CLIMATE CHANGE EFFECTS ON MIGRATORY BIRDS AND ON THE ECOLOGY AND BEHAVIOUR OF THE WILLOW WARBLER (PHYLLOSCOPUS TROCHILUS)

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Climate change effects on migratory birds and on the ecology and behaviour of the willow warbler (*Phylloscopus trochilus*)

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Nature's beautiful, random truth !

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II. **Hedlund JSU**, Jakobsson S, Kullberg C, Fransson T (2015) Regional differences in phenological response to climate change in willow warblers (*Phylloscopus trochilus*). *Manuscript*

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I am also a co-author of the following paper, which is not included in this thesis, but was published during my doctoral studies, in participation with colleagues in the EkoKlim Project at Stockholm University:

Elmhagen B, Destouni G, Angerbjörn A, Borgström S, Boyd E, Cousins SAO, Dalén L, Ehrlén J, Ermold M, Hambäck PA, **Hedlund JSU**, Hylander K, Jaramillo F, Lagerholm VK, Lyon SW, Moor H, Nykvist B, Pasanen-Mortensen M, Plue J, Prieto C, van der Velde Y and Lindborg R (2015) Interacting effects of change in climate, human population, land-use, and water use on biodiversity and ecosystem services. *Ecology and Society* **20**(1): 23

Abbreviations

GSO	Growing season onset
HSBO	Haparanda-Sandskär Bird Observatory
NAO	The North Atlantic Oscilliation
NDVI	Normalized Difference Vegetation Index
PCA	Principle Component Analysis
PLC	Powerline corridor
SBO	Sundre Bird Observatory
SCB	Sweden Statistics, Statistiska Centralbyrån
SFA	The Swedish Forestry Agency, Skogsstyrelsen
SLU	Swedish University of Agricultural Sciences, Sveriges Lantbruksuniversitet
SMHI	The Swedish Meteorological and Hydrological Institute

Prologue

It is no wonder that birds are among the most well-studied organisms in the world. They are conspicuous in appearance and sound, widely distributed among many different biomes and they master the one artform that is quite beyond the reach of mankind and consequently, ever intriguing to us: flying. Many bird species utilize this ability when migrating, thus joining one of the greatest animal mass movements in the world. The Eurasian-African flyway alone distributes an estimated 5 billion individual birds twice every year (Moreau 1972). The apparent absence of birds during European winter was noticed early on by antique scholars and probably pondered on long before the written word. Some very creative thinking was done by the early academics; Aristotle proposed that at summer's end the robin changed into the redstart, and the 17th century scientist Charles Morton suggested that birds disappeared in autumn because they took to the moon (Mahnken 1998). Well known is Carl von Linné's (Linnaeus) comment on swallows hibernating in the sludge of lake beds. He was not as sure of storks though:

> *"... if they travel to the warm countries, or if they rest on the lakebeds among the swallows, is yet unknown... "*
> — Carl von Linné, Scanian travel/ Skånsk resa, 1749.

The myth about swallow hibernation was first introduced by Aristotle (384-322 BC) and apparently still revered more than a thousand years later, which is unsurprising considering the astoundingly high regard Aristotle possessed for hundreds of years. Yet, sludge sleeping swallows did awake skepticism among Linnaeus' contemporaries. In the 1740s Johann Leonard Frisch tested the hypothesis by tying ribbons onto the legs of the swallows and when he found that the ribbons were not wet in spring, he concluded that the idea had been disproven (Moss 2009). Ribbons were later replaced by aluminum rings and in the 1890s the first scientific ringing of birds started (Preuss 2001).

Today it is no longer a mystery where birds go in autumn, but there are still unanswered questions regarding bird migration and ever new uncertainties arise, e.g. how the effects of climate change may alter phenology. In this thesis, I will present research topics, scientific results and discussions on how climate change may exert responses in birds by affecting their breeding and migration phenology (**Paper I, II, V**), distribution behaviour (**Paper III)** and habitat availability (**Paper IV**). One small migratory bird plays the leading role and constitutes the main study system: the willow warbler (*Phylloscopus trochilus*).

Introduction

Migration

Migration is a phenological trait that has developed independently during the adaptive history of many animal groups. Bird phylogeny reveals that a pendulation between residency and migration has occurred several times without apparent evolutionary constraint and that a variety of migratory modes exist within closely related avian species (Alerstam *et al.* 2003). Migratory behaviour can be differentially expressed within populations (Newton 2007; **Paper II**) and within species, e.g. depending on age and sex (reviewed by Alerstam & Hedenström 1998; **Paper I, Paper II**). There are for example species in which juveniles leave the breeding area before adults or use other routes than adults (Hedenström & Petterson 1987; Hake *et al.* 2003), subordinate individuals that migrate further than dominant (Lyngs 2003; Newton 2007) and males (protandry) or females (protogyny) that arrive before the other sex to the breeding ground (Oring & Lank 1982; Morbey & Ydenberg 2001; Rubolini *et al.* 2004; **Paper I**). A migratory programme, here referring to the combined elements of migration direction, distance, wintering ground and breeding ground, is susceptible to rapid micro-evolutionary alterations, as seen by the change in wintering ground by blackcaps (*Sylvia atricapilla*, Stafford 1956; Mokwa 2009) and the shift from sedentary to migratory behaviour in European serins (*Serinus serinus*) when they expanded their range northwards (Mayr 1926; Berthold 1999).

Birds migrate primarily as an adaptation for utilizing seasonal resource peaks and escaping seasonal resource depletions. Essentially, this means that migration serves as a way of changing habitat between periods of survival and reproduction. Seasonality is fundamentally associated with the life-history of migrating animals and a condition for the evolution of the behaviour. It is also at latitudes of extreme seasonality where the largest percentage of bird species are migratory; above the Arctic Circle more than 80% of all species migrates, whereas less than 10% do at the equator (Ferrer *et al.* 2008). In Europe, more than 70% of the approximated 407 breeding birds migrate if partial migrants are included, i.e. species in which some individuals are migratory but others are not (Berthold 1999). Interestingly, and perhaps appearing contradictory, migration is suggested to first have arisen in the tropics, or at least in sub-tropical environments (**fig.1**). The first bird species evolved in tropical climates and the precursor to migratory behavior most have been present among these early avian species before colonization of the temperate zones, or environments with corresponding conditions. Thus, initially, migration was over short distances and partial. As migration is an extremely adaptable and successful life-history trait, it is suggested to have quickly become common. Once partial migration was present, birds had acquired a basic behavioural component that could be tuned into various modes by simple selection and relatively rapid micro-evolution, so that a whole behavioural spectrum became available (Berthold 1999).

Figure 1. Wenceslas Hollar's (1607-77) "The creation of birds and fishes". Source: Wikimedia commons, public domain artwork.

Through the evolution of migration, many ecological components have been involved in shaping its development, e.g. parasite avoidance (Piersma 1997; Alerstam *et al.* 2003), predator avoidance, orientation ability, competition and life-history (reviewed by Alerstam *et al.* 2003). In addition, abiotic factors such barriers, e.g. oceans, mountain chains and deserts, have contributed to shaping migratory routes and behaviours. Barriers govern the location of stop-over sites for refuelling as energy expenditure is often great when crossing them, barriers can set or alter the direction for migration and they can simply stop migration from continuing beyond their borders. Barriers can also shape range expansion of migratory species and create seemingly strange distribution of migratory behaviour. In the willow warbler, a migratory divide separates the populations breeding in northern and southern Sweden (Salomonsen 1928; Hedenstrom & Pettersson 1987, Bensch *et al.* 1999; Chamberlain *et al.* 2000a; Ilieva *et al.* 2014). The southern population migrates westward and winters in West Africa, whereas the northern population migrates eastward, wintering in East and South Africa. The two populations are defined as subspecies, *P.t. trochilus* and *P.t.acredula*. *Trochilus* and *acredula* are not reproductively separated (Bensch *et al.* 1999 and 2009b; Liedvogel *et al.* 2014) and apart from a varying degree of morphological dissimilarities (Bensch *et al.* 1999 and 2009a), only classified as subspecies because of their different migration programmes (Hedenstrom & Pettersson 1987, Chamberlain *et al.* 2000a). The two populations are thought to have been founded by individuals originating from different peninsular refugia, isolated during the latest glacial maximum approximately 20 thousand years ago (Bensch *et al.* 2009b). When Europe was re-colonised after the ice sheets melted, the migration behaviour of the founders became the migration behaviour of the new populations that were established. Sweden is believed to have been colonised by two waves of willow warblers, one moving in from the south from a western refugium and one moving in from the north, from an eastern refugium (**fig. 2**). The two migration directions were in turn developed as a two pathways around the barrier of the Mediterranean, a sea is easier to cross at its western and eastern end points than across its central width.

Considering the above discussed plasticity that migratory behaviour exhibits, it appears contradictory that it is also suggested that migration can be rigid and inflexible. For example, several expanding bird populations have retained their original, but now often sub-optimal, migration route and wintering ground. Sutherland (1998) found when reviewing these species, that all were birds in which the juveniles relied on innate system to guide them during their first autumn migration. That there is inflexibility in parts of the genetic mechanism of migration is often cited as a concern in the context of climate change. The great list of studies that have shown that long-distance migrants are far less responsive to climate change than short-distance migrants (e.g. Nott *et al.* 2002; Tryanowski *et al.* 2002; Hubalek 2004; Lehikoinen *et al.* 2004; Macmynowski & Root, 2007; Rubolini *et al.*

2007; Thorup *et al.* 2007; Miller-Rushing *et al.* 2008b; Møller *et al.* 2008; Végvári *et al.* 2009; **Paper V**; but see Jonzén *et al.* 2006) is one example of such a concern. The hypothesis states that long-distance migrants are more restricted by their endogenous time program than those wintering closer to their breeding ground (Both & Visser 2001; Coppack & Both 2002; Jenni & Kéry 2003). This type of genetic encumbering, inflicted by the migratory programme, has also been used as an explanation for the perplexing fact that Eurasia sedentary species, and not long-distance migrants, have been the most successful colonist of North America (Böhning-Gaese *et al.* 1998).

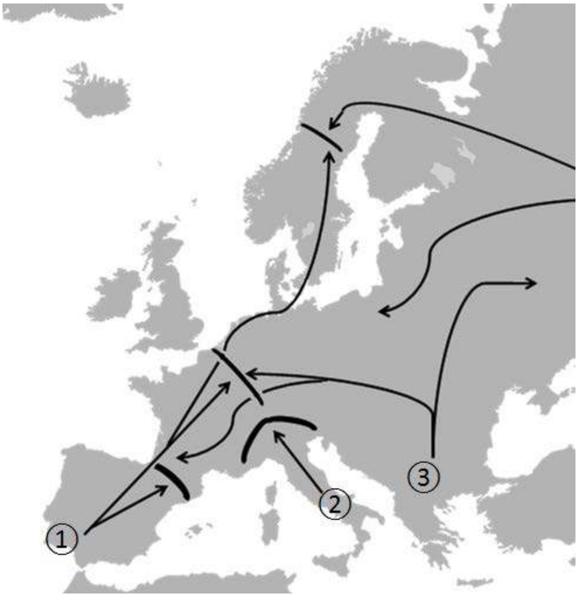


Fig. 2. Expansion routes of terrestrial species after the Last Glacial Maximum. Bold black bars depict main European suture or secondary contact zones and arrows the proposed expansion routes from the refugia in the (1) Iberian, (2) Apennine and (3) Balkan Peninsulas. The map is adapted from Taberlet *et al.* (1998).

As the genetics behind migration is still under investigation, the flexibility continuum of this behaviour will continue to be debated. However, there is much basic discernment of genetic components of migration. For example, the principal system that regulates migratory departure decision in a typical passerine migrant is known to be endogenously controlled, i.e. triggered by photoperiod (Gwinner 1977; Gwinner 1996). At the threshold of a certain day length (the phase of the photoperiod) the migrant experience *zugunruhe*, migratory restlessness, and prepares to leave. The actual departure is subsequently influenced by a variety of external factors, e.g. resource availability (Jenni & Schaub 2003; Schaub *et al.* 2008), local weather, e.g. winds, and predator risk (reviewed by Jenni & Schaube 2003).

Beside photoperiod, birds are known to use polarised light, visual cues, olfactory cues and electromagnetic fields to position themselves during migration (Able 1989; Walraff 2005; Wiltschko & Wiltschko 2005). In lab experiments, birds that have been placed in magnetic fields mimicking a geographic location close to a barrier, e.g. the Mediterranean, start to deposit fat needed for the crossing of the barrier (Fransson *et al.* 2001). Similar studies have also been able to show that birds that are placed in magnetic fields that correspond with a geographic location far off their original migratory pathway, start showing movements in a direction that would place them back on route towards their goal (Wiltschko & Wiltschko 1972). The physiology behind birds' ability to navigate is, as the genetics behind the migratory programmes, under investigation. Currently, the magnetic sense is explained by two hypotheses that both attain support from theoretical, behavioral and physiological evidence. The first suggests that a magnetite-mediated mechanism act as part of a magnetic map- or marker sense (Walker *et al.* 1997; Kirschvink *et al.* 2001; Fleissner *et al.* 2003), and the other hypothesis that there is a vision-mediated magnetic sense conveyed by processes in the birds' eyes (Heyers *et al.* 2007).

Global climate change

One thing that is absolutely certain in Nature is change. And in recent decades, change in climate has been the focus of an increasing amount of alarm, debate and research. Climate is the dynamics that affects the world at all scales; it constitutes atmospheric pressure, directs rainfall, tunes the temperature, guides winds and creates storms. It can alter local weather, global meteorology and glacial cycles. And as stated, it is certain to change. In the past, climatic shifts have occurred repeatedly and caused global, long-term and pervasive changes. A very apparent echo of past climate change is that of the isostatic post-glacial rebound seen in e.g. Scandinavia and Hudson Bay (Sella *et al.* 2007; Johansson *et al.* 2002), a consequence of when massive ice sheets weighed down whole landforms. Several mass extinction events of flora and fauna, such as at the Pliocene event three million years ago, have also been linked to climatic changes (Donovan

1989). The current change in climate however, is more rapid than ever before in recent geological history (IPCC 2007; Houghton *et al.* 2001; Karl & Trenberth 2003) and in contrast to past climatic changes, it is anthropogenic (IPCC 2007).

