consumed during stopovers (Wikelski et al. 2003). The third cost is associated with the elevated mortality risk due to other factors than energetic fatigue or starvation. For example, behavioural studies and experiments have shown that birds modulate behaviour during migration to evade predation, suggesting that predation is elevated during migration (e.g., Fransson and Weber 1997, Lank et al. 2003). This is partly due to the fact that birds take risks while fueling and that an increased body mass decreases manoeuvrability (Metcalfe and Furness 1984, Hedenström 1992). Other risks, such as increased exposure to disease and parasites have also been suggested to an important cost of migration (Piersma 1997).

Social mating system

Social mating systems can have a profound effect on differential timing of migration within populations and migration distance in general (Myers 1981a). During spring migration, individuals of the sex that establishes and defend territories, should be rewarded by arriving early at the breeding grounds relative to competitors (Kokko 1999). This is true for most social mating systems, but may be especially important in polygynous or polyandric systems (Oring and Lank 1982, Bensch and Hasselquist 1991). Protandry (earlier departure and/or arrival in males) or protogyny (earlier departure and/or arrival in females) in spring could be achieved either by leaving the non-breeding grounds before the other sex, migrating faster (increase air speed or fueling rates modulated by behaviour) or, more importantly in the context of differential migration patterns, winter closer to the breeding area (Myers 1981b, Ketterson and Nolan 1983, Morbey and Ydenberg 2001). Sex specific autumn departure date depends largely on the extent of parental care, in which the sex that provides less care is free to depart earlier (Reynolds and Székely 1997).

General methodology

Approaches

The main part of this thesis concern migration patterns and behaviours, in which various tracking devices (Fig. 2) have been used to describe, characterize and compare populations, age/sex groups and individuals (Paper I, II, III, V and VI). However, traditional ringing data from a stop-over site was also utilized for analysis of stopover behaviour (Paper IV). In Papers I, II and III, I used light level geolocators to determine wintering areas, stop-over sites, timing and speed of migration. In Paper V and VI, custom-built multi sensor data loggers, which record vertical acceleration generated by the birds' wing-beats, were used to investigate the process of migration (i.e., number and duration of flight bouts and stop-overs) in relatively high resolution compared to traditional geolocators (Bäckman et al. 2016). These data loggers also recorded light data periodically, primarily to identify wintering sites. In general, I used a comparative approach to analyse the resulting behavioural parameters and patters with respect to predictions from optimal migration theory and hypotheses concerning evolution of migration patterns.

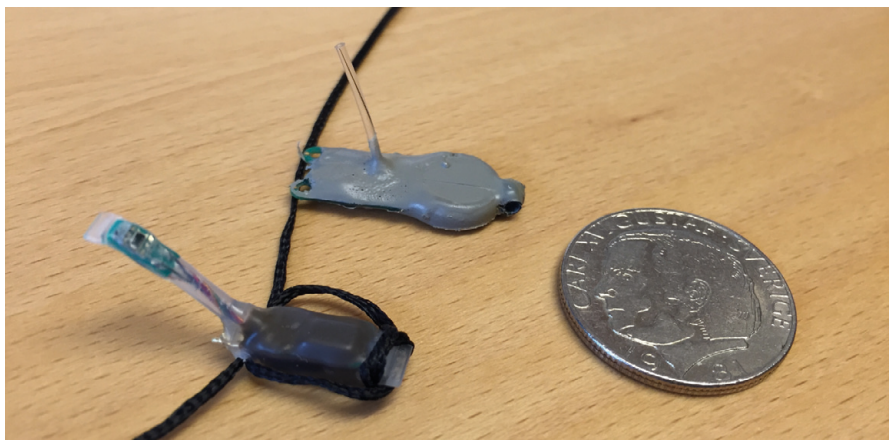

Figure 2. Differnect types of loggers used in this thesis. Closest is a traditional light-level geolocator (MK10s from Migrate Technology Ltd) and behinde a custom made multi-sesnor loger.

The common ringed plover

The common ringed plover (Fig. 3a) has a large global breeding range and three subspecies are currently recognized based on morphometrics and genetic markers (Fig. 4) (Engelmoer and Roselaar 1998, Thies et al. 2018). The subspecies *C. h. hiaticula* (*hiaticula* henceforth) breeds in temperate areas in northern Europe, southern Scandinavia and the Baltic Sea. *C. h. tundrae* (*tundrae* henceforth) has traditionally been identified to occupy alpine and tundra areas from the Scandinavian mountain range to Chukotka in far eastern Russia (Fig. 4). *C. h. psammadroma* (*psammadroma* henceforth) is breeding on Iceland (Delany 2009). Populations breeding on Greenland and in the East Canadian Arctic are also suggested to belong to *psammadroma*, although genetic evidence is still absent (Engelmoer and Roselaar 1998, Thies et al. 2018). Recently a hybrid zone between the nominate form and *tundrae* was discovered by analyzing the population structure, using eight polymorphic microsatellite loci, among ringed plover populations across the global distribution range (apart from Greenland and the Canadian Arctic). The hybrid zone is orientated in a northwest-southeast direction and range from northern Scandinavia to Belarus (Thies et al. 2018).

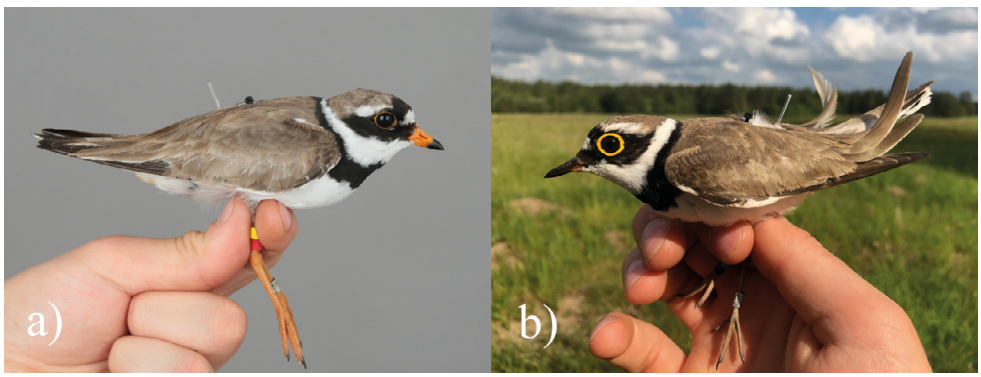

Figure 3. Study species after logger deployment. Adult male common a) and little ringed plover b). Photo: a) Ottrnby Bird Observatory, b) the author.

The global wintering range is also large, and includes coastal areas along the East-Atlantic coast (from the British Isles to South Africa), East Africa, the Middle East and the Indian subcontinent (Fig. 4). Inland wetlands, particularly in Africa, are also used during winter (Davidson and Scott 2009). *Hiaticula* mainly winters in western Europe, the Iberian Peninsula and some as far south as north-western Africa (Morocco), while *tundrae* and *psammadroma* migrates mainly to Africa (Taylor 1980, Wymenga et al. 1990, Davidson and Scott 2009, Thorisson et al. 2012, Lislevand et al. 2017, Léandri-Breton et al. 2019). Furthermore, populations breeding on the British Isles (which belongs to the subspecies *hiaticula*) are more or less resident (Taylor 1980).

The little ringed plover

The little ringed plover (Fig. 3b) also has a wide breeding range across the Eurasian continent and several subspecies have been described (Kirby and Scott 2009). The breeding populations in Europe consist of the subspecies *C. d. curonicus*, which is the only subspecies documented to conduct longer migrations, and the breeding range extends to the Russian Far East (Fig. 5). The other two recognized subspecies, *C. d. dubius* and *jerdoni* are mainly sedentary or nomadic (Piersma and Wiersma 1996). Populations breeding in Europe mainly migrate to Africa, south of the Sahara Desert (Kirby and Scott 2009), but recoveries from birds ringed in Sweden and Finland indicate a south-easterly migration route and at least one recovery from a wintering bird has been made in India (Fig. 5) (Fransson et al. 2008). Interestingly, Hedenström et al. (2013) found in a study using light-level geolocators, that one out of six individuals from a breeding population in southern Sweden migrated to India.

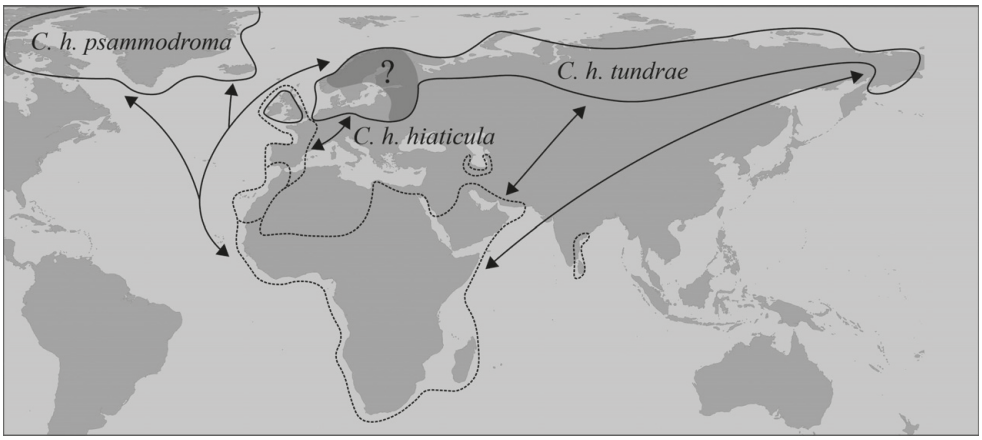

Figure 4. Distributions and migration routes of different populations/subspecies of the common ringed plovers *Charadrius hiaticula.* Solid lines represents breeding areas, dashed lines are wintering areas and arrows major migration routes. Shaded area (annotated with "?") in northern Scandinavia represents a recently discovered hybrid zone between *C. h. hiaticula* and *C. h. tundrae*. Based on: Taylor (1980), Davidson and Scott (2009), Lislevand et al. (2017), Tomkovich et al. (2017), Léandri-Breton et al. (2019), BirdLife International (2021).

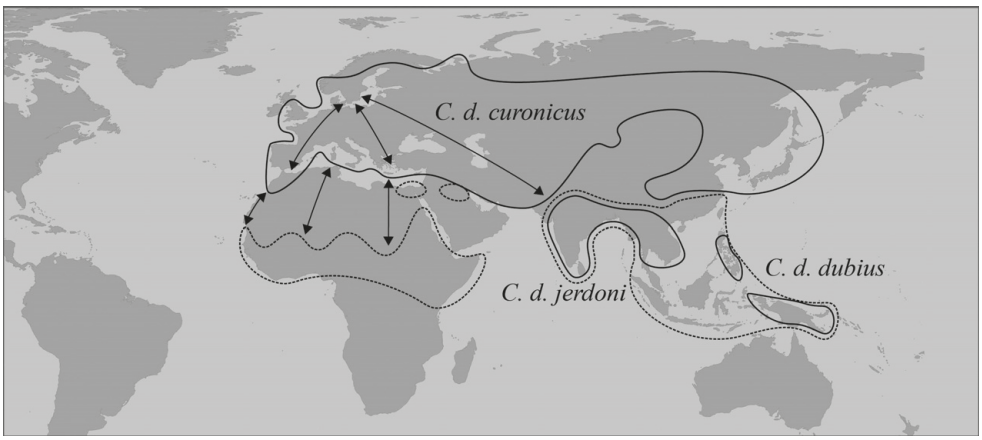

Figure 5. Distributions and migration routes of different populations/subspecies of the little ringed plovers *Charadrius dubius*. Solid lines represent breeding areas, dashed lines are wintering areas and arrows are major migration routes. Note that *C. d. dubius* and *C. d. jerdoni* are mainly or completely sedentary. Based on: Fransson et al. (2008), Kirby and Scott (2009), Hedenström et al. (2013), BirdLife International (2021a).

Study sites and field work

All studies except Paper IV, which concerned stopover behaviour, were conducted in the breeding area of different populations and thus, these birds were caught while

breeding using a circular walk-in trap or small clap-trap. However, one site (Ottenby; see Fig. 6), constitutes as both a breeding site and stop-over site for common ringed plovers. Ottenby is located in south-eastern Sweden and the breeding population belong to the subspecies *hiaticula*. In autumn, both *hiaticula* and *tundrae* are using this site for stopover and are trapped within the standardized wader trapping conducted by Ottenby Bird Observatory (Paper IV). Two sites, Abisko and Ammarnäs are located on the alpine tundra (900-1100 m.a.s.l) in Arctic and sub-Arctic Sweden, respectively (Fig. 6). In both areas common ringed plovers are breeding on gravel patches located around smaller lakes or on top of ridges and plateaus. Malören is a small island in the northern part of the Bothnian Bay, that is located within the sub-Arctic climate zone (Fig. 6). In Lund/Vomb, little ringed plovers have been studied for about a decade (Hedenström et al. 2013), where the breeding birds make use of man-made infiltration ponds (for water treatment), ponds and gravel pits.

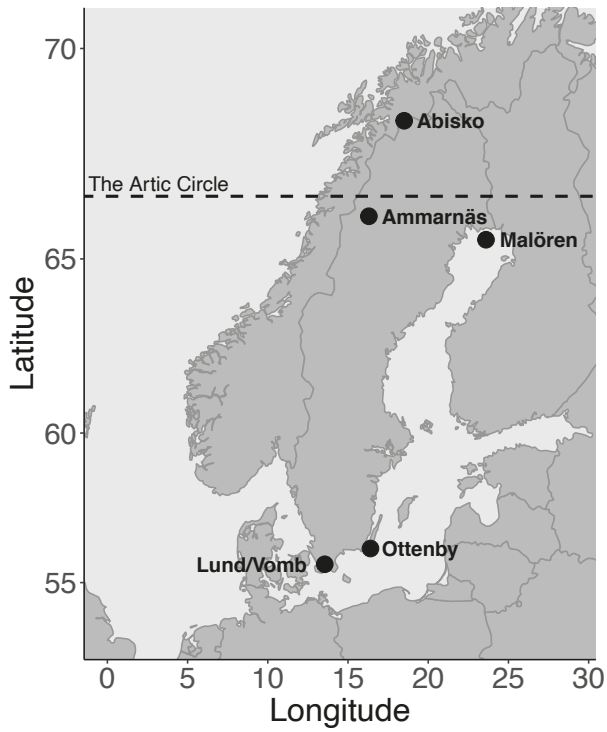

Figure 6. An overview of the breeding sites where loggers were deployed to study the migration patterns and behaviours of the common (Abisko, Ammarnäs, Malören and Ottenby) and little ringe plover (Lund/Vomb), presented in this thesis.

The different breeding sites of common ringed plovers were chosen to compare populations that experience diverse conditions during the annual cycle. First, the different sites provide widely different breeding environments with respect to the length and phenology of the breeding season, spring conditions at arrival and general seasonality (Fig. 7). Second, based on current knowledge, the common ringed plovers breeding in northern and southern Scandinavia differ both in migration distance and conditions at the wintering sites (Taylor 1980, Meltofte 1996, Lislevand et al. 2017). Ammarnäs and Malören were chosen specifically because they are located on nearly the same geographic latitude and thus have similar migration distance to the closest possible wintering sites (Davidson and Scott 2009). But the onset of spring, and hence breeding seasons, are slightly shifted in time between the two population (Väisänen 1977), because of the altitudinal cline between the Scandinavian mountain range and the coast of the Bothnian Bay.

Figure 7. Representation of the different study sites concerning the common ringed plover. The two top panels a) and b) depics the two alpine study sites, Abisko and Ammarnäs, in the beguining of the breeding season (mid June), c) Malören (beginning of June) and d) Ottenby (late March). Photo: the author.

Results and discussion

Between and within population patterns of migration in the common ringed plover

By comparing several populations of common ringed plover across latitudes (from temperate to Arctic regions in Sweden) in Paper I, the general pattern of leap-frog migration was recovered (Fig. 8). However, the population breeding on Malören, in the Bothnian Bay, overlapped in winter with the temperate population, which breaks the otherwise clear latitudinal pattern (Fig. 8) (Paper I).

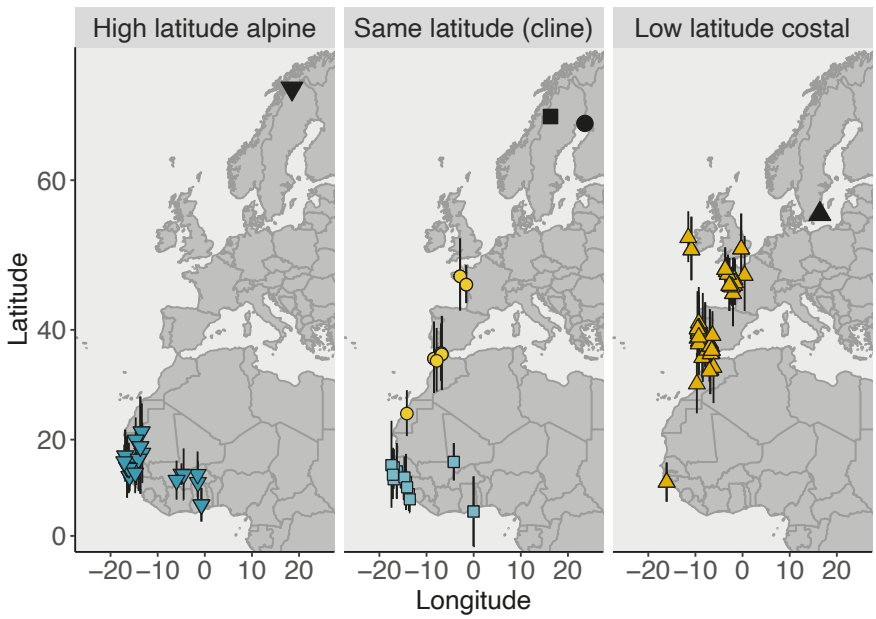

Figure 8. Wintering sites of common ringed plovers from four populations breeding in Sweden (Abisko: blue triangles, points down; Ammarnäs: blue squares; Malören: yellow points; and Ottenby: yellow triangles, points up). Symbols are mean positions with standard deviations. Breeding locations are represented as black symbols.. Maps are in Mercator projection. From Paper I.