The term recent climate change refers to the increase in temperature occurring continuously within the last decades in the three main spheres of the planet; the ocean, the terrestrial surface and the free atmosphere (IPCC

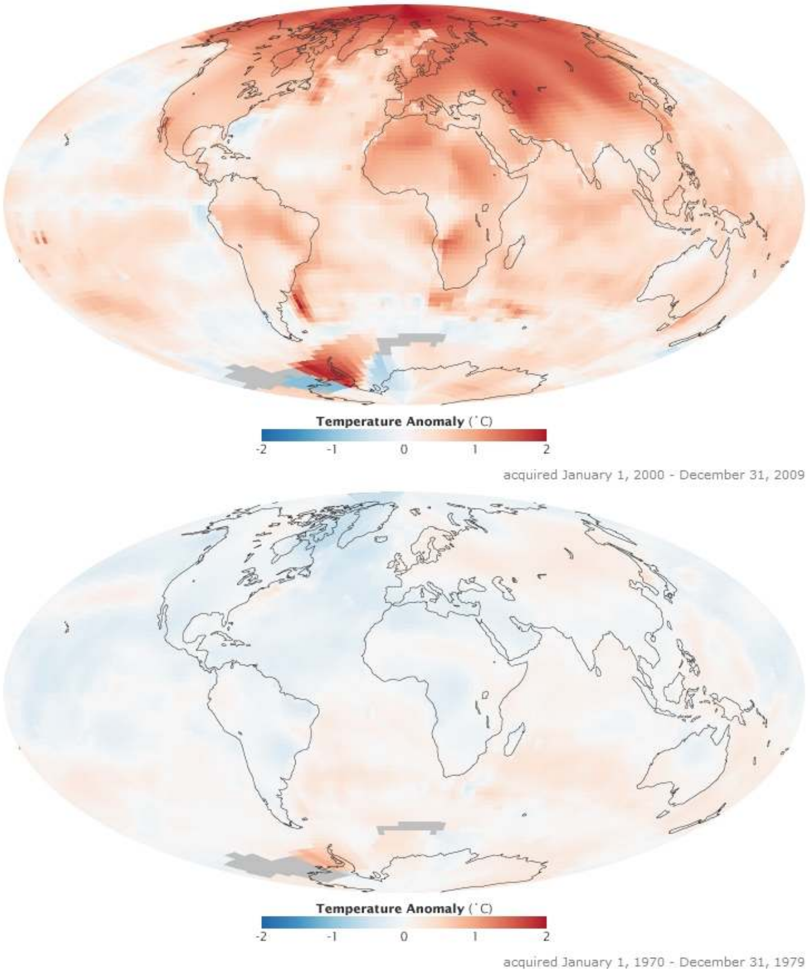


Figure 3. Differences in average surface temperatures between 1970-79 (bottom) and 2000-09 (top) in terms of temperature anomalies, not absolute temperature. Anomalies refer to the average temperature as of 1951-1980. Source: NASA, via Wikimedia Commons.

2007). Increased air surface temperatures are the most discussed and also the component most generally known outside the scientific community (**fig. 3**). The Intergovernmental Panel on Climate Change (IPCC) has reported that in the last 50 years, the rate of warming of surface temperatures has been near double that over the last century. The rate of temperature increase is now reaching an average of 0.7°C ± 0.02°C per decade (Hansen *et al.* 2005) and the 20th century is likely the warmest in at least 1300 years (IPCC 2007). Along augmentations in temperature, additional climatic components are also shifting. Extreme weathers, such as droughts and tropical storms are deemed to accelerate in frequency and intensity (IPCC 2001b ; Webster *et al.* 2005; van Vliet & Leemans, 2006). And the behaviour of far-reaching atmospheric events is projected to change; e.g. the occurrences of El Niño is expected to double (Cai *et al.* 2014) and the North Atlantic Oscilliation (NAO) has been modelled to presents wetter, windier and milder winters (Hulme *et al.* 2002; Wang *et al.* 2003) and to have become more variable in the decades contemporary with global warming (Goodkind *et al.* 2008).

Importantly, the climatic changes observed, as well as those predicted, are not homogenous. For example, the increase in temperature is not occurring at the same rate everywhere and not evenly through seasons or hemispheres. The Northern Hemisphere has seen the highest temperature rise and the contrasts are greatest at the most northern latitudes (IPCC 2001a; Karl & Trenberth 2003, **fig.3**). The temperature rise is also higher in these areas during winters and early spring than in summer or autumn and extensively greater at high altitudes (Houghton *et al.* 2001). These trends may likewise be less noticeable or even the opposite at local scale (e.g. Kozlov & Berlina 2002). However, the greatest changes to be seen are those predicted to occur in the future, when global temperatures are perhaps to rise to between 1.4 and 5.8°C by the year 2100 (IPCC 2001b).

Birds in a changing world

Birds are affected by climate change in as many ways as they are affected by climate in general. The three broad trait categories proposed by Jiguet *et al.* (2010a) summarize climate-responsiveness in birds as follows; i) climate sensitivity, referring to thermal tolerance (Bryan & Bryant 1999; Pendlebury *et al.* 2004; Jiguet *et al.* 2010b); ii) ecological sensitivity, referring to habitat preferences, food web dynamics and range size (Böhning-Gaese & Lemoine 2004; Cardillo *et al.* 2005; Jetz *et al.* 2007; Virkkala *et al.* 2008) and sensitivity in life history traits, referring to phenology, dispersal, fecundity and generation time (Cardillo *et al.* 2005; Jiguet *et al.* 2006; Brommer 2008).

Climate change and avian phenology

Spring migration phenology

The pronounced temperature increase in winter and early spring at northern latitudes has had, and is having, great impact on life in the temperate zone. Seasonal rhythms, which are essentially set by temperature thresholds and photoperiod, are used by many organisms as a proxy for phenology, i.e. for the timing of periodical, repeated life history events such as budburst, diapause and migration. When minimum threshold temperatures are being reached earlier in the year, an advancement of the growing season is also possible. In Sweden and Fennoscandia the growing season has become earlier by approximately 2 weeks between 1961-2014, and has also extended in length, reaching further into autumn than previously **(fig. 4**, SMHI 2015). According to some calculations the change is most apparent at the highest latitudes (SMHI 2015), but to others the shifts are greater further south in the region (Høgda *et al.* 2013).

The phenology of spring events has received great scientific interest since the first reports started to accumulate on earlier emergence of insects, earlier growing onset in plants and earlier appearance of migratory birds (Root *et al.* 2003). The cross-taxa summary of phenological shifts by Parmesan and Yohe (2003) has since its publication become a standard description of the wide impact climate change is having on the phenology of living organisms. In this compilation, the greatest number of studied animal species can be found in the taxonomic class of Aves, i.e. birds. Because of the long tradition of studying birds, their conspicuousness and the possibility to utilise ringing records for analysis, avian phenological response to climate change has become firmly established as a research topic. Foremost, it is the spring arrival of migratory birds that has been studied in this context and for this phenological event, the majority of evidence states that birds have started to arrive earlier at their breeding grounds (e.g. Sparks 1999; Cotton 2003;

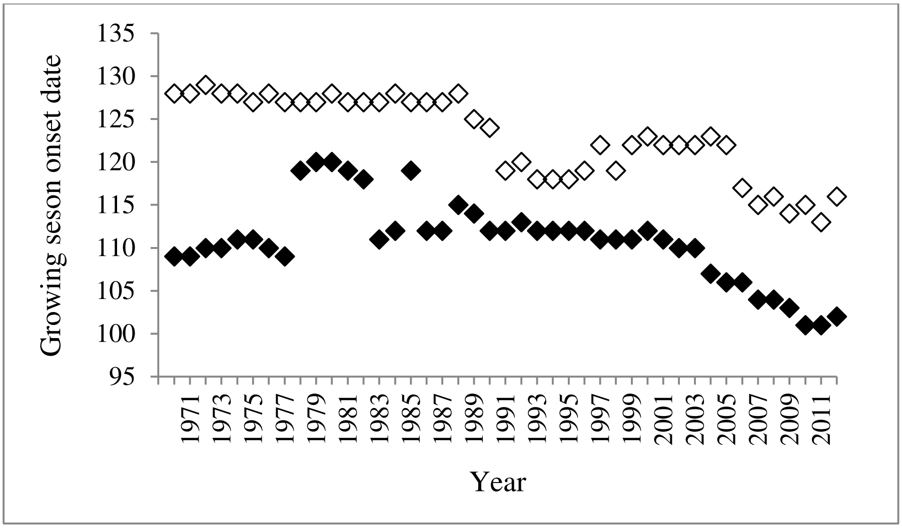


Figure 4. Growing season onset date presented in Julian calendar day (day 100 = April 10th) for southern Sweden (filled diamonds) and northern Sweden (open diamonds). Description of measuring method is available at SMHI (2015).

Sparks *et al.* 2005, Gordo & Sanz 2006, Jonzén *et al.* 2006, Hüppop & Hüppop 2011). Most of these studies concern changes seen in Europe, but the phenomenon of advanced arrival of migratory birds is present at other continents as well (North America: MacMynowski *et al.* 2007, van Buskirk *et al.* 2009; Australia: Beaumont *et al.* 2006, Chambers 2008). Though, the pattern is not uniform, and there are also reports of delayed arrival or non-change (e.g. Both & Visser 2001; Parmesan & Yohe 2003), a variation possibly reflecting the inconsistent warming trends around the world (Walther *et al.* 2012; Marra *et al.* 2005).

Primarily, earlier spring arrival has been connected to increased spring temperatures (e.g. Sparks 1999; Sokolov 2001; Tøtterup *et al.* 2010). For migrants, especially those species tending to migrate early in the season, arrival in early spring can be constrained by unfavourable weather (Forchhammer *et al.* 2002; Hüppop & Hüppop 2003; Wikelski *et al.* 2003). Harsh unpredictable weather events, e.g. cold spells, are more recurrent in early spring than in late spring (Brown & Brown 2000), and severe weather can have negative effects on the availability of food, e.g. insects, and at the same time increase energy demands on the birds (Pendlebury *et al.* 2004; Rubolini *et al.* 2005). With warmer springs, climate change has thus relaxed the natural selection against too early arrival.

Breeding phenology

The timing of spring arrival has important fitness effects as it sets the limit for breeding onset (Both & Visser 2001; Both *et al.* 2005). Early arrival is associated with reproductive success (Perrins 1970; Price *et al.* 1988; Hedenström *et al.* 2007) and there is strong selection for early breeding (Price et al. 1988; Both & Visser 2001). Individuals that arrive late to the breeding ground may suffer reproductive failure as availability of good nest sites, mates and territories decrease with time (e.g. Verhulst & Tinbergen 1991; Brown & Brown 2000; Bauer *et al.* 2008). In fact, before the effects of global warming were acknowledged, the lack of advancement in egg-laying dates puzzled researchers who saw that selection appeared to be favouring early breeding (Price *et al.* 1988). With warming springs and earlier growing season onset, the dominating trend reported for breeding dates in Europe is now a climate-induced advancement (e.g. Both *et al.* 2004; Dunn 2004; Root *et al.* 2003). Yet, timing of arrival and timing of breeding are not necessarily consequential in the sense that breeding always must be initiated immediately upon spring arrival. With climate change effecting phenology, there are examples of bird species both delaying breeding in relation to earlier arrival (Ahola *et al.* 2004) and advancing breeding in relation to unchanged arrival (Both & Visser 2001). Hence, it is essential not to draw conclusions based on just one phenological event when trying to understand changes in breeding area phenology, but strive for a holistic view, e.g. aiming to analyze timing of spring arrival, breeding and also autumn departure in synergy (Lehikoinen *et al.* 2010; **Paper I**).

The actual amount of time a migrant spend at the breeding ground also have important fitness effects as it is linked to ecological performance (Thorup *et al.* 2007). Positive correlation has been confirmed between the number of broods per season and spring advancement (Møller *et al.* 2008; Végvári *et al.* 2009), indicating that species able to rear multiple broods are under stronger selection for advancing their arrival date. Birds breeding in the temperate zone that are able to rear more than one clutch could also benefit from a lengthening of the growing season as they are given the opportunity to extend the breeding season and have multiple broods or re-nest (Jenni & Kéry 2003; Halupka *et al.* 2008). So far, few empirical studies have been able to document an increase in reproductive output as a consequence of an extension of the breeding season in a European species (but see Halupka *et al.* 2008 for references to unpublished data and Bullock et al. 2013 for an American example). In **Paper I** we show that the time between adult median passage date in spring and autumn at Sundre, Gotland, of willow warblers (*Phylloscopus trohcilus*) has not changed between 1990-2012, thus indicating that length of stay at the breeding ground has not extended. We further strengthen this conclusion by showing that both the autumn passage of juvenile migrants and the autumn peak appearance of locally hatched juveniles have become earlier, i.e. young are not being produced over a longer time period but rather, during a time period earlier commenced and earlier terminated in the season. This seasonally advanced but duration constant shift of breeding area phenologies is in line with the idea that long-distance migrants are more rigorously controlled by endogenous rhythms and genetics than short-distance migrants, and thus less prone to great phenological change (Both & Visser 2001; Møller 1994; Visser *et al.* 1998). However, extension of the breeding area residence time has been documented in both short- (Weatherhead 2005, Møller *et al.* 2010; Lehikoinen & Jaatinen 2012) and long-distance migrants (Halupka *et al.* 2008, Møller *et al.* 2010; Hüppop & Hüppop 2011). And as willow warblers are able to rear more than one clutch, even though it is very rare (da Prato 1982) and often re-nest if one clutch is lost (pers. observation), it is quite perplexing that they do not extend their stay at their Swedish breeding ground.

Autumn migration phenology

In order to increase breeding area residence time, if spring arrival has advanced, a migrant bird simply needs to keep autumn departure unchanged. Two questions thus emerge, what governs autumn migration and has timing of departure dates shifted with climate change? Four factors are usually listed to answer the first of these two questions, i.e. what governs autumn migration; i) completion of the breeding period; ii) moult; iii) conditions in the breeding area after the breeding period; iv) expected conditions during the autumn migration passage and at the wintering ground (Alerstam 1990; Jenni & Kéry 2003; Newton 2008). In a study examining 42 years of ringing records of 64 species migrating through Western Europe, it was found that when comparing breeding systems, species able to rear more than one brood per season delayed autumn departure, and that they did so irrespective of being short- or long-distance migrants. In addition, the study also showed that short-distance migrants most often delayed autumn migration, whereas most long-distance migrants had advanced departure (Jenni & Kéry 2003). In the context of climate change, autumn migration is often commented on as being less well studied than spring migration (Sokolov *et al.* 1999; Mezquida *et al.* 2007; Lehikoinen & Jaatinen 2012; Meller *et al.* 2013), and also to be a phenological event showing much more varying responses across species (e.g. Smith & Paton 2011**;** Sokolov *et al.* 1999, Jenni & Kéry 2003, Tøttrup *et al.* 2006, Sparks *et al.* 2007). Explanations for the inter-specific variation in autumn migration timing documented among European and North American species probably reside within species-specific adaptations to the four factors listed above. Long-distance migrants able to rear multiple broods are thus torn between the possible reproductive gain of staying longer at the breeding area, and the survival gain of leaving early for the wintering ground. The selective pressure on early arrival in Africa pertain to the benefits gained by timing arrival to the resource peaks during the rainy season and occupying higher quality territories (Telleria *et al.* 2001; Jenni & Kery 2003; Tellaria & Perez-Tris 2004; Mills 2005; Tøttrup *et al.* 2006; Hedenström *et al.* 2007). Favorable wintering in turn, may subsequently enable earlier departure and earlier arrival to the breeding ground the following year (Norris *et al.* 2004; Studds & Marra 2007).

Autumn migration appears to be as flexible spring migration, even if the cues responsible for its dynamics are different. In juveniles, initiation of autumn migration depends on hatch date; the later a bird is hatched the faster it develops and the earlier it starts migration (Meller *et al.* 2013; Pulido *et al.* 2001b), exemplified in the curlew sandpiper (*Calidris ferruginea*) where poor reproductive output is correlated with delayed autumn migration of juveniles (Barshep *et al.* 2012).In laboratory experiments, timing of autumn migration has been shown to a heritable trait and susceptible to selection. When captive blackcaps (*Sylvia atricapilla*) were subjected to selection for delayed autumn departure, only two generations were needed to delay mean autumn migratory activity by one week (Pulido *et al.* 2001a). The authors argued that these results indicate that change in autumn migration may occur over a very short time interval and that it will likely not be limited by lack of additive genetic variation.