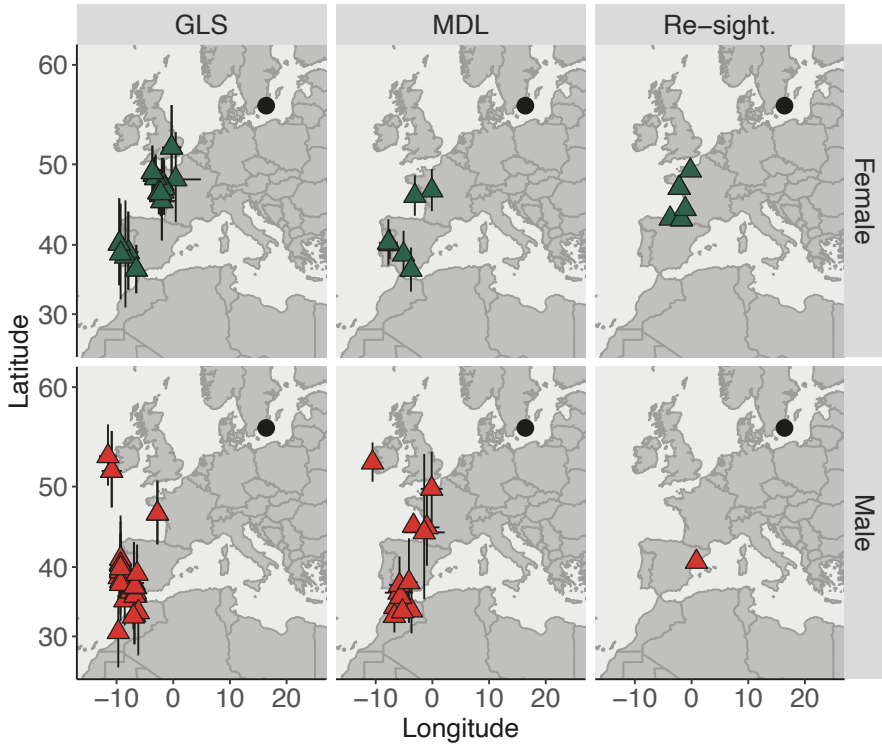

Figure 9. Wintering sites of male and female common ringed plovers breeding at Ottenby, a temperate breeding site in southern Sweden, as revealed from light level geolocators (GLS), light measurements from miniaturized multi sensor data loggers (MDL, Paper V) and re-sightings of individuals color-ringed (Re-sight., unpublished) within this project. GLS data from one additional female wintering (two consequtive winters) on the Iberian Peninsula have been added comapred to the map in Paper II. Note that positions of individuals tracked over two or more years are included in the map. The maps are in Mercator projection.

Notably, the population breeding in southern Sweden was spread out along more or less the whole European and Moroccan coast lines in winter, encompassing the whole known wintering range for temperate breeding populations (Paper I, II, V). This finding contrasts to Salomonsen (1955) suggestion that the leap-frog migration pattern in the common ringed plover is nested among the breeding populations in temperate Europe. He proposed that populations breeding in the Baltic Sea and southern Scandinavia winter from the Iberian Peninsula to Mauritania, and populations from southern most Sweden, Denmark and Germany winter farther north, but overlap with the Baltic populations on the Iberian Peninsula. Furthermore, an unexpected pattern of differential migration was found when examining the winter distribution of this population with respect to sex (Paper II). Males mainly wintered on the Iberian Peninsula and females in France (average difference in great circle distance was ~ 800 km, Paper II). This pattern still holds true when adding data on winter distribution data from the MDLs' and recoveries of colour-ringed

individuals in winter (Fig. 9). More overlaps, was however observed compared to that seen in Paper II. It seems that females tend to spread out more across latitudes, compared to males (Fig. 9). Differential migration by sex in ringed plovers was hypothesised by Wallander (2001) who found a female-biased recovery probability, based on a data set of winter recoveries of Swedish breeding birds wintering on the British Isles and in northern France. However, the data set contained too few recoveries at the time and only contained a few sightings from southern Europe. The pattern found in Paper II, that males migrate further from the breeding area compared to females is rare and most cases in which it occurs concern examples of reverse sexual dimorphism or polyandric social mating systems (summarised in Cristol et al. 1999; Newton 2008).

Testing ecological hypotheses explaining between and within population migration patterns

Several hypotheses for why different migratory patterns evolve between and within populations have been proposed (Table 1). Many empirical tests of these hypotheses have been made, particularly on within population patterns, such as differential migration between sexes (reviewed in Ketterson and Nolan 1983; Cristol et al. 1999). However, critical tests of the predictions and assumptions in hypotheses regarding the evolution of for example leap-frog migration are sparse. Some of the hypotheses concerning both between and within population patterns share the same assumptions, but differ in the ultimate ecological explanations. However, most hypotheses attribute competition, in one way or the other, as a main driver. Evidently, the predictions accompanying many of these hypotheses are not mutually exclusive (Ketterson and Nolan 1983). However, with the good resolution of winter destinations of individuals from several known breeding populations and the somewhat unexpected outcomes of the among and within population comparisons of common ringed plover, our data provided an excellent opportunity to test predictions and assumptions for a number of the existing hypotheses (Paper I, II). One hypothesis (the "Time allocation and seasonality" model, Table 1) was not testable given the data, because it requires winter range wide information on fueling rates prior to spring departure.

Table 1. Hypotheses aiming to explain between (B) and within (W) population migration patterns, in which assumtions and/or predictions were tested (or not tested) within this thesis.

Hypothesis	Ecological factor	Type	Tested	Reference
Dominance/winter competition hypothesis	Competition for wintering sites	B	Yes	Pienkowski et al. (1985)
Prior occupancy hypothesis	Competition for wintering and/or breeding sites	B	Yes	Lundberg & Alerstam (1986), Holmgren & Lundberg (1993)
Spring predictability hypothesis	Competition for breeding sites	B	Yes	Alerstam & Högstedt (1980)
Time allocation hypothesis	Seasonal time allocation	B	Yes/No	Greenberg (1980)
Time allocation and seasonality model	Seasonal time allocation and resource wave prior to spring migration	B	No	Bell (1996)
Dominance hypothesis	Competition for wintering sites	W	Yes	Ketterson & Nolan (1976)
Body size hypothesis	No competition	W	Yes	Ketterson & Nolan (1976), Ketterson and King (1977)
Arrival time hypothesis	Competition for breeding sites	W	Yes	von Haartman (1968), Ketterson & Nolan (1976)

The evolution of leap-frog migration in the common ringed plover

Building on the notion that body size is an important trait correlated with dominance, larger birds are suggested to settle in potential wintering sites closest to the breeding area, given the assumption that there is high competition for wintering sites and the cost of migration is severe (the "Dominance/winter competition" hypothesis, Table 1; Pienkowski and Evans 1985, Pienkowski et al. 1985). Considering the segregation between individuals breeding in Ammarnäs and on Malören (sub-Arctic populations) found in Paper I, we expected that individuals from Malören to have a larger body size than individuals from Ammarnäs. However, we did not find such a difference (Fig. 10) (Paper I). Furthermore, individuals breeding on Malören had a smaller body size compared to those breeding at Ottenby (Fig. 10). Taken together, there is no reason, based on body size, why individuals from Ammarnäs should not stay and winter in Europe as well (Paper I). Thus, we could reject the “Dominance/winter competition” hypothesis, in which migration distance is driven by body size mediated dominance, as an explanation for leap-frog migration in the common ringed plover.

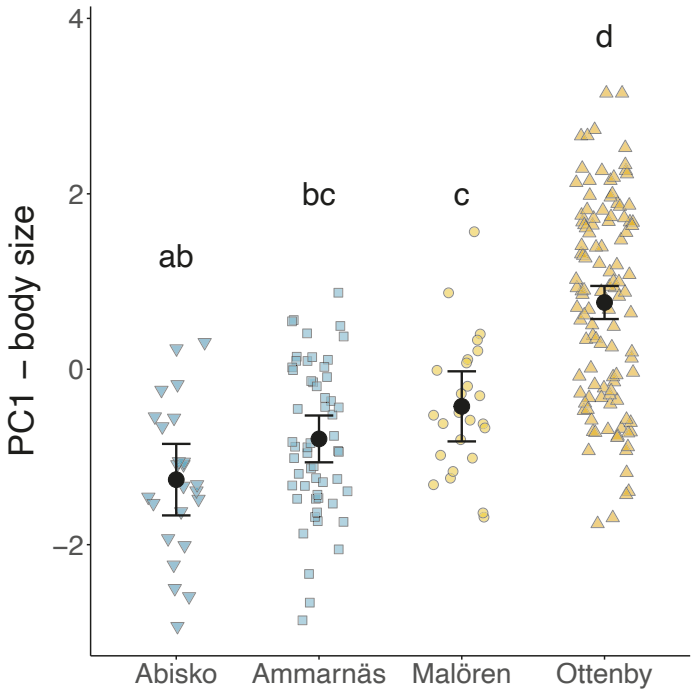

Figure 10. Body size, represented as the fist principal component of wing, tasus and total head length. Letter denotes significance differences as assesed by Tukey's HSD *post hoc* test (P < 0.05). From Paper I.

Early arrival in potential wintering or breeding site is considered a premium when competing for resources (von Haartman 1968, Alerstam and Enckell, Pehr 1979, Townshend 1985, Bensch and Hasselquist 1991). Theoretically, if competition for wintering and breeding sites occurs, dominance relationships related to being early, could lead to both stable (without fitness differences) and despotic patterns (with fitness differences) of leap-frog migration under different conditions related to latitudinal suitability gradients (the "Prior occupancy" hypothses, Table 1; Lundberg and Alerstam 1986, Holmgren and Lundberg 1993). In Paper I, both populations of common ringed plover wintering in Europe (Malören and Ottenby), left their breeding sites and arrived to continental Europe approximately 2 weeks earlier than the two populations wintering in Africa (Abisko and Ammarnäs) (Fig. 11). Thus, prior arrival to the closest wintering grounds is supported as an explanation for the development of leap-frog migration in the common ringed plover (Paper I).

Interestingly, experimental studies set out to test the effect of "prior occupancy" in wild birds have found little support for this to have a large effect on competitive ability in the long term. Rather, motivation to compete for a resource is more important and thus, competitive interactions may be shifting quickly in nature (e.g.,

Lindström et al. 1990). If this is true, it raises the question why newly arrived individuals from northern breeding populations are not able to compete for wintering grounds in Europe? After all, other traits, such as body size, do not seem to be of importance (Paper I). One possible explanation is that there may be a benefit of migrating to Africa, which may offer more benign environment seen to the energetic costs of thermoregulation and thus, potentially higher winter survival (Greenbegr 1980; but see Reneerkens et al. 2020) and potential positive carry over effects to the breeding season, may offset the extra migration cost (Drent and Piersma 1990, Meltofte 1996, Kersten et al. 1998, Carneiro et al. 2021). Temperate populations may stay in Europe for other reasons. One such reason was proposed by Alerstam and Högstedt (1980) by formulating the "Spring predictability" hypotheses (Table 1). They suggested that populations that are able to find wintering sites close to the breeding grounds, with tolerable conditions should do so, if they can make use of correlated environmental cues to time spring migration optimally in relation to the spring phenology at the breeding site (Alerstam and Högstedt 1980). As mentioned earlier, optimal arrival to the breeding site may facilitate higher reproductive output. But more importantly, in accordance with Alerstam and Högstedt's (1980) conjecture, is the arrival order in relation to competitors. The hypothesis further assumes that correlated environmental cues decrease with distance and, in general, populations that ultimately leave their climate zone, such as those from sub-Arctic and Arctic latitudes, would not be able to make use of such cues. Northerly populations should then pay the extra cost to migrate to more benign sites farther south (Alerstam and Högstedt 1980). However, the generality of this hypothesis falls when applied on all studied populations of common ringed plovers, as individuals from Malören segregate from those breeding at Ammarnäs in winter, despite that both are breeding in the sub-Arctic zone (Fig. 6 & 8) (Paper I).

Greenberg (1980) offered an alternative explanation for the development of leap-frog migration that does not include competition as a determining factor (Table 1). Instead, he suggested it is the relative ratio between time allocated in the breeding and wintering area, and the associated reproductive and survival costs/benefits in remaining at each given site, that dictated if individuals should pay an extra cost to migrate farther south. Similarly, to Alerstam and Högstedt (1980), Greenberg (1980) assumes that non-breeding survival increases at lower latitudes. We note that the time window for breeding, seen as the period between initiation of incubation to autumn departure, in the two populations breeding on the same latitude and in the same climate zone (Ammarnäs and Malören) is very similar (Väisänen 1977, Hedh, L., unpublished data, Paper I). Yet, they winter mainly separate, which is contrary to Greenberg's (1980) predictions (Paper I). However, critical tests of the seasonal survival rates between population have to be made before ruling out Greenberg's (1980) hypothesis.

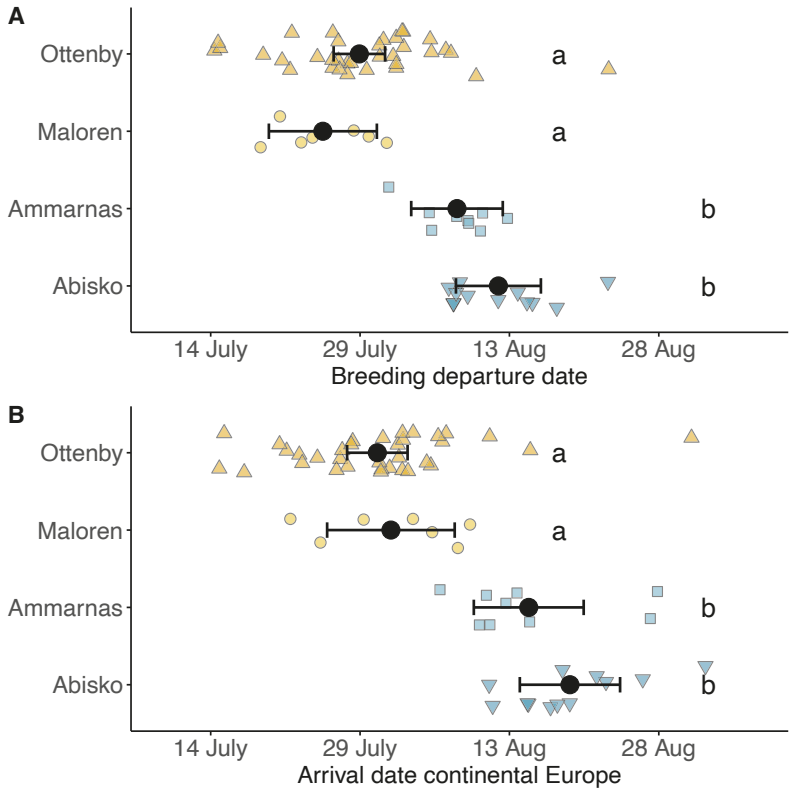

Figure 11. Autumn (A) departures and (B) arrivals to continental Europe in four populations of common ringed plovers *Charadrius hiaticula* breeding at different latitudes and climate zones in Sweden (Abisko: blue triangles, points down; Ammarnäs: blue squares; Malören: yellow points; and Ottenby: yellow triangles, points up). Points represents mean PC1, error bars 95% confidence limits and jitter individual data points. Letters denotes the significance level ($P < 0.05$) between groups. From Paper I.

Evolution of differential migration by sex in the common ringed plover

Similar to some hypotheses explaining leap-frog migration, within population segregation between sexes during the non-breeding season has been attributed to dominance related traits and competition for wintering resources (Gauthreaux 1978, 1982). Recapitulating that body size is considered to be positively correlated with dominance, the prediction based on the observed differential migration pattern in Paper II was that male common ringed plovers are smaller than females (the "Dominance" hypothesis, Table 1). However, males were, if anything, the larger sex in the population studied here (Paper II). The body size pattern also contradicts the suggestion that the larger sized sex would migrate shorter distance because body size is positively correlated with cold tolerance (the "Body size" hypothesis, Table 1) both in terms of reduced heat loss and the ability to conserve energy stores (Bergmann 1847, Ketterson and Nolan 1976). Also, the "Arrival time" hypothesis

(Table 1; Ketterson and Nolan 1976), which states that intrasexual competition among individuals in the sex that establishes breeding territories leads to shorter migration distance do not fit with the pattern observed because, in the common ringed plover it is the males that establishing the territory (Glutz von Blotzheim et al. 1975).

It is a possibility that females gain a competitive advantage by leaving the breeding site earlier than males (as observed in Paper II) and thereby arrive to the wintering sites earlier (Ketterson 1979), which was observed in the common ringed plover (Paper II). However, before accepting this as an explanation, one would first have to find the mechanism explaining why females leave earlier in the first place. Above, I concluded that prior occupancy could explain leap-frog migration between populations because initiation of autumn migration in northerly populations is restricted by the later breeding season. Such a mechanism is however not applicable within a single population. In some other wader species, females leave the males to take care for the offspring (Jenni 1974), whereby they theoretically could migrate earlier and gain prior access. However, there is to my knowledge no example in which this behaviour leads to sexual segregation in winter. Furthermore, the common ringed plover is strictly socially monogamous and both parents take part in the brooding (Blomqvist et al. 2001, Wallander 2001). Thus, finding the mechanism explaining earlier departure (or later departure by males) is essential to evaluate the option that females gain prior access and therefore can winter closer to the breeding area.