Returning to the two questions, autumn migration must be considered as a cogwheel in synergy with other phenological events, in the larger life-history machinery that dynamically responds to environmental shifts as well as being governed by genetics.

Wintering phenology

A great uncertainty is incorporated in bird studies on the migratory phenology of long-distance Palearctic migrants, and that is the often complete absence of data from the wintering ground (Gordo 2007). Only one third of the annual life cycle of the willow warbler is spent on the breeding ground, i.e. approximately 104 days (**Paper I, fig. 5**). The remaining part of the year is spent migrating and at the wintering ground. Compared to the amount of data available on migrants when they reside in Europe, data on life history events from the wintering ground are sparse. It is known that there are carry-over effects between life-history events (Webster & Marra 2005), e.g. the phenological synergy between migration, reproduction and moulting (Underhill *et al.* 2008; **Paper I**), and thus all parameters that shape the condition and survival of individual birds are of interest for the understanding avian biology. Hopefully, the skew towards Europe-focused studies will change and make way for a more holistic knowledge base.

Figure 5. Me with newly ringed willow warbler in South Africa, 2014.

Presently, there is a growing amount of research directed towards finding climatic variables in the wintering ground that can help explain phenological events in Europe. Even if these still have a European focus point, the scope has at least widened. For example, temperature and rainfall that migrants experience en route or while wintering in Africa, have been connected with timing of migration in Europe (Saino *et al.* 2007, Robson & Barriocanal 2011; Cotton 2003). These studies have generalized both climatic variables and migration routes over very large geographic areas, which give quite weak explanatory power but is adequate considering that a more exact location, duration and timing of the migration, wintering and departure of many of the small migrant species are still unknown. In larger species, capture-re-capture of individuals equipped with geolocators has given researchers detailed information about the duration of migratory stops and routes. The thrush nightingale, for example, appears to follow the rains in East-Africa, never stopping for longer periods in one place but using at least three different areas during wintering (Stach *et al.* 2012). The willow warbler has also been suggested to change locality depending on precipitation patterns in West-Africa (Salewski *et al.* 2002). This strategy to move in accordance with the ITCZ (Inter Tropical Convergence Zone) was called "itinerancy" by Moreau (1972) and is a behaviour present among many Palearctic migrants in West Africa (Jones 1998). Rain is a limiting factor in many African regions that migrants must pass, e.g. the African Sahel. During the period 1970-80, the Sahel suffered from severe desertification (Thiollay 2006; Wilson & Cresswell 2006) and, coinciding with this event and correlating with the amount of rainfall over Africa, was the prominent reduction seen in many long-distance migrant species (Winstanley *et al.* 1974, Peach *et al.* 1991, Böhning-Gaese & Bauer 1996; Payevsky 2006). The quality of winter habitats can also have long-term effects on the breeding strategy of individual birds (Webster & Marra 2005).

With the research focus of this thesis, it is especially information on timing of spring departure from the wintering ground of long-distance migrants that constitutes a missing piece of the puzzle. As documented in previous sections, many long-distance migrants, including the willow warbler, has advanced arrival in spring (e.g. Stervander *et al.* 2005; Spottiswoode *et al.* 2006; **Paper I**). Considering the distance and in-coherence in local conditions between the wintering ground and the breeding ground of long-distance migrants, how can individual birds in Africa time their departure to the earlier European spring? There are two possibilities in which a migrant can achieve earlier arrival to the breeding ground; either it departs earlier or it shortens the time spent migrating, i.e. reduce the stop-over duration or increase the migratory speed (van Noordwijk 2003). Ringing records from southern Europe (e.g. Jonzén *et al.* 2006; Robson & Barriocanal 2011) and North Africa (e.g. Both 2010) indicate that migrants are passing those sites earlier now than before. However, the closer to the European breeding ground a migrant gets, the more information it has available to evaluate spring conditions at its destination. For example, large-scale atmospheric pressure systems, such as the North Atlantic Oscillation (NAO), exert influence over a region including Scandinavia and North

Africa (Hurrell 1995), thus creating connectivity in environmental conditions over this entire area (Ottersen *et al.* 2001; Straile 2002) but not further south (Wang *et al.* 2003). Hence, it is sub-Saharan passage dates that must be sought in order to verify whether migration actually is initiated earlier or just increasing in speed at arrival to regions in environmental association with the breeding ground. In fact, there is data suggesting that departure from African wintering grounds has advanced with climate change, but it is limited. A study on the barn swallow (*Hirundo rustica*) in South Africa using information available in the South African Bird Atlas Project could declare that this species leave its wintering grounds 8 days earlier now than 20 years ago (Altwegg *et al.* 2012). Thus presently, there is little but concordant evidence supporting the hypothesis that earlier arrival of long-distance migrants to their European breeding grounds is being enabled by earlier departure from their African wintering grounds.

For the willow warbler, an earlier departure from the wintering ground could potentially be achieved by the same parallel advancement of phenological steps as those we have shown for breeding area phenology. In **Paper I** we argue that the earlier arrival of willow warblers in spring has resonated through all phenological steps (reproduction, moult, departure in autumn) and resulted in a seasonally advanced by temporally constant residence time at the breeding ground. Following this procedure, it is possible that arrival to the wintering ground is also earlier than before and that this resonate through the phenological steps at the wintering ground as well, resulting in a parallel advancement of the subsequent departure from the wintering ground.

Intra-specific differences in phenological response to climate change

How an individual responds to an environmental change will determine if it survives it. A basic three alternative model stipulates the possible options available to any given organism faced with a change in its living conditions; stay put and adapt; disperse to a more suitable habitat or, die (Holt 1990; Davis *et al.* 2005; Gienapp *et al.* 2008). In avian species, responses to climate change vary across species, but there is also some discrepancy between studies reporting on the same species and significant differentiation in response between populations and individuals.

In order to determine when species respond similarly and when they do not, researchers have investigated several behavioural and ecological parameters that might categorise phenological responses across taxa, e.g. number of broods (Jenni & Kéry 2003; Végvári *et al.* 2009); migration distance (Jenni & Kéry 2003; Thorup *et al.* 2007; Végvári *et al.* 2009; Hurlbert & Liang 2012); migration speed (Marra *et al.* 2005; Hurlbert & Liang 2012); moult period length (Végvári *et al.* 2009); diet (Jenni & Kéry, 2003; Végvári *et al.* 2009); intensity of sexual selection(Spottiswoode *et al.* 2006) and habitat and climate niche (Møller *et al.* 2008; Hurlbert & Liang 2012). The success in finding these "pheno-climatic guilds" has been very variable and some of the results are in contradiction, for example; Jenni and Kéry (2003) found no correlation in migratory response to climate change across taxa of similar food preferences whereas Végvári *et al.* (2009) did. However, migration distance appears to be a fairly accurate species-specific property for distinguishing between different phenological responses to climate change, i.e. long-distance migrants appear to respond with less intensity than short-distance migrant (see the section "**Migration**"). Less well studied than inter-specific differences are intra-specific differences, i.e. when members of the same species respond differently to environmental change. The interest for these within-species variation is beginning to increase (e.g. Rubolini *et al.* 2007; Gordo & Doi 2012; Gordo *et al.* 2013; **Paper I**)

Within some species, there appears to be differences in change in arrival date in spring depending on latitude (Hurlbert & Liang 2012; **Paper II; Paper V**). In their analysis of citizen science data collected 2000-2010 in Eastern North America, Hurlbert and Liang (2012) found intra-specific differences in migratory change in three species. Within these species, first arrival dates had advanced more in populations at southern latitudes than in populations at northern latitudes (latitudinal range: 32-46°N). Migratory speed also crystallized as an important factor in this analysis. The strength of phenological response to temperature was greater in species advancing more slowly northwards during spring migration than those moving at greater speeds. Thus effectively, species advancing more slowly may be better equipped in assessing conditions en route and in timing arrival with agreeable conditions in the breeding area. Long-distance migrants typically migrate at higher speeds than short-distance migrants (Fransson 1995; Alerstam *et al.* 2003; Hurlber & Liang 2012), and the further north an individual breeds, the greater is the time constraint due to increased migration distance. Thus, migration speed can also play an important role in latitudinal differences in phenological response within species. Another cause behind a latitudinal gradient in phenological response can be differences in local adaptation in temperature sensitivity. The earth's climate is not changing homogeneously, i.e. temperature change differs across latitude, seasons etc (see the section **Global climate change**), and contradictory to the weaker phenological response observed in northern breeding birds, it is at the most northern latitudes that the temperature changes are greatest (Houghton *et al.* 2001; IPCC 2001a; Karl & Trenberth 2003, Hurlbert & Liang 2012). Hurlbert and Liang (2012) argue that for birds in less seasonal environments to apply temperature cues in order to sustain the same degree of accuracy in phenological timing as birds in more seasonal environments, they need to be very sensitive to those cues. They state: “Because the rate of increase in temperature through the spring is faster at higher latitudes, a given temperature shift corresponds to a greater passage of time at lower latitudes”. Such latitudinal differences in rate of spring progression are also apparent in Europe (Stålhandske *et al.* 2014).

A similar large scale survey to that of Hurlbert and Liang (2012), focusing on latitudinal differentiation in spring migratory change in Europe, found that mid-European first arrival dates (54°N-60°N) had advanced more than southern (<54°N) and northern first arrival dates (>60°N). However, these differences were not as pronounced within species as between species (Rubolini *et al.* 2007) and the authors concluded that the 113-189 European migrants they had included in the analysis spanning from 1960 to 2006, displayed an overall intra-specific consistency in migratory response to climate change.

Beside migration timing, other phenological traits have been documented to change differentially according to latitude within species. An investigation in the timing of egg-laying in American tree swallows (*Tachycineta bicolor*) revealed that more southern breeding birds advanced reproduction more than those at higher latitudes (Dunn & Winkler 1999). Timing of reproduction has also changed differently within species in Europe. Great tits (*Parus major*) in the Netherlands appear to face an asynchrony between timing of reproduction and prey peak advancement (Visser *et al.* 1998), whereas great tits in Great Britain were not subjected to such a mismatch (Charmantier *et al.* 2008). In Finland, pied flycatchers (*Ficedula hypoleuca*) were found to arrive earlier in spring without advancing their breeding date (Ahola *et al.* 2004), whereas pied flycatchers in the Netherlands were breeding as early as possible following arrival (Both & Visser 2001). Within the two *Ficedula* species, a pan-European study found that breeding date varied within species according to local temperature increase (Both *et al.* 2004). Similarly, Visser *et al.* (2003) found that laying dates in different populations of great tits and blue tits (*Parus caerulescens*) variedly showed both change and lack of change across Europe, though not corresponding to temperature increase.

The sexual differences in phenology that exist within species have also been found to change variedly with climate change. Foremost, it is the degree of protandry, the earlier arrival of males than females to the breeding ground, that has been suggested to (Tøttrup & Thorup 2008; **Paper I**), and found to, increase (Møller 2004; Harnos *et al.* 2015, but see Bauböck *et al.* 2012 and Raino *et al.* 2007). As the selection on the timing of migration can act differentially and independently on the sexes, the costs and benefits of a climate-induced phenological change in females and males will be a shifting balance, depending on climate consequences acting independently on each sex, and on climate consequences indirectly influencing costs-to-benefits in one sex through the other. Since males seem to experience greater benefits than females from early arrival, protandry should increase at latitudes where climate change has advanced spring events (Spottiswoode & Saino 2010). In addition, decrease survival rates induced by climate change could further increase protandry, as females are subjected to higher mortality (Liker & Székely 2005) and a surplus of males would increase mating competition. Despite the published reports where in increases in protandry has been shown to occur over quite short time periods, it has been argued that this behaviour can only change by microevolution (Tøttrup & Thorup 2008) as it has been experimentally documented to be endogenously governed (Maggini & Barlein 2012).

Intra-specific differences in climate-induced phenological change can exist also between individuals that migrate differently, e.g. because of individual condition or age (Cramp & Simmons 1977; Lehikoinen & Jaatinen 2012; **Paper I**), which may modulate the migration dynamics of the whole population. It was recently shown that in a population of waders with advanced spring arrival, the change was not due to between-year individual plasticity in migratory timing, but rather to the behaviour of new recruits that changed in frequency temporally (Gill *et al.* 2013). Similar to this population of waders, marsh harriers (*Circus aeruginousus*) alo show considerable individual concitency in spring migration between years, but for this species, concistency declined the further north the individual bred in relation to its Sahelian wintering ground (Vardanis *et al.* 2011).

Climate change and avian range shifts

The high mobility of birds provides them with unique opportunities to respond to a change in their surroundings by dispersing. In the paleontological record, there are numerous examples of taxa reacting to climate induced habitat change by geographical range shifts (Clarke 1996). Some examples from the transition between glacial and interglacial periods indicate that the distribution shift happened as rapidly as within 50 years of the climatic change (Coope 1995). During the last inter glacial period (117 000 -130 000 years ago) temperatures were about 4°C warmer than today in United Kingdom. When the fossil record of this region was analyzed, it revealed that it was inhabited by species that today inhabit south-western Europe. Thus historical data suggest that the avifauna can respond to warming episodes by shifting their range northward (Tyrberg 2010).

Conclusively, recent climate change is very likely to result in range expansions and range shifts in avian species. In corroboration, there are already numerous reports of such distribution responses to be happening, with a poleward shift to be most common (Burton 1995; Pounds *et al.* 1999; Thomas & Lennon 1999; Brommer 2004; NIPCC 2011) and mountainous species changing range to ever higher altitudes (Pounds *et al.* 1999). However, some predict that range contractions are to be more common than range expansions (Böhning-Gaese & Lemoine 2004). For migratory birds there is a multitude of constraints for range shifts, as suitable habitats must be present at several spatial and temporal points, i.e. for breeding, migration and wintering. Species whose distribution is already located close to distribution barriers, e.g. arctic and alpine taxa, may be especially threatened by diminishing living space (ACIA 2005). Beside topographic barriers, temperature (cold in the north and heat at the equator), competition, predation and parasitism are other factors that may set limits to the possibility of different bird species at different latitudes to shift their range (Böhning-Gaese & Lemoine 2004).

At northern latitudes, climatic changes in precipitation and temperature are expected to be particularly strong. For Fennoscandia, bioclimatic envelope models suggest that out of 27 northern land bird species, most will lose the main part of their climate space, i.e. 83.6% respectively 73.6% range loss depending on the severity of the climate scenarios (Virkkala *et al.* 2008). The willow warbler is a common breeder at temperate latitudes (se **fig. 9** in **Methods**), and largely absent as a breeding species in southern Europe. It is, along with species of similar thermo-optimal distribution, expected to shift its range northwards in pace with climatic warming of higher latitudes (Huntley *et al.* 2007). However, as the willow warbler already exist at the northern edge of the European landmass, a further move polewards is hindered by the end of connected land. A cross-ocean colonization of Iceland is suggested based on environmental suitability (Huntley *et al.* 2007), but perhaps unlikely. A northward range expansion could also include a colonization in altitude and an increase in breeding density at higher latitudes, as is happening in Finland (Virkkala & Lehikoinen 2014).

Range shifts, philopatry and nomadic breeding behaviour

In **Paper III** we report on the remarkable absence of philopatry in a breeding willow warbler population in Abisko, northern Sweden (**fig. 6**). When an extensive literature review was performed, we found no previous document reporting on reoccurring, complete absence of site fidelity in this species, rendering our find unique. We deem it likely that the phenomenon can be attributed to an influx of individuals representing another breeding strategy than the common philopatric one: a nomadic breeding strategy made favourable by low breeding density in the north and climate-induced environmental change.

Figure 6. Abisko Scientific Research Station, May 2014, photo: Sven Jakobsson.

Philopatry, the return to the same area in successive years, is believed to be associated to the benefits gained by returning to where the individual already has established knowledge on certain resources (food, territory, mates) or threats (competitors, predators, parasites) (Greenwood & Harvey 1982; Krebs 1982; Maynard Smith 1982; Cezilly *et al.* 2000; Stanback &

Dervan 2001). Philopatry is very common among avian species, and can vary intra-specifically in degree between years and populations, e.g. because of reproductive success (Jakobsson 1988; Wiklund 1996; Zając et al. 2011), habitat quality (McNicholl 1975; Bollinger & Gavin 1989; Ortega *et al.* 2006; Zając *et al.* 2011) or breeding density (Bensch & Hasselquist 1991; Doncaster *et al.* 1997). However, not all bird soecies display philopatric breeding behaviour and consistent or high degree of site infidelity is referred to as nomadic breeding behaviour.

Nomadic breeding behaviour is typically reported for bird species in which reproductive success is highly dependent on certain fluctuating resources (Newton 2003). In boreal pine forests, tree seed feeders as the crossbills (*Loxia spp.*) may leave their usual breeding grounds and move southwards in years of massive coniferous seed failure (Newton 1998). For insectivores, breeding densities may increase during episode of insect outbreaks: populations of the brambling (*Fringilla montifringilla*) in Sweden are an example of a species known to increase in peak years of the autumnal moth (*Epirrita autumnata*) (Enemar *et al.* 2004). One very close relative of the willow warbler, the wood warbler (*Phylloscopus sibilatrix*) also exhibit little or no philopatry and has been designated as a nomadic breeder (Herremans 1993, Wesołowski *et al.* 2009 and references therein). One reason behind nomadism in wood warblers has been ascribed to predator avoidance (Wesołowski *et al.* 2009), as there have been indications of them breeding in lower numbers during rodent outbreaks, i.e. at periods/locations to which more predators are attracted.

There are some indications that willow warbler population dynamics can be influenced by the cyclic peaks of autumnal moth at northern latitudes (Enemar *et al.* 2004; Hogstad 2005). In two instances where low breeding densities of willow warblers were followed by outbreak years at a north-western site in Sweden, breeding density increase drastically the following years (Enemar *et al.* 2004). Interestingly, the Abisko willow warbler population differs from other avian nomadic breeders by not fluctuating greatly in numbers (with the exception of old reports from Finland where densities in the 1920s-50s are reported to have fluctuated greatly: Siivonen 1949). For example, when philopatry is not displayed in wood warblers, it is because no birds have returned at all. The same applies to the brambling. At the Abisko site, the same territories were occupied in successive years, but by all new individuals, which suggests that the habitat was not of poor quality and that the absence of returning birds was not due to the whole population tracking a resource present elsewhere. Thus, willow warbler philopatry may be influenced by resource availability but is not governed by it to any great extent.

An example of when return rates can be very low in the willow warbler is during choice of wintering sites. Philopatry can be expressed as faithfulness to a certain winter quarter, a behaviour present in for example the pied flycatcher (*Ficedula hypoleuca*) (Salewski *et al.* 2002). Interestingly, in a study performed at Comoé National Park in Côte d'Ivoire, none of the banded willow warblers, in contrast to other migrant taxa, were ever found to reoccur, which the authors suggested must be a lack of selective advantage for doing so in this species (Salewski *et al.* 2002).

Populations breeding isolated from other populations, i.e. breeding on true islands surrounded by water or on habitat islands on the mainland, generally exhibit higher degree of philopatry (Newton 2003). Our data in **Paper III** supports this as the island population generally had both higher density and site fidelity than the populations on the mainland. Tryjanowski *et al.* (2007) suggest that the absence of returning red-backed shrikes (*Lanius collurio*) at their study site, a stark contrast to the high site fidelity recorded elsewhere (25%), could be due to the increased opportunity their study population had to move elsewhere. The Abisko population is situated on the mainland and indeed has great opportunity to find new territories in close vicinity, especially as breeding densities are low at the site and in the wider area. However, philopatry is also high in the mainland Tovetorp population, and in many other mainland sites where dispersing opportunities are plenty (**Paper III**), suggesting that in willow warblers, opportunity to disperse does not typically cause low philopatry.

As before mentioned, Wesołowski *et al.* (2009) explain reoccurring absences of breeding wood warblers as a symptom of a nomadic breeding strategy, but this phenomenon has also been attributed to ongoing range expansion (Lapshin 2009, referring also to Sokolov *et al.* 1996). The populations studied by Lapshin (2009) and Sokolov *et al.* (1996) were peripheral in relation to the core distribution of the species, and thus the nonreturn of adult wood warblers to previous nesting sites was interpreted as a consequence of them expanding their range at this site. Willow warblers have already colonized suitable habitats in northern Scandinavia and occur as far north as above Abisko, i.e. up to 70°N by the Barents Sea (Cramp 1992; Bensch *et al.* 2009b). However, two forms of the willow warbler are present in Scandinavia, the southern sub-species *P.t. trochilus* and the northern sub-species *P.t.acredula* (see **Methods**) and thus a range expansion can involve distribution shifts within these. The closely related chiffchaff

(*P.collybita*) was at the start of the last century absent from southern Sweden and only present as a northern form (*P.c. abietinus*) above 60°N. Since then, the southern chiffchaff *P.c. collybita* has gone through a rapid northwards range expansion across Fennoscandia, replacing the northern form (Hansson *et al.* 2000; Lampila *et al.* 2009). A northward range expansion of the southern form (*P.t. trochilus*) could also be occurring in the willow warbler, enabled by climate change and the subsequent milder conditions at higher latitudes, e.g. longer growing season (Karlsen *et al.* 2007, Høgda *et al.* 2013). Dispersal-prone individuals could even be favored under the present conditions in the north and in Abisko (**Paper III**), resulting in a dominance of the nomadic breeding strategy of the expanding colonizers.

Climate change and land-use change

Many living organisms have the ability to change the physical structure of the environment they inhabit; elephants create clearings in dense bushlands, beavers flood river plains and insect outbreaks can deprive whole forests of leaves. *Homo sapiens* may have had impacts on its habitat even as scattered hunter-gatherers (Doughty *et al.* 2010), but the utterly profound effects of the period defined by anthropomorphic force, the epoch sometimes referred to as the Anthropocene, started with the Neolithic Revolution and the birth of agriculture about 12000 years ago (Ellis *et al.* 2013). With agriculture and denser, resident society structure, the growing human civilization demanded ever greater areas to grow and harvest timber, fibre and food.

To a certain extent, biodiversity adapted to the changes of the Anthropocene and species richness can still be high in localities where traditional agriculture is practiced (Poschlod & Bonn 1998; Söderström *et al.* 2001; Eriksson *et al.* 2002). However, biological adaptation is not as rapid as anthropomorphic change can be, and the industrialisation and intensification of agriculture and forestry that has happened during the last 70 years has completely transformed past landscapes. Generally, it is these human activities that are more recent in origin and that have accelerated in intensity and scale, that one refers to when land-use change is discussed (Steffen *et al.* 2007).

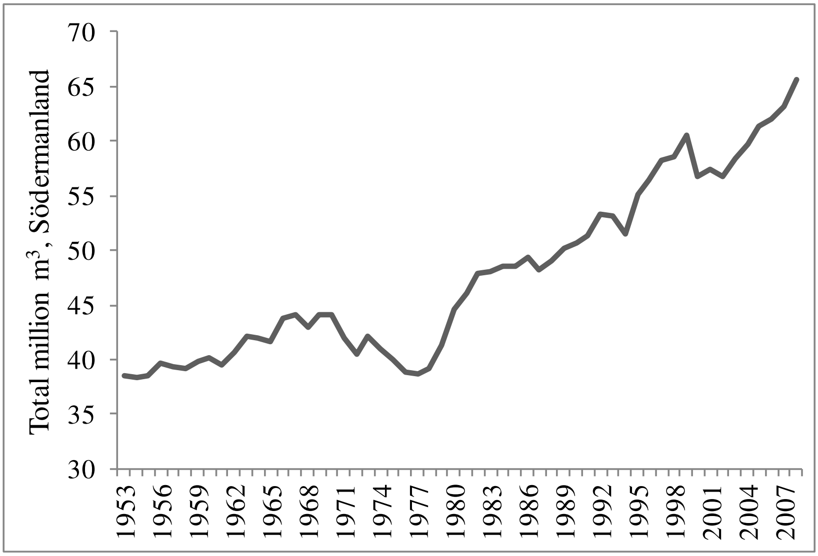
Currently, in 9 of the world's 14 biomes 20-50% of the land area has been converted by human use. In the past 300 years, about 20% of global forests have disappeared whereas cropland has increased by 466% (Richards 1990). Land-use change is the main driver of habitat loss and habitat fragmentation, two of the great global threats against biodiversity (Baillie *et* *al.* 2004; MA 2003). For birds, it is well established that the intensification of agriculture has had pronounced impacts on species connected to the old farmland landscape (Fuller et al. 1995; Aebischer *et al.* 2000, Chamberlain *et al.* 2000b). Explicitly, it is for example the increased use of pesticide, poisoning birds that forage around the crop fields, and cease of mixed farming that has had negative effects (Bright *et al.* 2008). Many avian habitats associated with old farmland is also disappearing as a result of industrialised agriculture and socio-economic changes (Ostermann 1998); hedgerows and brush that used to frame fields and pastures are being cleared and at the other end of the axis, land- and farm abandonment has resulted in a reduction of semi-open grasslands and encroachment by forest (Debussche *et al.* 1999; Poyatos *et al.* 2003; Roura-Pascual *et al.* 2005).

Commonly, the effects of land-use do not act on biodiversity alone, but interacts with other drivers (Sala *et al.* 2000; MA 2003; Baillie *et al.* 2004; Brook *et al.* 2008). The synergistic effects of land-use change and climate change can both increase the rate and magnitude of a negative impact or act in opposition, balancing the influence. One effect of change in land-use and climate is facilitated range expansion. As human activity (e.g. forestry, agriculture, infrastructure) has increased at higher latitudes, ecological corridors and new, suitable habitat has become available for southern species, enabling dispersal. With increased temperatures and extended growing season, temporal connectivity has also increased the opportunity for colonization of the north (e.g. Elmhagen *et al.* 2015; Auffret *et al.* 2015). Historical land-use might once have allowed northern breeding bird species to expand into marginal southern habitats (Svensson *et al.* 1999). The distribution pattern of invasive species may also be affected by the synergistic feedbacks between climate and land-use changes (Bellard *et al.* 2013): new invasive taxa may emerge (Hellmann *et al.* 2008) and current invasive taxa may increase (Butchart *et al.* 2010) or even experience population limitations following reduced climatic suitability (Pyke *et al.* 2008; Bradley *et al.* 2009; Bellard *et al.* 2013).

Loss of habitat, which is commonly driven by anthropomorphic land conversion, may be exhilarated by climate change. Using Millennium Ecosystem Assessment scenarios on the distribution of 8750 bird species, it was predicted that even under environmentally favorable scenarios, at least 400 species may suffer >50% range reductions by the year 2050 and over 900 by the year 2100 (Jetz *et al.* 2007).

The spread of avian infectious diseases has also been attributed to a combined negative effect of land-use change and climate change. In Hawaii, honeycreepers (*Drepanidae*) are experiencing an ever increasing risk of avian malaria since land-use change and rising temperatures are diminishing the distribution of low-risk habitats (Atkinson & LaPointe 2009).

In northern biomes, where temperatures are expected to increase the most, interaction between climate and land-use change can come to have a pronounced effect. In Sweden and Finland, timber production has been increasing since the 1950s (Järvinen *et al.* 1977; Nilsson 1990; Virkkala *et al.* 1993; Kumm 2003, **fig. 7**), as a consequence old-growth forests with deadwood are declining whereas young trees are increasing (Ylitalo 2012; SFA & SLU 2008). Following increased temperatures, tree growth rates are expected to accelerate in temperate climates. For forestry in the boreal zone, this means that the turn-over rate will shorten and that harvest of completed tree stocks can occur after 80 years of age instead of the current 106 years of age (SFA & SLU 2008). Subsequently, if timber production continues to grow and claim more land, tree demographics will change. In Sweden, the Swedish Forest Agency (SFA) predicted that logged forest and young stands will increase from 21% to constitute about 34% of the Swedish forested area by 2100 (SFA & SLU 2008). Outside Fennoscandia, the northern boreal and tundra biome of Russia and Canada have experience relatively little land-use change and remained relatively unexploited (Brooks *et al.* 2006). However,



Figre 7. Timber outtake (shown in million m^3) in Södermanland county, southeastern Sweden, between 1953-2008. Data source: Riksskogstaxeringen.

both climate and land-use change are projected to become strong drivers of biodiversity change at these latitudes over the next century (Sala *et al.* 2000), thus indicating that with their combined effect, the northern hemisphere may come to experience substantially change in the future (Elmhagen *et al.* 2015).

Phenotypic plasticity and micro-evolutionary adaptation

The question whether a documented response in nature has a genetic basis or reflects the individual's phenotypic ability to change according to circumstance should not, essentially, be viewed as a dichotomy. The degree to which an individual is capable to respond with phenotypic plasticity, indeed the mere occurrence of this reaction syndrome, are essentially governed by genes and thus a result of selection (e.g. De Jong 2005; Pigliucci 2005). However, in the presence of current and rapid climate change, it has become crucial to not only acquire the necessary understanding of the functional impacts of different modes of adaptations but also to better predict future developments. Phenotypic plasticity is adaptive within a certain width of environmental settings and may thus become inadequate or even maladaptive outside expected conditions (e.g. see Coppack & Pulido 2004). As climate change is presumed to be incessant for numerous decades to come, phenotypic plasticity may fail to keep individuals in pace with the environmental change. Micro-evolutionary adaptation, in contrast, takes shape through a selective process, and thus ultimately enables generations of individuals to stay ever modified. Restrictions to evolutionary change are present primarily in the genes, as genetic variation in the traits under selection determines the possible responses available to the population (Bradshaw 1991). Birds have an advantage in this aspect, since their high mobility facilitates gene flow between populations. This is exemplified by the fact that avian families exhibit lower rates of endemism than less mobile taxa (Simmons *et al.* 2004). Genetic drift and mutation are other evolutionary processes that, beside gene flow, act with natural selection to determine the adaptive potential of populations (Davis *et al.* 2005).