The general view is that longer migration distance, or migrating at all, always comes with a fitness penalty (Pienkowski and Evans 1985, Lok et al. 2015, Buchan et al. 2020), but recent studies indicate that this is not necessarily the case (Alves et al. 2012, 2013, Kentie et al. 2017). In Paper II, we propose an alternative hypothesis for the differential migration pattern observed. We postulate that migrating farther could be adaptive, given differential energetic needs upon spring arrival and dynamics of spatiotemporal fueling rates. We observed that 1) the pre-egg laying time in the common ringed plovers breeding in southern, temperate Sweden is up to 1.5 month (Väisänen 1977, Hedh, L., unpublished data, Paper II, III) and 2), males initiate display behaviour and defend breeding territories immediately after arrival (Hedh, L., unpublished data). Upon arrival, sub-zero temperatures are not uncommon in temperate areas and one could hypothesize that additional fuel stores accumulated at the wintering site, as an insurance for reduced foraging time in males after arrival, may increase male fitness (Holmes 1972, Ens et al. 1994, Morrison et al. 2005). Given that predation risk increases with increased body mass, fueling time prior to departure should then be minimized (Hedenström 1992, Witter and Cuthill 1993). Based on the premises described above, we used the flight range equation (Pennycuick 1975), which describes the required fuel load to fly a given distance, to calculate the time it would take to accumulate the necessary fuel stores to cover the migration distance for males and females, respectively (Paper II). We then added

the assumption that males carry additional fuel stores (10% of lean body mass) into the breeding area. By using these calculations, we found that longer migration distance in males would be preferred as long as the fueling rate is at least 2.18 times higher compared to the average female wintering site. If we assume that females, which we hypothesize carry little or no additional fuel stores after arrival, were to favour the same wintering site as males, fueling rate has to be 2.63 times higher compared to the average female wintering site (Paper II). Thus, given the assumptions and assumed adaptive values, longer migration distance for one sex could potentially be beneficial given certain conditions.

Annual cycle adaptations

The partitioning and scheduling of the annual cycle, with respect to the three main stages (breeding, moult and migration), depends largely on seasonal patterns, migration distance, and body size (Hedenström 2006, Buehler and Piersma 2008, Newton 2011). For instance, in Arctic or sub-Arctic areas the window of opportunity to breed is short compared to temperate areas. Temperate areas, on the other hand, allow for longer residency and earlier springs, and show larger variation in spring onset (Paper III). Particularly in larger birds breeding on the Arctic tundra, such as swans and geese, the breeding period becomes even more restricted because of the long incubation periods and low growth rate in the young (Hedenström 2006). Therefore preparation for breeding in some species (or populations) may start well before arrival to the breeding sites, generating an overlap between life-history activities, which may create energetic bottlenecks (Drent et al. 2003, Buehler and Piersma 2008, Williams et al. 2017).

Time allocation and potential bottlenecks in the common and little ringed plover

By comparing the annual cycle of two populations of common ringed plovers breeding in Arctic and temperate Sweden (Paper III), we found that the latter population spent more than twice as long time in the breeding area (136 vs. 60 days) and arrived up to 1.5 months before egg laying, compared to approximately 2 weeks in the former (Paper III, Hedh, L. *unpublished data*). Longer active breeding time havs been found in temperate populations of common ringed plover, compared to the Arctic, and it is not unusual with several replacement clutches or double brooding, which could partly explain the longer breeding site residency (Pienkowski 1984, Blomqvist et al. 2001, Wallander 2001). However, there was a considerable overlap in autumn migration timing between adults and juveniles in the temperate subspecies as revealed from ringing data at a temperate stopover site (Paper IV). Among most Arctic shorebirds adults usually migrate ahead of juveniles in autumn

(Kolthoff 1896), a pattern which was also observed among the tundra breeding subspecies of common ringed plovers (Paper IV). The differences in relative autumn timing between age groups in the two subspecies suggest that adults in populations breeding in temperate areas prolong their stay in the breeding area. Possibly the additional time is to initiate, or even complete, wing feather moult. Moult in temperate breeding populations of common ringed plovers is usually completed early in the autumn (Clapham 1978). However, at the moment, no moult data from the studied temperate population is available, but anecdotal evidence suggests that primary moult can be initiated already during incubation (Hedh, L., unpublished data). Wing feather moult is energetically expensive and do not usually overlap with migration (Lindström et al. 1993, 2010, but see Holmgren et al. 1993), but the climate on the wintering site may set limits on the possibility to carry out moult, due to for example low temperatures and less available food (Machín et al. 2018). If moult is conducted in close proximity to migration or even overlap with migration, this may result in an energetic or time associated bottleneck (Buehler and Piersma 2008), which may have consequences for the behaviours employed during the migratory journey, such as employing an energy minimizing strategy (Hedenström and Alerstam 1997, Hedenström 2008)

Interestingly, we found that all but one little ringed plover had long interruptions during autumn migration (lasting up to 77 days in one individual, which utilized a site in south-eastern France) (Paper VI). This time period is far longer than needed to fuel up for the next migratory flight (even with modest fueling rates), as the little ringed plover seem to make many but relatively short flights (Paper VI). Accounts of moult in the little ringed plover have been found short after the main breeding period or during early migration in, for example, Camargue, France (Glutz von Blotzheim et al. 1975). This suggests that the interruptions of migration in the little ringed plover found in Paper VI could be associated with moult. If this is true, it raises the question why little ringed plover interrupt autumn migration to moult, instead of postponing it to after winter site arrival? One reason could be that they make use of productive, ephemeral wetlands on the route. To answering this question requires further tracking with devices offering higher spatial resolution, coupled with studies in the field.

Migration timing in relation to migration distance and breeding site climate in the common ringed plover

Not surprising, the Arctic population of common ringed plovers always arrived and departed later to the breeding and wintering sites compared to the temperate population, indicating that the two populations are adapted to their respectively breeding site specific phenology (Conklin et al. 2010; Briedis et al. 2016 Paper III). However, as mentioned earlier, proximity to the breeding site during winter can allow birds to use weather cues, such as ambient temperature, to determine

when to optimally time spring migration in relation to the conditions at the breeding site (e.g. Burnside et al. 2021; Powers et al. 2021). We estimated yearly variation in spring arrival date by using citizen science data from the two provinces in which the breeding areas of the Arctic and temperate populations are located, and found that that the temperate population had a larger interannual variation in arrival date than the Arctic population. This suggests a more flexible migration schedule in the temperate compared to the Arctic population (Fig. 12) (Paper III). However, currently we lack data from repeated tracks to analyse if this variation is due to flexible spring departure or if arrival time is adjusted after migration is initiated, and depends on conditions experienced *en route* (e.g. Amélineau et al. 2021).

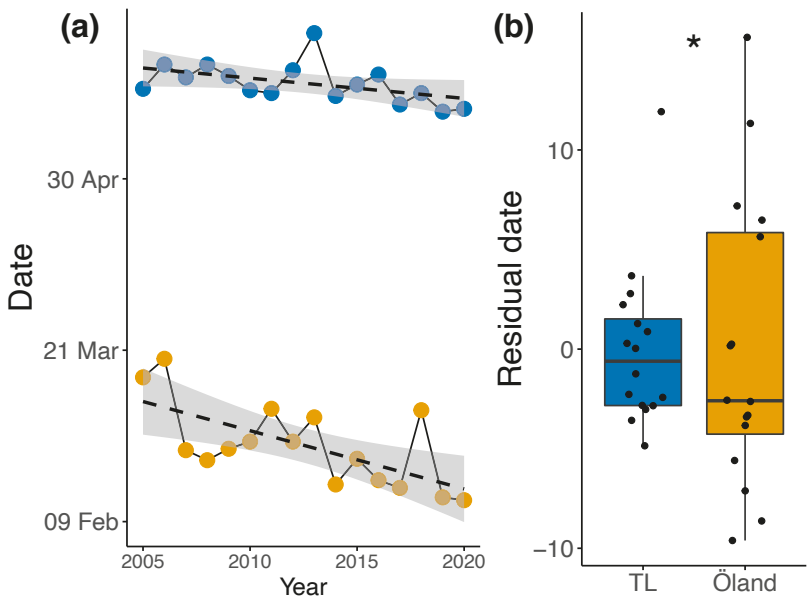

FIgure 12. Variation in spring arrival dates between common ringed plovers breeding in the region of Torne Lappmark (TL), northern Sweden (in which the NBP breeds) and the province of Öland, southern Sweden (in which the SBP breeds) based on citizen science data obtained from the Swedish Species Observation System (Swedish Species Information Centre) collected between 2005 and 2020. Data are presented as (a) yearly variation of spring arrival to Torne Lappmark (blue dots) and Öland (yellow dots) around the fitted regression lines (dashed lines), and (b) the residuals around the fitted regression lines. Boxes show the 25 and 75% quartiles, whiskers the 1.5 times inter quartile range. Jitter shows individual data points. From Paper III.

Migration speed

Because competition for breeding resources and early initiation of breeding may be associate with higher reproductive output (Perrins 1970, Kokko 1999, Morrison et al. 2019, Halupka et al. 2021), the time spent on spring migration should be minimized (Hedenström and Alerstam 1997). However, arriving too early to the breeding ground may reduce fitness due to inclement and adverse weather conditions (Kokko 1999). Building on the reasoning regarding the ability to time spring migration in relation to weather cues, which may be correlated between breeding and wintering sites, minimizing time should be particularly important for a population wintering far from the breeding area. This is because timing of arrival should preferably be after the average date of spring onset at the breeding grounds (Bauer et al. 2020) and thus, timing of migration in long distance migratory populations are set by the circannual clock (Alerstam and Högstedt 1980, Gwinner 1996). Indeed, migration speed in spring has been found to be higher compared to autumn (Nilsson et al. 2013; but see Norevik et al. 2017; Carneiro et al. 2019, Paper III, VI), which can partly be explained by increased air speeds (Hedenström and Alerstam 1995, Karlsson et al. 2012). However, higher air speeds in spring have been found in both short and long-distance migratory birds (Nilsson et al. 2014). One may also consider that an increased migration distance may create more time constraint seen to the annual cycle and indeed, in multi-species comparisons, higher migration speeds have been found among long-distance migrants in autumn (Ellegren 1993, Alerstam 2003).