In order to determine whether there are advancements in migration time that constitute a micro-evolutionary response to climate change, two things need to be demonstrated; first the presence of directed selection on migration timing caused by shifted climate conditions and secondly, the presence of heritability of migration timing To determine selection on migratory timing, reliable fitness estimates are needed, preferably offspring recruitment in relation to individual arrival dates. As multiple, contradicting selection factors may be acting on timing of migration and since not all cues bird apply to regulate phenology may have been altered by climate change, estimating directional selection on migration is difficult. So far, no study has directly demonstrated climate change-induced selection on migratory timing, presumably because of these difficulties and the logistic exhaustive filed work needed (Gienapp *et al.* 2007). However, it has been experimentally shown that selection for altered migration timing is possible both during spring (Möller 2001, but see Potti 1998) and autumn migration (Pulido *et al.* 2001a). Also other traits associated with migration, i.e. migratory activity, migratory direction and fat repositioning have been demonstrated to be heritable (Pulido & Berthold 2003), and the mere initiation of migratory behaviour can respond quickly to selection (e.g. Berthold *et al.* 1992, Bearhop *et al.* 2005).

The adaptive fundaments of phenological responses have received much debate and proposals, but few empirical conclusions have been made (Rubolini *et al.* 2007). Thus far, most studies argue that the phenological changes seen in birds are products of phenotypic plasticity (Sheldon *et al.* 2003; Stervander *et al.* 2005; Both 2006; Gienapp *et al.* 2007; Charmantier *et al.* 2008; Charmantier & Gienapp 2013), even if there are tentative claims of actual genetic phenological adaptation to climate change (Jonzén *et al.* 2006). As microevolution on migration phenology demands consistency in the direction of the selection pressure and as climatic factors, e.g. NAO winter index, have great interannual variation, evolutionary adaptation to climate change is often claimed to delay (Stervander *et al.* 2005; Both 2006; Gienapp *et al.* 2007). However, the fact that evidence for micro-evolutionary change is largely absent, does not signify that such processes are not happening, but perhaps that they are so marginal that they so far evade detection.

Methods

Study species: The willow warbler

Figure 8. To the left: Willow warbler female, colour-banded 996 “Basta”, ringed at Sundre, southern Gotland in 2012. To the right: Willow warbler male, colour-banded 004 “Delphi”, ringed at Sundre, southern Gotland in 2011. Photo: Johanna Hedlund.

The willow warbler (*Phylloscopus trochilus*) is a small insectivorous passerine, weighing approximately 8grams (**fig 8**). It has a wing span ranging from 58-78mm, with males being slightly bigger. Of all adult birds measured at the Sundre, Tovetorp and Abisko field sites during this PhD project, the averages for females were 64.4mm (Sundre, N=28) and 64.6 mm (Abisko, N=18) and the averages for males 69.0mm (Sundre, N=128), 68.9mm (Tovetorp, N=62) and 70.0mm (Abisko, N=74). The heaviest bird ever weighed within the project was a chick at Abisko in 2011, which at approximately 9 days of age weighed 12.7grams. Males and females are dimorphic in size, with female wing length reaching <67 and male wing length reaching ≥66 (Svensson 1975; Tiainen 1982; Norman 1983), but the sexes do not differ in colouration.

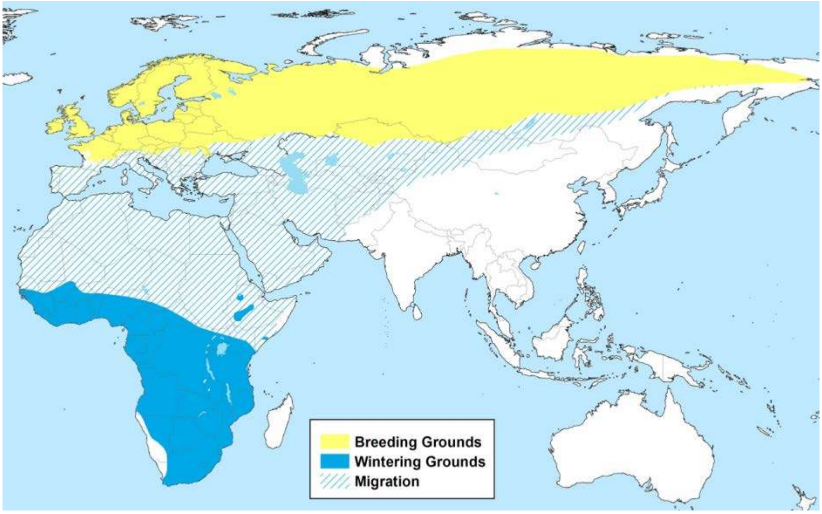


Figure 9. World map showing the distribution of the willow warbler, indicating breeding and wintering range. Source: created by Keith Larsson 2012, using distribution reports provided by BirdLife International.

The breeding distribution includes most of temperate Europe, with the biggest densities occurring in Fennoscandia and Russia. The most southern populations are found in northern Spain and in the Balkans but the species is largely absent in the Mediterranean region accept during migration (**fig. 9**). This apparent temperature threshold places the willow warbler in a group of species that are at risk of experiencing a decrease in potential habitat as climate change increase temperatures in Europe. In the pan-European project mapping the possible range shifts of European breeding birds 100 years into the future, the willow warbler was projected to lose 40% of its former range (Huntley *et al.* 2007). Possible new habitat was estimated to be made available on Svalbard and Iceland, islands quite far from the current range borders.

There are three acknowledged sub-species of willow warbler; *P.t. trochilus, P.t. acredula* and *P.t. yakutensis.* Only the two former reside in Sweden, *trochilus* in the south and *acredula* in the north, whereas *yakutensis* reside in northern Eurasia, mainly Russia. Carl von Linné, Linnaeus, was first to describe the willow warbler in *Systema Naturae* in 1758. He placed it in the genus *Motacilla*, from where it was later removed and transferred to *Phylloscopus* in 1826 by Boie. Linnaeus recognised two sub-species, *acredula* and *trochilus*, a separation based mainly on differences in colouration of specimens captured in England and Sweden. With eagerness and with fame rather than science in mind, several naturalist has since joined the quest of describing the diversity of Nature and many willow warbler sub-species have been named and claimed. The two sub-species *acredula* and *trochilus* that divide Sweden between them are still recognised, even if they may not represent the exact definition they once received from Linnaeus. Today they are awarded sub-species status because of their difference in migratory programme, i.e. they migrate in two different directions and winter in different areas in sub-Saharan Africa. In Sweden, birds breeding below 60°00'N are considered to be *trochilus* and birds breeding above 63°00'N to be *acredula*, with a suggested hybrid zone existing where they meet (Bensch *et al.* 2002). While it is not known when the two subspecies came into secondary contact, willow warblers were reported as common across the whole of Sweden by the early 19th century (Nilsson 1817).The difference in migratory program has been verified through analysis of isotope δ^{15}N (Chamberlain *et al.* 2000a; Bensch *et al.* 2009b), autumn migratory direction (Ilieva *et al.* 2014) and by ringing recoveries (Hedenström & Petterson 1987). There has also been effort devoted to finding a genetic basis of the migratypes/ sub-species (Bensch *et al.* 1999; Bensch *et al.* 2009a). At the AFLP-derived markers WW1 and WW2, Bensch *et al.* (2002, 2009b) found clear differences between northern and southern birds in allele frequencies. The AFLP-WW2 is a locus that could be associated with genes encoding the variation in migratory program between the sub-species, whereas the AFLP-WW1 locus appears to be an anonymous non-coding autosomal region (Bensch *et al.* 2002, 2009b), that could be linked to environmental adaptation to high altitudes and short growing season (Lundberg *et al.* 2011; Larsson *et al.* 2014).

Other aspects that separate willow warblers breeding in southern Sweden from willow warblers breeding in northern Sweden is susceptibility to stress (Silverin *et al.* 1997), size (Fonstad & Hogstad 1981; Lindström *et al.* 1998; Bensch *et al.* 1999; **Paper II**) and to some degree, colouration (Bensch *et al.* 1999). In **Paper II**, we describe a comparison in wing length between birds banded at Sundre Bird Observatory (SBO) on Gotland in southern Sweden and birds banded at Haparanda-Sandskär Bird Observatory (HSBO) in northern Sweden. When males (defined as having wing lengths over 66mm, i.e. 67-75mm) and females (defined as having wing lengths under 66mm, i.e. 58-65mm) from the two sites were compared, the results revealed that both sexes were significantly bigger at BSBO (Wilcoxon rank sum test, females: $W=1686$, $p<0.001$, males: $W = 3257$, $p<0.001$). Difference in colouration is the trait with least explanatory reliability (Bensch *et al.* 2009b), but it has been argued that northern breeding willow warblers are less green and more grey than those breeding further south (Bensch *et al.* 1999).

Although it is known that the two European sub-species, together with the Eurasian *P.t. yakutensis*, winter at different locations in sub-Saharan Africa, little is known about the extent of the distributions there. In western Africa, where *trochilus* individuals winter, willow warblers tend to change wintering area depending on precipitation patterns (Salewski *et al.* 2002), i.e. employing itinerancy (Moreau 1972). They are also reported to sing occasionally during wintering (Salewski *et al.* 2002) and to compete for food with local resident warblers (Rabøl 1987). Willow warblers are very unusual in their moult programs, as they undergo primary moult two times per year, with one episode taking place during wintering (e.g. Underhill *et al.* 2008).

Arrival to the breeding grounds in Europe starts in March-April, but Swedish birds start to arrive to the southern parts of the country mid-April. At the three study sites included in this thesis, the first males start to claim territory around 25th of April on Gotland and Tovetorp and about a month later at Abisko. Males arrive about a week earlier to the breeding grounds than females, a phenomenon known as “protandry”. Upon territory establishment, males are aggressive against competitors and defend territories of about 5000m^2 (Jakobsson, pers. comm.). When females arrive, they chose mates depending on singing rate and territory quality (Arvidsson & Neergard 1991) and build nests on the ground. Both males and females may mate promiscuously (Lawn 1982) and males may have more than one female with a nest within his territory. Five to seven eggs are laid (Bjørnstad & Lifjeld 1997; Evans *et al.* 2009), but in the north eight eggs are not uncommon (pers. obs.). The female incubates for about 13 days and when the chicks are hatched, they remain in the nest about 13 days. After fledging, the young moult and are fed by the male and female (who divide the brood in between them) for an additional 10 days (Jakobsson, pers. comm). Nest predation is high, about 50% of nest are lost (Silverin *et al.* 1997; **Paper III**), and re-nesting is common. Secondary broods are very rare, but do occur (Nilsson 1983; Marchant & Wernham 2003; del Hoyo *et al.* 2006). The willow warbler departs from Europe between the end of July and the beginning of September, depending on breeding latitude (Tiainen 1991).

The willow warbler is the most common bird species breeding in Sweden, and approximated number of breeding pairs is 13.2 million (Ottoson *et al.* 2012). Of all bird species engaging in trans-Saharan migration, the willow warbler is believed to be one of the most numerous

(Ulfstrand & Hogstedt 1976; Cramp & Brooks 1992). However, the population status is concerning. Even though the species is deemed to be "of least concern" according to IUCN (IUCN 2015), it is declining in most European countries where it is breeding (EBCC 2015). In Sweden, the north population is decreasing, whereas the southern appears to be stable (Green & Lindström 2014). The population trend in the north is negative in all of Fennoscandia, particularly in high altitude areas (Lehikoinen *et al.* 2014; Thingstad *et al.* 2015).

Longevity in the willow warbler is about 1–4 years (Bairlein 2006) with the oldest ever reported bird being 11.8 years (Fransson 2010) and estimates of annual survival rate vary between 30 - 40% (Tianen 1983, Baile & Peach 1992; Siriwardena *et al.* 1998).

The word *Phylloscopus* is a combination of the Greek words φυλλον phyllón, meaning "leaf", and σκοπεω skopeo, meaning "too look at" or "to see". *trochilus* is also greek and belongs to τροχος trochos, which means "wheel" (Whiter 1811). The association with a word for wheel is interpreted as the motion of the bird, i.e. that it twist and turns about. In English, the willow warbler was also originally referred to as the willow wren, until William Yarrell named it willow warbler in 1843 (Lockwood 1984). Interestingly, the word wren is also derived from a branch of words associated with meanings of varied motion, i.e. the word *wring* which means "to twist / turn about" (Whiter 1811). The name *acredula* is believed to be have been used first for the nightingale. Cicero says in his Prognostics: "Et matutinos exceret acredula cantus", meaning "Acredula performs its morning song" (Throop 2005), but it was later broadened and came to mean just a singing bird.

Willow warbler in other languages: lövsångare (Swedish), løvsanger (Danish), løvsanger/ lauvsangar (Norwegian), pouillot fitis (French), Fitis (German), pajulintu (Finnish), Пеночка-весничка (Russian), mosquitero musical (Spanish), luì grosso (Italian), felosa-musical (Portugese), עלווית אפורה (Hebrew), نقشارة (Arabic), Fitiszfüzike (Hungarian), Puig-haleg (Brezhoneg), piecuszek (Polish), fitis (Dutch), Rievssatcizáš (Sami), Salu-lehelind (Estonian), Вівчарик весняний (Ukrainian), Θαμνοφυλλοσκόπος (Greek), ķauķis (Latvian), hofsanger (Afrikaans).

Study species: The chaffinch

Figure 10. To the left: chaffinch female (photographer: Jacob Spinks 2014), source: Wikimedia commons (Creative Commons Attribution 2.0 Generic license). To the right: chaffinch male (photographer: John Haslam 2007), source: Wikimedia commons (Creative Commons Attribution 2.0 Generic license).

The chaffinch (*Fringilla coelebs*) is a medium sized, insectivorous and seed feeding passerine (**fig. 10**), weighing 17-29 grams and having a wing length of 114-118mm (del Hoyo *et al.* 2006). In Europe, it is widely distributed, being almost omnipresent (BirdLife International 2015). It is a short-distance migrant, wintering in western, continental Europe, but in southern Sweden the species is also common as a winter resident (Payevsky 2010; BirdLife International 2015, **Paper V**). The chaffinch has also been introduced to New Zealand, where it has become one of the most widespread bird species (Allen & Lee 2006).

The chaffinch and the willow warbler are kindred birds in regard to song melody, which is very similar, and in that they are the most common species in many countries within their northern range. The chaffinch is second to the willow warbler in breeding numbers in Sweden, reaching 8 million breeding pairs (Ottoson *et al.* 2012). The population status in Europe is stable (EBCC 2015), and the European breeding population is large, reaching >130 million breeding pairs (BirdLife International 2015). One factor behind the species' success could be its adaptability to different habitats. The chaffinch is sometimes considered to be a farmland species, but it also common in forests and in close association with urban nature, e.g. parks and gardens (Cramp & Perrins 1994), and in sharp contrast to other farmland bird species, it has increased in numbers during the latest decades (Baillie *et al.* 2002;

Whittingham *et al.* 2001). The chaffinch is a tree nester and usually lays 4-5 eggs (Newton 1964) in a nest secured in the wedge between branches, concealed with moss and lichens (Mullarney *et al.* 1999). Previous studies have documented a positive correlation between chaffinch densities and tree densities in hedgerows (Osborne 1984, Macdonald & Johnson 1995) and breeding success has been found to be positively associated with scrub cover (Møller 1991). Nest predation in chaffinches can be high, reaching 50% (Whittingham *et al.* 2001).

Territory size in the chaffinch is about 6700m^2 (Marler 1956) and males arrive and sing long before the breeding activity commence. In the UK chaffinches sing from March to June (Riebel & Slater 2000) and in central Europe for as long as two months prior to egg-laying (Bauer *et al.* 2005).