In accordance with general predictions, we found that spring migration speed was higher in an Arctic population of common ringed plovers compared to a temperate population (Paper III). Furthermore, there was no difference in migration speed between the two populations in autumn (Fig. 13). However, spring migration speed in the temperate populations was lower compared to the autumn migration speed (Fig. 13) (Paper III). These results are surprising, because the total flight time was found to be 36% lower in spring compared to autumn in the temperate population as revealed by MDLs (Paper IV). Thus, the most likely explanation, considering that the average time between departure and arrival was only 5 days in Paper III, is the fueling time prior to the first migratory flight.

One intriguing potential explanation for why individuals from the Arctic population in Paper III achieve relatively high spring migration speeds compared to the temperate population, despite that they are dependent on larger fuel stores to cover their first migratory flight, could be because they migrate later in spring, when food stuffs are more accessible along the route (i.e. on European stopover sites). Thus, they may be using European stopover sites as a well-timed "stepping-stone" generating high instantaneous migration speeds (Drent and Piersma 1990, Gudmundsson et al. 1991). However, to explore this possibility, which could also partly be an explanation for leap-frog migration (Drent and Piersma 1990, Bell

1996), one must measure the dynamics of food availability over large spatial and temporal scales.

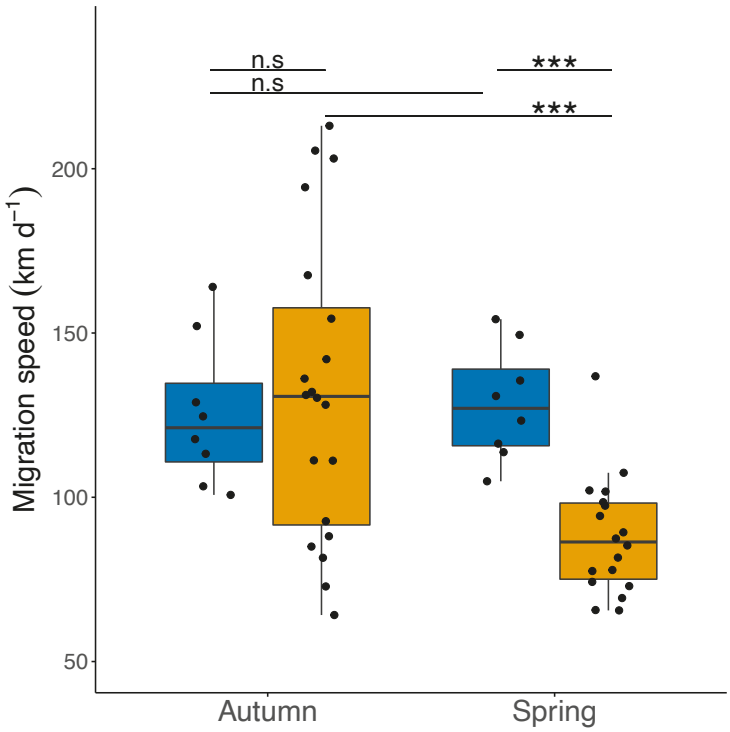

Figure 13. Autumn and spring migration speeds (km d-1) in common ringed plovers breeding in an Arctic population (Abisko; blue boxes) and a temperate population (Ottenby; yellow boxes). Boxes show the 25 and 75% quartiles, whiskers the 1.5 times inter quartile range. Jitter shows individual data points.From Paper III.

The process of migration in relation to migration distance and adaptive values

Division between migratory flight and stopovers

As mentioned earlier, the migratory process is divided between migratory flights and stopovers, which are used to accumulate fuel reserves used during flight. Because fuel is metabolized at a higher rate compared to the rate of fuel accumulation (Lindström 1991, 2003, Pennycuick 2008), more time should be spent on fueling during migration. Based on estimations of maximum daily metabolizable energy, maintenance costs (i.e. basal metabolism and thermoregulation) and flight

metabolism, Hedenström and Alerstam (1997) calculated that the time ratio between flight and fueling time should be 1:7 (12.5% flight time) over the whole migratory journey. We found empirical support for this ratio in both common and little ringed plovers (Paper V, VI). However, the ratio was lower in spring for the common ringed plover, which may be explained by wind-support as suggested by the shorter total flight times in spring compared to autumn (mentioned above; paper V) or low fueling rates.

Number and duration of migratory flights

Some birds, like the bar-tailed godwit *Limosa lapponica baueri* breeding in Alaska, are able to cover the whole migratory journey in one single flight after one longer fueling episode (Gill et al. 2009). However, most birds need to stop several times for re-fueling, generating distinct episodes of migratory flights and fueling. Piersma (1987) described three hypothetical outcome patterns ("hop", "skip" or "jump") depending on constrains in fueling conditions and possible effects of wind. The bar-tailed godwit, mentioned above, is an example of a typical "jumper". However, fueling conditions may directly prevent long "jumps" and will result in smaller "hops" instead (Piersma 1987). However, the process of migration may also be related to the adaptive value of the behaviour performed. For instance, if the goal is to minimize the time of migration a bird should put on large stores to cover long distances ("jumps"), given that the fueling rate is sufficiently high (Alerstam and Lindström 1990). However, if the resource landscape is homogenously high, the fastest way to travel could be to make more, but shorter, flights with equal step length (Weber and Houston 1997). One reason for this, particularly related to waders, could for example be to reduce the time required to remodel the digestive tract (Weber and Hedenström 2001). Similarly, if the migratory direction is pointed against a resource gradient (i.e. fueling deposition rates are increasing) lower departure fuel loads and shorter flights would be expected at the beginning of the migratory journey, but should gradually increase with increasing rates of fuel deposition (Ellegren 1990, Lindström and Alerstam 1992, Weber and Houston 1997, Lindström 1998, Lindström et al. 2002).

Based on the reasoning above, the number, duration and division of migratory flights suggest that common ringed plover breeding in southern Sweden are attending a time minimization strategy in autumn (Paper V). The number of autumn migratory flights did not increase with increasing migration distance, instead 75% of all individuals migrating > 2000 km made at least one flight longer than 20 hours (Fig. 14a) (Paper V). Furthermore, 90% of all flights > 20 hours occurred after the second stopover (Fig. 14c) This suggests that common ringed plover move towards stopover sites, e.g. the Danish/German/Dutch Wadden Sea, with potentially higher fuelling rates, whereby the individuals migrating farther fuel up extensively and perform one relatively long migratory flight (Paper V). If the birds were energy

minimizing one would expect those individuals migrating farther to continue making more but shorter "hops" (Hedenström and Alerstam 1997). In spring, common ringed plovers migrating longer distances made more stopovers compared to individuals migrating shorter distances. This pattern could indicate that they are time-minimizing in accordance to the theoretical prediction made by Weber and Houston (1997). However, other factors could explain the spring pattern. For example, individuals may modulate the progression of spring migration in accordance with available resources or the progression of spring (Pakanen et al. 2018, Bauer et al. 2020). Therefore, based on the current data, it is impossible to determine which currency is ought to be minimized in during spring migration.

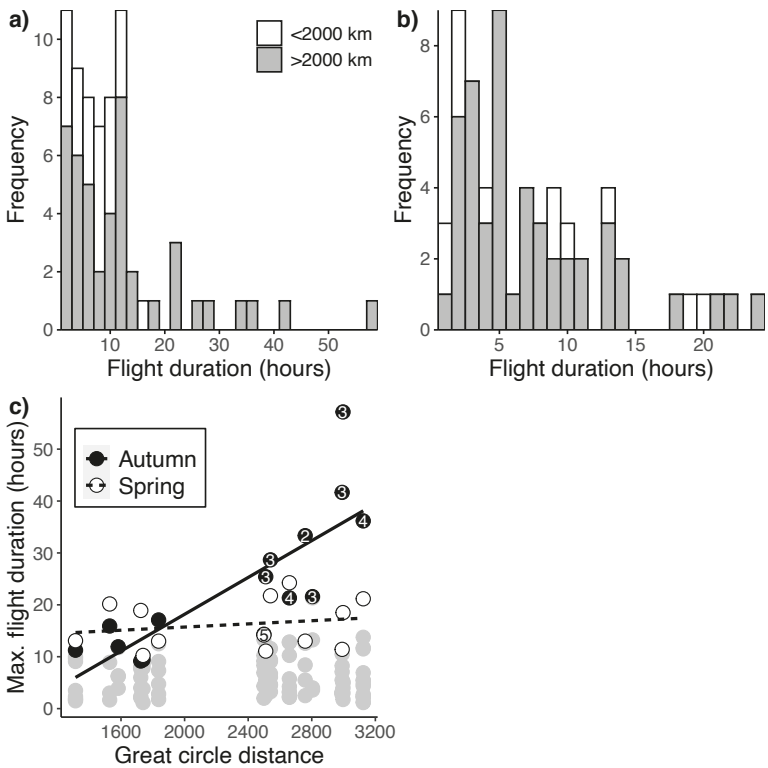

Figure 14. Durations of individual migratory flights a) distribution of individual flight durations in autumn and b) spring migration, and c) maximum duration of individual migratory flights in autumn and spring in relation to GC distance. In c) trendlines indicate significant interaction between season and GC distance, grey background scatter represents the duration of all remaining individual migratory flights, and numbers indicate individual flight number, i.e. 3 = 3rd flight in order (note that the black 5 denotes an autumn maximum migratory flight which is hidden).

As mentioned in an earlier section, the total flight duration during spring migration, in a temperate population of common ringed plover, was 36% lower compared to autumn (Paper V). Since the detour in autumn was very low (1.8%) the shorter total flight duration cannot be explained by a shorter route in spring. Rather it may be explained by either tail-winds or increased air speed, or both (Kemp et al. 2010, Klaassen et al. 2010, Nilsson et al. 2014). If air speeds are increased it may be indicative of a time-minimization strategy (Alerstam and Lindström 1990). However, future studies aiming to partitioning the effect of winds and seasonal modulation of air speeds is needed to draw further conclusions.

Conclusions and future outlook

In this thesis I have revisited some fundamental questions and theories regarding the evolution of migration patterns and behavioural adaptations during migration, which may be linked both to completing the journey itself and to the adaptive value relating to the next step of the annual cycle. To do so I used individual based tracking techniques to comparatively study among and within population differences in seasonal, spatiotemporal distribution patterns and migratory behaviour in the common and little ringed plover.

Individual tracking studies have furthered our knowledge about population specific winter destinations and connectivity (McKinnon and Love 2018). In Paper I and II three important findings related to the migratory connectivity were made, which adds to the current natural history of the common ringed plover. Firstly, we found that birds from two populations breeding only 350 km apart and on nearly the same latitude (in sub-Arctic Sweden), segregated latitudinally during the winter (Paper I). Secondly, individuals in the temperate breeding population utilized wintering sites along the whole known European wintering distribution (Paper II). And lastly, we found that male common ringed plovers, on average, winter farther from the breeding site than do females (Paper II). Apart from these findings we confirmed the general pattern of leap-frog migration pattern, i.e. that northerly populations associated with alpine/tundra environments winter at lower latitudes compared to temperate breeding populations (Paper I).

The findings in Paper I provide a good starting point to evaluate and test hypotheses aiming to explain the evolution of migration patterns in general, and leap-frog migration in particular. Based on the furthered knowledge of the wintering distribution and body size relationships between populations breeding in Sweden, the "Dominance/winter competition" hypotheses, predicting that populations with larger body sizes should winter closer to the breeding grounds, could be rejected - in the case of the common ringed plover (Paper I). Similarly, the "Spring predictability" hypotheses cannot explain the difference in migration distance between the populations breeding on the same latitude (Ammarnäs and Malören) (Paper I). If, for example, only the Arctic and temperate populations would have been used in the tests, all hypotheses would ultimately have been supported. This highlights the importance of natural history in basic life science (Travis 2020).

One alternative explanation to the results in Paper I is that the breeding population on Malören (one of the sub-Arctic populations) could originate from populations breeding farther south, which have recently colonized northwards. Thus, one may speculate that the current pattern (i.e. that they utilize wintering sites in Europe) can be explained by history rather than any competing hypotheses e.g. that they arrive to the wintering site earlier and therefore outcompete individuals arriving later (Paper I). To address this, studies to establish the genetic structure of the populations included in this work (and preferably more intermediate populations) need to be carried out, and is an obvious next step forward.

Neither of the hypotheses concerning the evolution of differential migration by sex could explain the pattern found in Paper II. Such a situation is rare, as support for all or many of the hypotheses are usually found (Ketterson and Nolan 1983). Building on the insights provided by recent tracking studies, showing that birds are able to migrate longer distances than previously believed (considering theoretical physiological constraints) and that longer migration not always incur a fitness penalty (Pennycuick 1975, Hedenström 2010a, b, Niles et al. 2010, Alves et al. 2012, Lindström et al. 2015), we suggest a new hypothesis proposes that a longer migration distance in one sex can be adaptive (Paper II).

In contrast to many empirical studies (e.g. Nilsson et al. 2013), we found lower spring migration speeds compared to autumn, in the temperate population of common ringed plovers (Paper III). This was mainly due to our inclusion of the fueling period prior to the first flight. We calculated the length of the first fueling period based on a conservative but reasonable fueling rate and the measured distance/duration of the first migratory flight in both autumn and spring. This may result in migration speeds that are not entirely true, but most likely closer to real migration speed. Nevertheless, inclusion of a fueling period prior to the first flight, highlights the impact this period may have on speed calculations and the potential danger to draw conclusions about strategy based on estimates where only the period between departure and arrival is included (Winkler et al. 2014, Carneiro et al. 2019, Lindström 2020).

Studying within population differences in migratory behaviour in the common and little ringed plovers by using multi sensor data loggers revealed exciting behavioural patterns in relation to migration distance (Paper V, VI). The pattern of individual flight durations suggests that common ringed plovers, in a temperate population, are time minimizing during autumn migration. This notion goes against the general belief that birds are less time constrained in autumn than spring and may be of importance when considering competition as an important driver for the evolution of between population migration patterns.

Although tracking reveals new and exciting opportunities to revisit old hypotheses, it still has many limitations. Throughout this thesis I have mainly compared outcomes from tracking devices with predictions and assumed adaptive values.

Thus, I have not measured environmental factors or fitness (survival and reproductive success). Instead I have used information from the literature to make assumptions about the condition different populations of particularly common ringed plover may experience at different seasons and locations. Many of the new insights drawn from this work still need to be confirmed with good old, tedious and time-consuming ecological field work. For instance, the predictions from the new hypothesis presented in Paper II, which explains why male common ringed plovers migrate farther than females, require to both measure site specific spring fueling rates and arrival fuel loads. Similarly, the potential gradient in fueling rate, with gradually increasing fueling rates towards the migratory direction, during autumn, as suggested in Paper V needs to be confirmed by studying fueling rates along the whole migratory route.

Finally, the implication of the breeding environment on the development and canalization of the behavioural phenotype (i.e. winter destination or timing) has not been considered. It has been shown that different environments have different impact on migratory phenotypes, such as homing to natal grounds (experienced after displacement during ontogeny) (Verhoeven and Loonstra 2020). To assess the role of environment during ontogeny, particularly just after hatching, may help to elucidate new aspects and insights about the evolution of migration patterns, such as leap-frog migration. The merit of the study system put forward in Paper I (e.g. the among population variation in migratory behaviour and that all populations largely utilize the same migratory fly-way) may constitute an excellent opportunity for future displacement experiments combined with tracking to assess the effect of the environment on the phenotype (Wikelski et al. 2007, Piersma 2011). A similar question concerns the choice of wintering site among males and females in the temperate population (Paper II). Studies have indicated that individual wintering site is decided early in life (e.g. Townshend 1985), but there is also evidence that, for example, migratory routes improve over life-time with respect to the optimal choice (e.g. Sergio et al. 2014). Thus, assuming that the new hypothesis put forward in Paper II explains the observed pattern, are males settling at sub-optimal wintering areas selected against or do they learn over the course of their life-time (Verhoeven et al. 2019)? Future tracking devices that are small enough even for medium sized birds (like the ringed plovers) and can last for several years, which is required to address these kinds of questions, already lay at the door step.

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Interpretation of the study species made by Phillip Downing.

Populärvetenskaplig sammanfattning

Flyttfåglar har fascinerat människor i århundraden. Att fåglar flyttar är särskilt märkbart på våra svenska breddgrader, där skillnaden mellan säsongerna är påtagliga. När hösten och tillika de första frostnätterna kommer är det dags att flytta söderut, särskilt för insektsätande fåglar. I folkmun pratar vi ofta om flytt eller stannfåglar, vilket inte alltid är helt rätt begrepp. Många av de fåglar som vi upplever som stannfåglar, liksom koltrast och i södra Sverige även rödhake, är i själva verket ofta individer som faktiskt har flyttat från nordligare platser.

Det är inte ovanligt att nordligt häckande fåglar flyttar söderut och etablerar vinterrevir där en annan individ av samma art häckat tidigare under sommaren. Men som senare har lämnat Sverige för kontinenten. Detta är ett flyttningsmöster som kallas ”kedjeflytt”. Det är heller inte helt ovanligt att fåglar från populationer som häckar långt norrut, övervintrar längst söderut. Även kallat ”spegelflytt”. I det här fallet skiljer sig inte bara flyttningsavståndet, men också klimatförhållandena på de olika platserna de olika populationerna upplever under årscykeln. Det är inte heller ovanligt att flyttningsavståndet skiljer sig åt mellan hanar och honor, inom samma population. Vanligtvis brukar hanar övervintra närmast häckningsplatserna. Detta är ett mönster som Carl von Linné beskrev redan på 1700-talet.