Figure 11. A chaffinch female in The Sherborne Missal, an illustrated manuscript from the 1400s, currently at the British Library, source: Wikimedia Commons public domain artwork.

Unlike the willow warbler, the chaffinch is conspicuous, easy to recognise and dissimilar from other bird species. As such, it has made an impression on scholars, writers and poets. The Swedish poet and composer Carl Michael Bellman (1740-95) sang about the chaffinch (bofink in Swedish) in one of his more famous ballads Fredmans epistel N° 72 "Glimmande nymph". In 1544 the chaffinch was described by William Turner in his book "*Avium praecipuarum, quarum apud Plinium et Aristotelem mentio est, brevis et succincta historia*" (The main birds, as described by Plinius and Aristotle, a short and concise history), there called “spink” or “Sheld-appel”. Spink presumably refers to the call of the bird and “sheld” means multicoulred. Apple can be associated with the name of the bullfinch, Alp (Swainson 1885). In **figure 11** it is demonstrated how well medieval artist knew the appearance of the chaffinch, there portayed as decorative bird om one of the pages of the Sherborne Missal, a richly illustrated manuscript from the 1400s..

Chaffinch in other languages: bofink (Swedish), bogfinke (Danish), bofink (Norwegian), pinson des arbres (French), pinzón vulgar (Spanish), Buchfink (German), pint / pintig (Brezhoneg), Φρυγίλλος ο άγαμος (Greek), peippo (Finnish), حسون الظالم (Arabic), fringuello (Italian), bófinka (Iclandic), žubīte (Latvian), ნიბლია (Georgian), erdei pinty (Hungarian), vink (Dutch), ズアオアトリ(Japanese), beibboš (Sami), tentilhão (Portugese), zięba zwyczajna (Polish).

Study sites

The data for this thesis originates from a multitude of sites scattered across Sweden and reaching as far back in time has the late 19th century. Personally, I have been actively involved in collecting field data on migration, reproduction and behaviour of willow warblers at four sites; Gotland, Tovetorp, Södermanland county and Abisko. Beside these locations, I have been granted access to long time series and detailed information collected by others at two ringing stations; Sundre Bird Observatory and Haparanda-Sandskär Bird Observatory and field data collected by Sven Jakobsson, Anna-Karin Fridolfsson, Frida Jaremark, Robert Stach, Frida Sjösten and Kristaps Sokolovskis. In addition, for **Paper V**, I as a co-author was given the opportunity to participate in an analysis of historical data sets of bird observations spanning 140 years, collected all over southern and central Sweden from 1873 to 2013 by volunteering and governmentally organised individuals.

Figure 12 depicts the locations of the study sites where an exact position can be given: southern Gotland (56°55’N, 18°07’E); Tovetorp Research Station (58°94’N, 17°14’E); Haparanda-Sandskär Bird Observatory (65°32’N, 23°44’E), Abisko Scientific Research Station (68°32’N, 18°80’E) and the county of Södermanland. Gotland is an island in the Baltic Sea, situated 80km from mainland Sweden and within the boreo-nemoral

Figure. 12. To the right: map over Sweden, marking the locations of Sundre on southern Gotland, Tovetorp and Södermanland county in south-eastern Sweden, Haparanda-Sandskär in north-eastern Sweden and Abisko in northern Sweden. To the left at the top: Abisko with view over lake Torne (photo: Johanna Hedlund); in the middle: view over juniper moorlands in Sundre (photo: Johanna Hedlund); and at the bottom: mixed forest at Tovetorp (photo: Frida Sjösten).

vegetation zone (Ahti *et al.* 1968). Data on spring arrival and autumn departure of willow warblers, used in the analyses for **Paper I and II**, was derived from ringing records from Sundre Bird Observatory which is situated on the southernmost tip of Gotland. Ringing at Sundre Bird Observatory was first initiated in 1976 and has been continuous since.

Gotland and Sundre were also the location of one of the field sites continuously monitored during the development of this thesis. The field site consists of two environmentally different areas in close vicinity; one is a dry, open alvar plateau sparse in vegetation and mainly dominated by juniper (J*uniperus communis*), pine (*Pinus sylvestris*) and whitebeam (*Sorbus intermedia*) (**fig. 12**), whereas the other area is a wet semi-wild grassland rich in herbaceous plants and deciduous trees. Data on egg-laying dates and spring arrival of breeding birds was collected at this field site, and included in the analysis of **Paper I.**

Tovetorp Research Station is part of the Department of Zoology at Stockholm University. Here, data collection on arrival, breeding and behaviour of willow warblers has been conducted since 1979, with some interruptions. The area is dominated by coniferous forest and is a typical rural landscape in the Scandinavian boreo-nemoral zone (Ahti *et al.* 1968). Information on philopatry and nest biology collected at this site was used in **Paper III**. Tovetorp is situated in Södermanland county which also was the location for the historical landscape survey performed in a study area of 165200ha (midpoint 59°00'N, 17°11'E) for **Paper IV**.

Haparanda-Sandskär Bird Observatory lies in the North Bothnian Sea archipelago outside Haparanda in Norrbotten county in the main boreal vegetation zone (Ahti *et al.* 1968). Here, birds have been continuously ringed since 1981, with main focus on autumn migration. Abisko Scientific Research Station is also situated far north in Sweden but further into the mainland, at the shore of lake Torne in Swedish Lapland. At this location, similar monitoring studies as those at Tovetorp and Gotland on spring arrival, reproduction and behaviour of willow warblers were conducted 2011-2014. Abisko lies within the sub-alpine birch woodlands of the boreal vegetation zone (Ahti et al. 1968) and is a stochastic environment where cyclic peaks of rodent and autumnal moth outbreaks are common (Jepsen *et al.* 2008; Elmhagen *et al.* 2011).

Ringing records and citizen science

The Sundre and Haparanda-Sandskär ringing records utilized in this thesis (**Paper I and II**) are slightly different in composition and coverage. Sundre Bird Observatory (SBO) was founded 1976, but I chose to only include records from 1990 onwards for **Paper I and II**. The aim was to eliminate a possible effect of the move of the ringing site in 1990, from Skoge (56°55'13'N,18°11'49'E) to Hoburgen (56°55'11'N, 18°07'29'E). Since 1990, SBO has continuously documented ringed birds during both spring and autumn. The ringing effort is standardized, continued daily from sunrise and always include the two periods April 25th – June 6th, and July 25th – September 15th. For willow warblers, the following details are recorded: wing length, weight, age, fat score and post-juvenile moult score. For **Paper I and II**, post-juvenile moult scores were used to separate juveniles into two groups; locally hatched juveniles and migrating juveniles and wing lengths were used to separate males and females. A total of 11842 individuals ringed during spring were included in the analysis from SBO, of these 7068 were males and 4774 were females. In autumn, a total of 17800 individuals were included in the analysis, of which 890 were adults and 8200 were juveniles. Of the juveniles, 8200 were locally hatched (3917 males and 4342 females) and 8700 were on migration (4390 males and 4339 females).

At Haparanda-Sandskär Bird Observatory (HSBO), ringing has been less well standardized as full staffing has not always been possible and many of the years (1991, 1992, 1996, 1999; 2000, 2006) within the study period 1990-2012 had to be removed from the analysis since the trapping effort was too irregular. Irrespective of this exclusion, the total number of individuals analysed in **Paper II** from HSBO reached 17441. As data on wing lengths and age was also recorded at HSBO differentiation between males and females was possible and of the 17441 individuals analysed, 9771 were juvenile males and 7670 juvenile females.

The scoring of post-juvenile moult, which is only done at SBO, is based on the guide developed by Bensch and Lindström (1996) and involves seven stages. When birds are in the stages 0-4 moulting is in a very active process: 0) post-juvenile molt not yet initiated, chicks under 15 days of age (**fig. 13**); stage 1) growth of primaries not yet complete, waxy sheaths present on outer primaries; stage 2) wing growth complete, new feathers growing on sides of breast with throat feathers sill in pin; stage 3) growing feathers on throat and sides of breast (three moulting areas distinguishable), some throat feathers have now emerged from the sheaths; stage 4) the three mouling areas have merged, there is an uninterrupted band of new feathers from the throat along each side of the breast and flanks. We deemed it very unlikely that juveniles in these stages would be in active migration and thus unable to be on the island of Gotland unless they were hatched there (**Paper I, II**). Gotland is situated far from mainland Sweden, about 90km from the nearest coast, and post-juvenile moult is not combined with longer flights (Lawn 1984, Norman & Norman 1985). Thus, individuals with moult score 0-4 were subsequently designated as "locally hatched juveniles". Juveniles in stage 5 are described by Bensch and Lindström (1996) as having "new feathers only, but with waxy sheaths still present on belly feathers" and juveniles in stage 6 as having "completed post-juvenile moult". Individuals with moult score 5-6 were subsequently designated as "juveniles in migratory mode", i.e juveniles that could have been hatched on Gotland or elsewhere and that when ringed were actively migrating.

As the willow warbler is sexually dimorphic, wing lengths can be used to separate males and females, and this was done for the data from both SBO and HSBO. Males have wings ranging between 66-78mm in length and females have wing lengths ranging between 58-66mm (Svensson 1975, Tiainen 1982). In our two studies that utilized ringing records from SBO and HSBO, individuals of wing length 66 were removed from the analysis, as these could be of either sex. When analyzed separately using linear regression analysis, it is revealed that the median passage date of individuals of this wing length have advanced arrival in spring to SBO ($r^2_{adjusted}=0.20$, $p=0.01$), but show no change in autumn departure from either SBO ($r^2_{adjusted}=0.04$, $p=0.15$) or HSBO ($r^2_{adjusted}=0.007$, $p=0.93$).

Figure 13. To the left: adult willow warbler female with colour rings and a metal ring re-captured in a net at the field site in Sundre, Gotland, 2013; to the right; willow warbler juvenile at approximately 11 days of age, Abisko 2011, photo: Johanna Hedlund.

Birds offer great opportunity for studies on the effects of climate change because of the long-term records made available by ringing efforts (**fig. 13**). Depending on the resolution of the data (size, wing length, moult score, fat score, weight, sex etc), the ringing records provide differential detail, and thus varying certainty and ultimately varying explanatory power (Meller *et al.* 2013, **Paper I**). There are however some methodological caveats associated with ringing records, population size may influence probability of capture and in days of adverse weather and heavy winds, sampling effort is skewed (Miller-Rushing *et al.* 2008c). The negative effects of these limitations increase in records that are less standardized and collected by less experienced observers, as is the reality with citizen science and volunteer observations. When documenting migratory arrival, means and foremost medians and percentiles are better descriptions of the behaviour of populations than first arrival dates, as the latter is highly dependent on probably of detection (i.e. population size) and merely reflects the extreme behaviour of certain individuals than the migration cohort as a whole (Miller-Rushing *et al.* 2008b; Lehikoinen & Sparks 2010; Hüppop & Hüppop 2011).

Citizen science initiatives have been facilitated by the digital globalization and are growing in numbers as never before. This development is in contrast to the otherwise largely absent interface between civil society and science, and presents great opportunity for public involvement, conservation and education. Human intelligence is so far superior to any computer in achieving the complex task of identifying a bird species in the field, as the observer must process the impressions of shape, size, and behavior under differing conditions and simultaneously reconcile this data against a list of species likely to occur at that specific location and date (Wood *et al.* 2011). The public has contributed significantly to the understanding of bird distribution and abundance for more than two hundred years (Barrow 1998) and in **Paper V** two types of such volunteer records were utilized. The historical record (1873-1917) was an aimed initiative, initiated by the government and focusing on participation of farmers through specific submission forms. The present day record (1984-2013) however, was part of the still ongoing report system called Artportalen (Species Observation System), where the public join freely and report on sitghings of birds, insects and flowering.

Figure 14. Me holding a 7 days old willow warbler chick at one of our field sites in Abisko 2011, photo: Sven Jakobsson.

Field observations

Daily field observations of willow warbler territories were conducted 2011-13 at Sundre, Tovetorp and in Abisko (**fig.12**, **fig.14**). Observations started upon male arrival (late April in southern Sweden and late May in northern Sweden). When males had been singing for more than one day, the territory was considered established and the male was caught and ringed. All marked birds received one metal ring with a unique number, issued by the Swedish Natural Museum, and three colour rings, with every colour representing a number (**fig. 13**). At each site and year, males and females were equipped with a particular starter number, facilitating recognition between sexes and years, for example: on Gotland in 2013 all males received a pink ring, nr 2, as the starter number and all females nr 6, orange as the starter number. Between 25-35 territories were followed at each site. About a week after male territory establishment, the females arrive and chose a mate. At this point, we recorded the date at which all individuals formed pairs and then attempted to find where females built nests. Identified nests were then monitored for the first day of egg-laying and start of incubation. One egg is laid per day and usually, between six-seven eggs are laid at the first nesting attempt. Many nests are lost before hatching and when re-nesting is attempted, fewer eggs are often laid. At day three, six and nine after hatching, all known nests were filmed for three and a half hour using

Figure 15. At the top: still shot of a willow warbler female at her nest in Abisko 2011; to the left at the bottom: camouflaged nest camera at Tovetorp; to the righ at the bottomt: willow warbler young weighed in at 8.9grams at 9 days of age, Sundre 2013. All photos: Johanna Hedlund.

camouflaged nest cameras (**fig.15**) and the young were weighed. The young of each nest are followed until fledging, which generally happens at day 13after hatching. Between day 10-13 the young are able to survive outside the nest and cannot be handled or disturbed as this triggers escaping, thus they are given metal rings before day 9.

Historical maps and GIS, Geographic Information Systems

For **Paper IV** we utilize a historic cadastral map (in Swedish Häradskartan, resolution 1:50000) developed between 1899-1901, that had been prepared for digitalized usage and employed by Cousins *et al.* (2015), and three present-day maps: the 2013 terrain map (in Swedish Terrängkartan, resolution 1:50000), the CORINE land-cover map from 2012, and the Swedish Property map (in Swedish Fastighetskartan).

The purpose of the old cadastral maps was to accurately describe the area and location of crop-fields and meadows, as these land-uses were economically important, but the maps also depicts forested areas, lakes, buildings, roads and wetlands (**fig. 16**). The type of cadastral maps used in

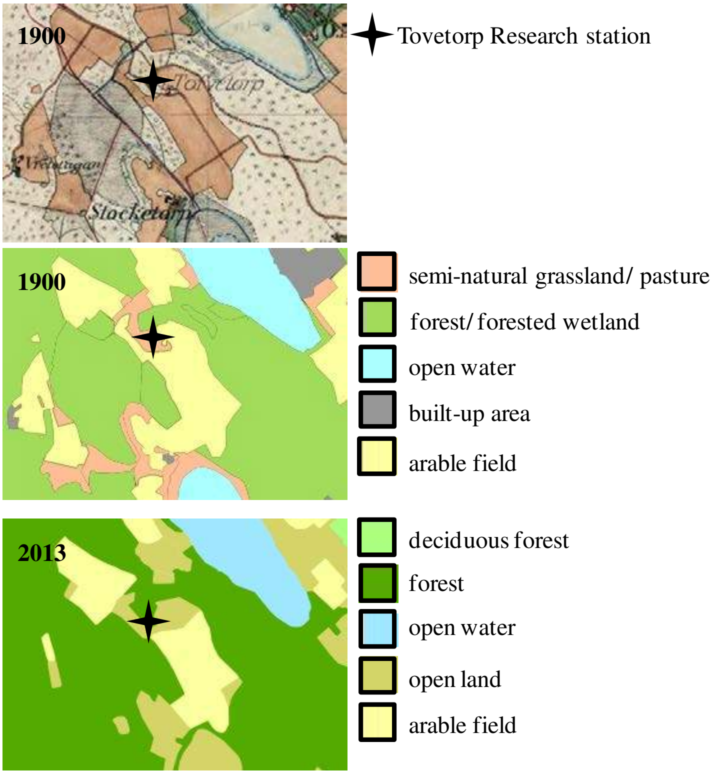


Figure 16. Cadastral map from 1900 followed by the corresponding digitized version, and a terrain map from 2013.The maps depict the area around Tovetorp Research Station (marked with a star) in southeastern Sweden.

Paper IV have a high resolution and accuracy (Jansson 1993), but small irregularities may form when converting them into digitalized form (Cousins *et al.* 2015) and the different land covers were manually digitized to maximize precision.

During the analysis, the cadastral map and the modern maps were handled in ArcMap™ (version 10), a Geographic Information System software program developed by ESRI (Environmental Systems Resource Institute, California). GIS allows fast and exact calculations of for example coverage of different digitalized areas and with the help of different tools, the association between different layers can be calculated. Thus large-scale, fast and accurate estimations are made possible. For example, to estimate the amount of forest used for grazing and firewood, polygon areas reaching 500m from all dwellings were created and all forested areas falling within these were classified as utilized, grazed forests.

Measuring climate change

Temperature

Investigators attempting to determine whether an observed change in a living organism can be associated with a proxy of climate change have most commonly chosen to make the comparison with some form of temperature measurement, e.g. average local temperature, average minimum temperature or degree days (Ahola *et al.* 2004; Cotton 2003; Both *et al.* 2005; van Burskirk *et al.* 2009; Hurlbert & Liang 2012). The benefits of using temperature to describe climate are that long and precise time series are available and that means can be calculated for many different scales and dimensions (minimum, maximum, daily average, monthly average etc). Meteorological analyses have also confirmed that local measurement can be used as a reliable indicator of a fairly large sourroudning area (Heino 1994; Sokolov *et al.* 1998). Temperature is the main indicator used in descriptions of climate change and highly topical for analysis of phenological responses to climate change. For studies on climate responsiveness in birds, explanatory climate parameters are generally chosen as measurements of changes in resource availability and/or changes in indicators of meteorological favourability (i.e. favourable in terms of physiological temperature threshold and again, resource availability). Temperature is a valid indicator of phenology in many insects (Tauber *et al.* 1982; Visser *et al.* 1998; Visser & Holleman 2001; Poseldovich *et al.* 2015), important resource for numerous bird species, and temperature may also have an impact on reproduction and thermoregulation in birds (Nager & van Noordwijk 1992; Bryan & Bryant, 1999, Smithers *et al.* 2003, Pendlebury *et al.* 2004, Jiguet et al. 2010b).

For **Paper II**, we included estimates of average local monthly temperatures as a proxy of climatic change at my two study sites (one southern and one northern). Only months during which willow warblers are present in the area were chosen, i.e. April-September at the southern site and May-September at the northern site. The data was downloaded from SMHI (the Swedish Meteorological and Hydrological Institute) an analyzed for the period 1990-2012. The results indicated no change over time, except for September, during which temperature had increased at both sites. However, if the period investigated is lengthened to incorporate time before the start of global climate change, i.e. to 1961-2012, the picture is another. Temperature has then risen at the southern site during April (Linear Regression, $p<0.001$, $r^2_{\text{adjusted}} = 0.29$), May ($p<0.001$, $r^2_{\text{adjusted}} = 0.21$), July ($p<0.001$, $r^2_{\text{adjusted}} = 0.19$), August ($p<0.001$, $r^2_{\text{adjusted}} = 0.19$) and September ($p<0.05$, $r^2_{\text{adjusted}} = 0.09$), and at the northern site: in May (Linear Regression, $p<0.01$, $r^2_{\text{adjusted}}=0.11$) and July ($p<0.05$, $r^2_{\text{adjusted}} = 0.07$), but not in September.

The North Atlantic Oscillation (NAO)

Indices of large scale atmospheric systems have also been tested against phenological events in avian species. The North Atlantic Oscillation (NAO) is a natural atmospheric pressure system that re-disseminates atmospheric volumes from the Arctic to the southern Atlantic (Hurrell *et al.* 2001). The NAO influences temperature and rainfall over large areas, including Europe, North Africa and the Middle East but not the Sahel region (Hurrell 1995; Cullen & de Menocal 2000; Wang 2003). Due to the inherent magnitude of the NAO's influential capacity, it causes a coherent, temporal symmetry in the interaction of trophic levels in both terrestrial and aquatic systems (Ottersen *et al.* 2001; Straile 2002). Therefore, the NAO has been argued to have greater explanatory power than for example local temperature (Hüppop & Hüppop 2003) and to influence both long- and short distance migrants (Forchhammer *et al.* 2002). Effects of the NAO on timing of avian phenology have been repeatedly shown, e.g. egg-laying and spring arrival correlates with NAO (Forchhammer *et al.* 2002; Hüppop & Hüppop 2003). Interestingly, it is also one of the climate parameters used that appears to produce most varying result of influence: correlation between spring migration (Hüppop & Hüppop 2003,Vähätalo *et al.* 2004, Stervander *et al.* 2005), no correlation (Cotton 2003) or partial correlation (Jonzén *et al.* 2006, Hüppop & Hüppop 2011)

In **Paper II**, we included the winter index of the NAO as a proxy of large scale climate change. In winters with high NAO index, conditions become warm and wet in Europe, causing earlier emergence of spring plants and insects (Sparks & Carey 1995; Post *et al.* 2001; Ottersen *et al.* 2001). In the Baltic region, there is a positive relationship between increased winter values of the NAO and spring greenness. Thus vegetation productivity and fluxes of the NAO are associated, a relationship that also was corroborated in our analyses in **Paper II**, where winter index of the NAO and growing season onset (GSO) always aggregated together in our Principle Component Analyses (PCA). The NAO and the GSO also demonstrated explanatory significance for migratory change in willow warblers passing SBO.

Growing season onset and NDVI

The timing of the growing season onset (GSO) is rarely considered in research on climate change effects on avian phenology (e.g. Sanz *et al.* 2003; Visser *et al.* 1998), which is surprising considering the potential of this measuring factor. The growing season is defined as the period during which the vegetation is actively developing, e.g. producing leaves, flowers and general growth. Growing season onset can be estimated indirectly though temperature thresholds which vary for different plant species depending on species-specific endurance (SMHI 2015), or directly through e.g. satellite surveillance of greening (e.g. Høgda *et al.* 2013). Once such remote sensing technique with which increases in primary productivity and growing onset can be measured is the Normalise Difference Vegetation Index (NDVI) (reviewed by Pettorelli *et al.* 2011). As vegetation is a necessity for most insects, NDVI can for example be used to assess abundance of prey insect species (Lassau & Hochuli 2008; Jepsen *et al.* 2009) and has through this ecological mechanism been suggested to influence timing of bird migration (Visser *et al.* 1998). There is an increasing number of studies that use NDVI as an explanatory variable in investigating changes in avian phenology and correlations between earlier arrival and high NDVI have been suggested for the sub-Saharan wintering ground (Saino *et al.* 2004) and North African and Sahel stop-over sites (Balbontin *et al.* 2009; Robson & Barriocanal 2011).

In Sweden, the growing season has increased in length, primarily through earlier onset but also by delaying the end (SMHI 2015, **fig. 4**). These changes has occurred at most latitudes in Sweden and Fennoscandia (Karlsen *et al.* 2007; Høgda *et al.* 2013), but not uniformly, and thus populations may respond differently accordingly. It has been demonstrated in herbivores that shifts in the timing of vegetation onset may have different effects on populations at different latitudes (reviewed by Pettorelli *et al.* 2011). In **Paper II**, growing season onset was utilized as a proxy for climate change and showed significant seasonal advancement, in both southern and northern Sweden.

Sammanfattning

Den globala uppvärmningen har påverkan på beteende och ekologi hos världens arter. Temperaturen på våren ökar, vegetationsperioden tidigareläggs och i interaktion med ytterligare pådrivande faktorer, som tex förändring i markanvändning, håller det ekologiska landskapet på att skifta både temporalt och spatiallt för många arter. Detta ålägger organismer med stor anpassningsbelastning. Fåglar utgör ett exemplariskt system att undersöka i denna kontext, eftersom de är lättstuderade, traditionellt välstuderade samt, då merparten fågelarter i tempereareade klimat är migrerande, utsatta för ett vitt spektrum av miljömässiga faktorer och ekologiska effekter. I den här avhandlingen brukas historiska ringmärkningsserier, fältobservationer, historiska kartor och frivilligobservationer med syftet att utröna beteendemässiga och ekologiska responser hos fåglar på den pågeånde klimatförändringen. Migrerande fåglar utgör en av världens största massrörelser utav djur och en av de talrikaste europeiska arterna som pendlar mellan de euroasiatiska och afrikanska kontinenterna är lövsångaren (*Phylloscopus trochilus*). Lövsångaren är Sveriges vanligaste fågel och som långdistansflyttare antagen att vara särskilt utsatt av klimatförändringen. I min första artikel visar jag hur samtliga tre häckningsfenologiska händelser; vårankomst, reproduktion samt höstavfärd, har titigarelagts parallellt hos lövsångare som häckar och migrerar förbi ett studieområde i södra Sverige (65°N, 18°E). Således ankommer, häckar och lämnar fåglarna Sverige tidigare, samtidigt som häckningsperioden inte har förändrats i längd. Genom att undersöka migrationsresponsen hos olika individer kunde det även påvisas att särskilt tidigt ankommande hanar och tidigt höstflyttande ungfåglar har tidigarelagt sin migration. I en påbyggande studie, där ringmärkninsgdata från ett nordligt studieområde (65°N, 23°E) inkluderats, blir det emelelrtid uppenbart att lövsångare som häckar längre norrut i Sverige inte har förändrat sina migrationmönster på hösten någonting. Migrationsdatat från de två områdena analyseras även mot tre faktorer som beskriver klimatförändringen: lokal temepratur, vinterindex hos North Atlantic Oscillation (NAO) samt vegetationsperiodens start i norra och södra Sverige.

Resultaten antyder att de grupper som uppvisar förändrade migrationsmönster har förändrat den i relation till vegetationsperiodens start samt NAO. Men trots att vegetationsperioden har tidigarelagd start både i norra och södra Sverige så har dock inte lövsångare i norr förändrat sin höstmigration. I min tredje artikel visar jag att nordliga lövsångare även uppvisar en anmärkningsvärd avsaknad av ett beteende som annars är normalt förekommande: filopatri. Här föreslås det att de klimatpådrivna förändringarna i vegetatonsperiodens längd och start, i samverkan med en ökning i antalet tillgängliga revir, kan ha gynnat ett mindre filopatriskt häckningsbeteende och möjliggjort en tillströmmning utav spridningsbenägna, nomadiskt häckande individer. Tillgänglighet utav revir studerades även i relation till 100 år av förändring i markanvändning i södra Sverige och i samverkan med framtida klimatförändringars effekt på skogsbruk. Den massomvandling utav betad skog till produktionsbarrskog som har skett i Sverige mellan åren 1900-2013 kunde påvisas ha en negativ effekt på revirtillgänglighet hos lövsångaren, emedan en annan vanlig art, bofinken (*Fringilla coelebs*), visade sig vara i stora drag opåverkad. I ett framtida scenario där stigande temperaturer har ökat tillväxten hos träd, kommer fällningsrotationen ske snabbare och både produktionsbarrskog och hyggen öka i storlek. Detta kommer att gynna både lövsångaren och bofiknen. I min femte artikel görs en relativ jämförelse mellan två dataset, båda sammanställda av frivilliga observatörer, som sträcker sig över 140år och som beskriver vårankomst hos 14 flyttfåglar. Resultaten pekar på att kortdistansflyttande fåglar har tidigarelagt sin ankomst mer än långdistansflyttande fåglar, speciellt i södra Sverige och att detta tills viss del beror på att kortdistansflyttare har börjat övervintra i södra Sverige. Sammanfattningsvis så ger resultaten i den här avhandlingen inblick i klimatförändringens effekter på fåglars beteende och ekologi, dokumenterar unika observationer samt bidrar med ett vitt spektrum av kunskap, från exakta detaljer hos individuella fåglar, långsiktiga förändringar på populationsnivå och historiska perspektiv på skiften i hela landskap.

Abstract

Recent global climate change is influencing the behaviour and ecology of species worldwide. Birds are typical systems to study in this context, as they are often migratory and thus subjected to a variety of environmental effects. This thesis employs the use of long-term ringing records, field observations, historical maps and historical volunteer observations with the aim of describing behavioural and ecological responses of birds to the current environmental change. An investigation into the spring arrival, reproduction and autumn departure in willow warblers (*Phylloscopus trochilus*) breeding at a southern study site in Sweden (65°N 18°E) showed that all three phenological events had advanced in parallel. Thus birds arrive earlier, start breeding earlier and leave Sweden earlier, with the breeding period staying the same in length. By teasing apart the migratory responses of different individuals, it became clear that particularly early arriving males and early departing juveniles had advanced migration. However, willow warblers migrating past a northern study site in Sweden (65°N 23°E) displayed no change in autumn departure. When migration in the two regionally separate populations were analyzed in relation to climatic variables, the results indicated that foremost a combined effect of growing season onset and the North Atlantic Oscillation influenced migratory timing, and only in individuals that had advanced migration. As growing season onset had advanced at both regions, but only elicited migratory change in southern willow warblers, it is proposed that intraspecific difference between populations prepare them differently to climate change. Willow warblers breeding at northern latitudes were also displaying absence of an otherwise common behaviour of the species: philopatry. It is suggested that the climate induced change in onset of the growing season, coupled with an increase in available territories, could have enabled a southern influx of dispersal-prone birds adopting a less philopatric breeding behaviour. Availability of territories was also studied in southern Sweden, in relation to 100 years of land-use change and future climate change effects on forestry. The mass-conversion of grazed forest into coniferous sylvicultures that has occurred in Sweden 1900-2013 was shown to have negatively affected territory availability for willow warblers. The second most common bird species in

Sweden, the chaffinch (*Fringilla coelebs*), was however shown to be largely unaffected. In a future scenario where rising temperatures will increase growth rates of trees, harvest rotation will be faster and both sylvicultures and logged areas will increase in coverage, favouring both species. Thus commonness in terms of landscape and species occurrence has altered historically and is dynamically linked. Historic perspectives were also applied to observations of spring arrival of 14 migratory bird species. A relative comparison of two data sets, collected over 140 years, revealed that short-distance migrants have changed their spring arrival more than long-distance migrants in southern Sweden. In conclusion, the results of this thesis provide insights into climate change effects on avian behaviour and ecology, document unique observations and contribute with a great spectrum of knowledge, from exact details on responses by individual birds, through long-term changes in populations to historical perspectives on shifts in entire landscapes.