Men varför uppstår flyttningsmöster som ”spegelflytt”? Och hur ska en flyttande fågel bete sig på bästa sätt för att genomföra flytten så optimalt som möjligt i förhållande till flyttningsavståndet och de varierande miljöerna de kan tänkas utsättas för? För att försöka svar på de här frågorna har jag studerat större och mindre strandpipare under deras flyttning. Jag har använt mig av så kallade ljus- och aktivitets-loggar för att följa deras rörelsemönster under ett helt år. Anledningen till att just de här arterna studerats är att båda arterna uppvisar stor variation i flyttningsavstånd. Både mellan och inom populationer. Större strandpipare häckar i södra och norra Sverige. Den större strandpiparen är en typisk ”spegelflyttare” där de nordligaste populationerna övervintrar i Afrika och de sydligaste längs med den europeiska atlantkusten. Populationer av den mindre strandpiparen från södra Sverige har tidigare visat sig övervintra på lägre breddgrader, men från Afrika i väster hela vägen till Indien i öst. Faktum är att en hane och en hona som häckat tillsammans i Skåne, flera år i rad, har befunnit sig på nästan 4000 kilometers avstånd från varandra under varje vinter!

Fyra olika populationer av större strandpipare, utspridda över Sverige från norr till söder, undersöktes. Vi fann liksom tidigare att den allra nordligaste populationen övervintrade i Afrika, och den allra sydligaste i Europa. Men, vi fann att två populationer i norra Sverige, som häckar på samma latitud, men i olika miljöer, hade olika övervintringsplatser. Den ena, häckande i fjällen, övervintrade liksom den nordligaste populationen i Afrika, och den andra, häckande i Bottenviken, övervintrade i Europa.

Så tillbaka till frågan. Varför flyttar nordliga populationer längre, och förbi, sydliga populationer? En hypotes är att det råder konkurrens om övervintringsplatser så ligger så nära häckningsområdena som möjligt. Större fåglar anses var mer konkurrenskraftiga och fåglar som anländer tidigt har en fördel jämfört med nykomlingar. Intressant nog hittade vi ingen skillnad i individuell kroppsstorlek mellan populationerna som häckar på samma breddgrad, men som övervintrar åtskilda. Dessutom var det en stor skillnad i kroppsstorlek mellan den av de två populationerna som övervintrar i Europa och den sydligt häckande populationen. Kroppsstorlek har alltså inget att göra med vilken breddgrad övervintringen sker på. Däremot anländer båda populationerna som övervintrar i Europa tidigare än de två andra. Således skulle den senare häckningssäsongen i fjällen göra att årscykeln blir senarelagd och när de anländer till potentiella övervintringsplatser i Europa är dessa redan uppfyllda.

En annan hypotes är att det kan finnas en fördel att häcka nära häckningsområdet, särskilt om det är möjligt att förutspå vårens ankomst med hjälp av de stora vädersystemen. Då finns det möjlighet att anpassa avgångstiden för vårflytten efter vårens frammarsch, så att häckningen kan starta tidigast möjligt. Populationer som flyttar ut ur sin klimatzon under vintern, tillexempel arktiskt häckade populationer, kan inte utnyttja vädersystem för att förutspå vårens ankomst från övervintringsplatsen. I sådant fall skulle det snarare vara en fördel att förlänga flyttsträckan och övervintra i tillexempel Afrika, istället. Där är födotillgången mer konstant och temperaturen är högre (notera dock att för hög temperatur också innebära en kostnad). Det faktum att de två populationerna som häckar på samma breddgrad, i den subarktiska klimatzonen (fjällen och Bottenviken), skiljer sig åt under vintern innebär att den här förklaringsmodellen inte är särskilt trolig. Varför skulle den ena populationen, men inte den andra, kunna förutspå väderutvecklingen, givet att det är mer eller mindre samma avstånd mellan de två häckningsplatserna till de europeiska övervintringsplatserna?

Jag fann vidare att individer från populationen häckande i södra Sverige spred ut sig över hela det kända europeiska övervintringsområdet (från norr till söder). Dessutom flyttade hanar längre än honorna. Ett mönster som är extremt ovanligt. Ingen av hypoteserna som förklarar detta mönster kunde styrkas. Därför formulerade jag en ny hypotes som, till skillnad från de flesta andra, går ut på att det ibland kan löna sig att flytta längre sträckor om förutsättningarna för att lägga

på sig fett där är högre jämfört med övervintringsplatser som ligger närmare häckningsområdet.

Nästa fråga rörde hur fåglar anpassar sitt beteende till olika flyttningsdistanser och de förutsättningar de direkt erfar eller förväntar sig. För det första: flyttning tar tid. För att kunna flyga längre sträckor måste tillräckligt mycket energireserver fyllas på. Detta gör fåglar genom att äta och lägga på sig fett, vilket är det primära flygbränslet. Men energikonsumtionen under flygning är betydligt högre än fettupplagringshastigheten. Därför spenderar flyttfåglar allra mest tid till att äta. Baserat på teoretiska uträkningar som inkluderar flygkostnad, energiinnehåll av flygbränsle (fett) och kostnaden för basala livsuppehållande system, borde mindre flyttande fåglar spendera 87,5% av sin totala tid till att leta föda och resterande 12,5% till att flyga. Vi fann bevis för detta förhållande för större och mindre strandpipare.

Alltså, ju längre flytten är, ju mer måste fett måste lagras och desto mer tid tar flytten. Långdistansflyttare borde därför försöka minimera tiden de spenderar på själva flytten. Vidare så är individer tillhörande populationer som häckar långt norrut, tillexempel Arktis eller fjällen, begränsade av en kort häckningssäsong. Därför förväntas det att långdistansflyttare borde flytta snabbare än kortdistansflyttare. Vi fann detta förhållande mellan en arktisk och sydlig population på våren. Däremot fann vi att den tempererade populationen av större strandpipare och mindre strandpipare flyttade långsammare på våren än på hösten. Detta är förvånande. Generellt bör vårflytten vara snabbare, eftersom det är bråttom till häckningslokalerna för att etablera revir i de allra bästa områdena. Den långsammare vårflytten för de sydligt häckande större strandpiparna kan förklaras på olika sätt. En trolig förklaring är dock att de lägger på sig större mängd fett innan den första flygningen (vilket vi vet tar tid). En annan förklaring är att de måste anpassa sin frammarsch eftersom det fortfarande kan vara vinter när de anländer. Vi fann baserat på data från Artportalen (ArtDatabanken), som samlats in och rapporterats genom åren av fågelskådare runtom i Sverige, att större strandpipare som häckar i södra Sverige anländer med mer mellanårsvariation än de som häckar längre norrut. Detta indikerar att strandpipare som häckar i Europa och anländer tidigare på våren anpassar sin ankomst efter väder och att strandpipare som övervintrar i Afrika och häckar i Arktis baserar sin flytt på en inre tidtabell.

Hur flyttningen delas upp i olika etapper av flygningar och stop för fettupplagring kan te sig på många olika sett. Myrspovar Limosa lapponica bauri som häckar i Alaska och övervintrar på Nya Zeeland, lägger på sig fett en gång och gör sedan en enda flygning på hösten. På våren å andra sidan, flyttar den längs med östra Asien och gör fler stop på vägen. Man kan tänka sig flera olika anledningar till varför detta varierar mellan säsonger och flyttningsavstånd. Det första är såklart vart födan finns. Om det är långt mellan rastplatserna måste de göra längre flygningar. Om det däremot är kort, kan det löna sig att flytta i kortare etapper. EN annan variabel är vindmönster. Om det finns en möjlighet att få hjälp av lite extra medvind kan det

löna sig stanna och lägga på sig mer fett för att sedan snabbare flyga en längre sträcka. Uppdelningen beror såklart också på vilken strategi en fågel ämnar anta. Om det finns gott om resurser längs med hela flyttsträckan skulle vi förvänta oss att en fågel som vill flytta så snabbt som möjligt borde ”hoppa” mellan rastplatser och lägga på sig lite fett i taget. Om rastplatser med goda fettupplagringsmöjligheter däremot är utspridda så bör fågeln lägga på sig mer fett och göra längre flygningar. En fågel som å andra sidan ämnar minimera energiåtgången under flytten ska alltid göra små hopp, med små fettreserver, eftersom en högre vikt ökar flygkostnaden (detta är analogt med att en lättare bil drar mindre bensin per mil). Som tidigare antar vi att fåglar är under tidspress på våren, men mindre så på hösten. Vi fann att större strandpipare som häckar i södra Sverige verkar tidsminimera sin flyttning även på hösten. Genom att mäta flygtiderna kunde under hela höstflyttningen verkar det som om de börjar med att göra små hopp i början av flyttningen innan de når de stora, produktiva tidvattensområdena i Vadehavet. Härifrån följer två mönster beroende på vilka vinterkvarter en given strandpipare är destinerade för. De som flyttar längre, tillexempel till Portugal och Spanien, gör totalt lika många flygningar som de som endast ska till Frankrike, men de gör en långflygning (ofta över 20 timmar). Detta tyder på att strandpiparna börjar med att göra korta flygningar för att de är begränsade av fettupplagringshastigheterna i södra Sverige. Vi fann att fettupplagringshastigheten vid Ottenby, där strandpiparna häckar, bara var 1,7% av den fettfria kroppsvikten per dag, vilket är relativt lågt jämfört med andra uppmätta värden. När de senare kommer till Vadehavet, där upplagringshastigheten troligare är högre, vilket vi kan anta eftersom de bara stannar en kortare tid följt av en långflygning.

Detta är några exempel på vad modern spårningstecknik kan lära oss om fåglars flyttningsbeteende. Som alltid så har de här studierna genererat fler frågor än svar och framtida studier av den större och mindre strandpiparen ligger redan på ritbordet.

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