Paper I

Long-term phenological shifts and intra-specific differences in migratory change in the willow warbler *Phylloscopus trochilus*

In this paper we investigated phenological change in the willow warbler using a holistic approach where the three main parts of breeding area phenology were studied in synergy; spring arrival, egg-laying and autumn departure. To identify possible temporal shifts in these life-history components, we utilized long-term data from ringing records from a Swedish island bird-ringing site (Sundre Bird Obseravtory, southern Gotland, 56°55'N, 18°07'E, see **fig. 12**) and two temporally separated data sets of arrival and reproduction of the breeding population at the same locality. The ringing record covered 22 years (1990-2012) and was uniquely detailed, thus allowing for the distinction between individuals according to; sex (determined by wing lengths), age (determined by post-juvenile moulting), migratory phase (determined by population percentile date of migratory passage, i.e. 5th, 50th and 95th percentile) and juvenile origin (determined by post-juvenile moult stage), all further explained in **Methods**.

With these data as basis, we aimed to answer two questions; 1) has there been a change in the timing of spring migration, egg-laying and autumn migration and have the potential changes in these phenologies occurred in parallel? 2) Are there differences in migratory response between groups in reference to age, sex, migratory phase and juvenile origin?

The analysis revealed a general parallel advancement occurring through all three phenologies, but also interesting differences in the migratory response between individuals during both spring and autumn.

During spring migration, individuals migrating in the two earliest phases of the migration period, i.e. those pertaining to the first and median percentile of the population in the ringing record, showed the strongest responses and advanced their spring arrival most (**table 1**), whereas individuals in the latest phase were not changing arrival at all.

According to the data collected on individuals breeding at the island site, egg-laying dates had advanced ($N_{1992-199}3=30$, $N_{2011-2013}=46$, Welch Two Sample T-Test, $t= 734$, $p< 0.001$) and the median egg-laying day (Julian day 141, i.e. May 21st) for the period 2011-2013 occurred five days earlier than the median egg-laying day of the period 1992-1993 (Julian day 146, i.e. May 26th). The spring arrival of the breeding population showed a less clear change than in the ringing records and presented a small shift to earlier

Table 1. Linear regression analysis on temporal change in spring migration in willow warblers at Sundre Bird Observatory, southern Gotland. The table shows results for males and females in three different phases of migration: early (5th percentile) phase; median (50th percentile) phase and late (95th percentile) phase. Columns display r^2-values (r^2), p-values (p) and calculated rate of change in days. Significant p-values are highlighted in bold.

Migratory phase	Sex	r^2	p	Rate of change
5th percentile	males	0.32	**0.003**	-0.22 days/year; 4.8 days
	females	0.31	**0.003**	-0.20 days/year; 4.4 days
50th percentile	males	0.57	**<0.001**	-0.29 days/year; 6.3 days
	females	0.13	**0.053**	-0.17 days/year; 3.9 days
95th percentile	males	-0.0005	0.332	-0.08 days/year; 1.7 days
	females	-0.01	0.449	-0.06 days/year; 1.3 days

arrival ($N_{1992-1993}$ =101, $N_{2011-2013}$= 146, Wilcoxon Rank Sum Test, W= 10815, p= 0.008) changing median arrival day from Julian calendar day 129 to 128.

During autumn migration, locally hatched juvenile males advanced their median peak appearance by 4.2 days whereas females showed no change in median peak appearance (**table 2**). Among migrating juveniles, i.e. juveniles in the last stages of post-juvenile moult, males and females in the first migratory phase showed the strongest advancement in departure, followed by males and females in the median migratory phase (**table 2**). Similar to the trends during spring migration, migrating juveniles in the latest phase of migration showed no temporal change (**table 2**). Very few adults were ringed during autumn migration (approximately 0.7 individuals/day), and thus only the median migratory phase was considered for this age group, and here, no change in passage date was detected (**table 2**).

In order to further investigate whether the association between breeding area phenologies might have shifted in relation to each other, we compared the number of days between median arrival of all adults in spring and median departure of all adults in autumn across the 1990-2012 ringing record. However, the comparison revealed no change over time in the number of days, i.e. in time spent at the breeding ground had ramined the same in length ($F_{1,20}$ =0.903, r^2= – 0.004, p =0.353).

Table 2. Linear regression analysis on temporal change in autumn migration in willow warblers at Sundre Bird Observatory, southern Gotland. The table show results for three age groups; locally hatched juveniles (local juv), migrating juveniles (migr juv) and adults. Migrating juveniles are further divided according to sex (m= males, f=females) and migratory phase: early (5th percentile) phase; median (50th percentile) phase and late (95th percentile) phase. Columns display r^2-values (r^2), p-values (p) and calculated rate of change in days. Significant p-values are highlighted in bold.

Phase	Age	Sex	r^2	p	Rate of change
50th	local juv	m	0.17	**0.031**	-0.19 days/year; 4.2 days
50th	local juv	f	0.08	0.101	-0.12 days/year; 2.7 days
5th	migr juv	m	0.36	**0.001**	-0.45 days/year; 9.9 days
5th	migr juv	f	0.42	**<0.001**	-0.46 days/year; 10.1 days
50th	migr juv	m	0.29	**0.005**	-0.37 days/year; 8.4 days
50th	migr juv	f	0.12	**0.056**	-0.28 days/year 6.2 days
95th	migr juv	m	-0.04	0.69	-0.02 days/year; 0.5 days
95th	migr juv	f	-0.04	0.83	-0.03 days/year; 0.7 days
50th	adults	m+f	0.05	0.15	-0.23 days/year; 5.2 days

In this paper we demonstrated that an overall advancement consistent in all phenological events had occurred, clearly suggesting that a parallel shift has taken place throughout the whole breeding area schedule of this species. This answered the first of our two questions. Further, we presented details on individual differences in phenological change of the willow warblers migrating past southern Gotland, showing that foremost early migrating individuals were advancing migratory timing, answering the second of our two questions.

Paper II

Regional differences in phenological response to climate change in willow warblers (*Phylloscopus trochilus*)

In Paper II, we built on the data set and findings of **Paper I**, extending the analysis to identify the climatic drivers behind the migratory changes. In addition, we incorporated ringing records complied during juvenile autumn migration at another bird observatory, located far north in Sweden (Haparanda-Sandskär Bird Observatory, 65°32’N, 23°44’E, **fig.12**). Similar to **Paper I**, the ringing records from the northern site included the study period 1990-2012 and had great detail, enabling distinction between individuals according to age and sex, and also migratory phase. Contrary to our previous study however, adults were excluded from this analysis, as catch rates were so low for this age group; 1.7/day at the northern site and 0.7/day at the southern site. Three different climate variables were utilized to describe environmental and climatic change, representing three different scales; local average monthly temperature, regional growing season onset and index of the North Atlantic Oscillation.

The aim of this paper was to use a spatiotemporal approach to investigate regional within-species differences in phenological response to climate change and to associate these potential differences with environmental change at different spatial scales. As a growing number of previous studies have confirmed latitudinal differences in phenological response, and have reported weaker responses in high latitude breeders (e.g. Dunn & Winkler 1999; Ahola *et al.* 2004; Hurlbert & Liang 2012), we were interested in further investigating such possible differences in our study species the willow warbler. We predicted; i) that individuals ringed at our northern study site would display less pronounced changes in migration than what we had already confirmed at our southern site (**Paper I**); ii) that if northern individuals displayed any migratory change this would be in the earlier migratory phases; and iii) that the climate variables we applied as predictors would be most effective in explaining changes in earlier phases of migration.

Autumn migration at the northern site differed greatly in comparison to autumn migration at the southern site: no advancements in autumn departure were found in any of the migratory phases and in any of the sexes. In **figure 17**, the dissimilarities between juvenile autumn migration at the two study sites are visualised.

The analysis of the climate variables revealed an uneven change. None of the local average monthly temperatures had increased during the study period, neither in spring, nor in autumn, at any of the two sites, except for an increase in September: (Linear Regression Analysis, northern site: p= 0.046, r2=0.189; southern site: p=0.054, r2=0.131). The growing season onset date had however advanced in both northern (Linear Regression Analysis, p=0.015, $r^2_{adjusted}$ =0.303, advancement rate: 1.2 day/year) and southern Sweden (Linear Regression Analysis, p<0.001, $r^2_{adjusted}$= 0.85, advancement rate: 0.6 days/year). The NAO winter index showed no change over time during the period 1990-2012 (p=0.082, $r^2_{adjusted}$=0.100).

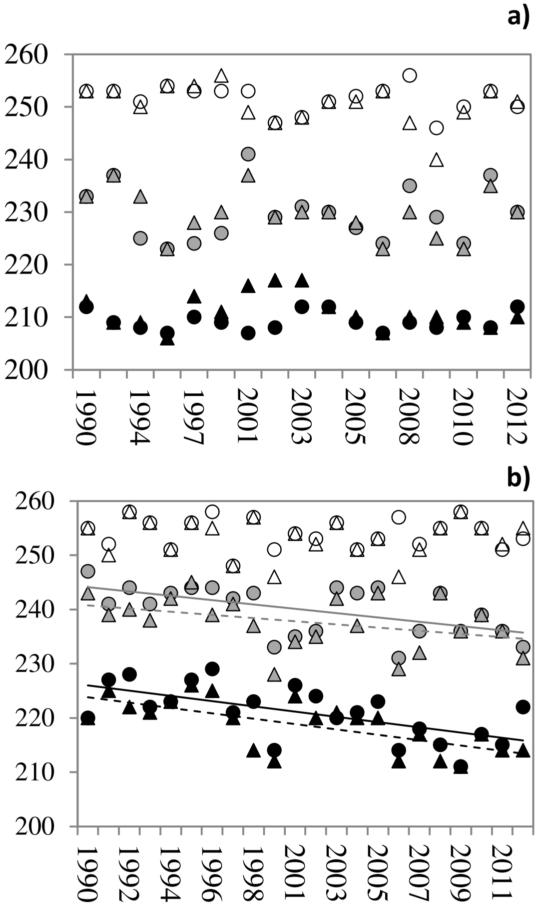


Figure 17. Autumn passage dates in the three temporal phases of juvenile willow warbler migration over time: a) at the northern site and b) at the southern site (only juveniles in moult stage 5-6 are included). Circles represent males and triangles represent females, black denotes 5th percentile migration dates, grey denotes median migration dates and white denotes 95th percentile migration dates. The y-axis shows Julian calendar days, starting at day 200 which during non-leap years is July 19th. Solid trend lines signify change in male juvenile migration and dashed trend lines signify change in female juvenile migration.

In order to analyse the effect of the different climate variables on the three different migration data sets (spring and autumn migration at the southern site and autumn migration at the northern site), three Principle Component Analyses (PCA) were performed. For each migration data set, a relevant compilation of climate variables was composed. Minimum eigenvalue for principle components (PC)s was set to 1 and we defined absolute loadings greater than, or equal to, 0.40 as salient. We rotated all

Table 2. Results of the stepwise multiple regression analyses testing the relationship between the components of three PCA and three migration data set; spring and autumn migration at the southern site and autumn migration at the northern site. For each migration data set, individuals were divided according to sex and migratory phase. The models with best p-values for each sex and percentile are shown and models with significant p-values are in bold.

Male spring migration at the southern site

Percentiles	Best model	p	r^2	F
5th	**PC1+PC2**	**0.055**	**0.184**	**$F_{2-19} = 3.36$**
50th	**PC2**	**0.006**	**0.286**	**$F_{1-20} = 9.41$**
95th	PC1	0.105	0.081	$F_{1-20} = 2.87$

Locally hatched juv. male peak appearances at the southern site

Percentiles	Best model	p	r^2	F
50th	PC3	0.14	0.060	$F_{1-20} = 2.35$

Juvenile male autumn migration at the southern site

Percentiles	Best model	p	r^2	F
5th	**PC1+PC3**	**0.007**	**0.340**	**$F_{2-19} = 6.41$**
50th	PC3	0.142	0.059	$F_{1-20} = 2.33$
95th	PC2	0.274	0.012	$F_{1-20} = 1.26$

Juvenile male autumn migration at the northern site

Percentiles	Best model	p	r^2	F
5th	PC2	0.686	-0.054	$F_{1-15} = 0.16$
50th	PC1	0.337	-0.001	$F_{1-15} = 0.98$
95th	PC1	0.107	0.107	$F_{1-15} = 2.92$

Female spring migration at the southern site

Percentiles	Best model	p	r^2	F
5th	**PC2**	**0.016**	**0.215**	**$F_{1-20} = 6.78$**
50th	PC2	0.200	0.034	$F_{1-20} = 1.75$
95th	PC1	0.370	-0.007	$F_{1-20} = 0.83$

Locally hatched juv. female peak appearances at the southern site

Percentiles	Best model	p	r^2	F
50th	PC3	0.346	-0.003	$F_{1-20} = 0.92$

Juvenile female autumn migration at the southern site

Percentiles	Best model	p	r^2	F
5th	**PC1+PC3**	**0.013**	**0.299**	**$F_{2-19} = 5.48$**
50th	PC1	0.336	-0.001	$F_{1-20} = 0.97$
95th	**PC2**	**0.055**	**0.130**	**$F_{1-20} = 4.14$**

Juvenile female autumn migration at the northern site

Percentiles	Best model	p	r^2	F
5th	**PC2**	**0.043**	**0.195**	**$F_{1-15} = 4.88$**
50th	PC2	0.856	-0.064	$F_{1-15} = 0.03$
95th	PC1	0.086	0.128	$F_{1-15} = 3.36$

components using the varimax procedure. To measure the possible effect of the climate variables, the PCs were tested against the three migration data sets using stepwise multiple linear regression analysis, ranked according to the most significant p-value (**table 2**).

We were able to confirm two of our predictions; i) individuals ringed at our northern study site did not change migration at all (**fig.17**) and iii) the climate variables we applied as predictors were most effective in explaining changes in earlier phases of migration (**table 2**). As no migratory change was found at our northern site, prediction ii) was nonapplicable. The findings of our analyses suggested that willow warbler migratory response to environmental change in Sweden differ between the north and the south; individuals passing the northern site had not change autumn migration timing at all whereas individuals passing the southern site had advanced their greatly. These differences existed irrespective of the similar advancement found in growing season onset in both regions.

Paper III

Point of no return –absence of returning birds in the philopatric willow warbler (*Phylloscopus trochilus)*

The willow warbler display high levels of philopatry, e.g. reaching up to 50% in males (Jakobsson 1988; Foppen & Reijnen 1994) and even if return rates can differ between sites, philopatry is an established and acknowledged behavioural trait in this species. It is therefore very surprising that in this study, we could show that at one of our three study sites, none of the known 74 males and 21 females returned during the four year study period.

During the years 2011-2014 we conducted detailed surveillance of breeding area behaviour (i.e. spring arrival, male territoriality, pair-bonding, nest building, breeding, juvenile hatching and fledging) at three study sites in Sweden: two located in south-eastern Sweden, Tovetorp and Gotland, and one in north-western Sweden, Abisko (**fig.18**, **fig.6**; see **Methods**). In order to observe individual birds and document return rates, both males and females were given metal rings and were colour-ringed. As breeding density, predation and reproductive success are parameters documented to affect the rate of returning birds, we analysed these factors in conjunction with site fidelity and predicted that absence of philopatry should co-occur with low breeding success, low breeding density and high nest predation. In addition, we made a literature review to establish the published knowledge on rate of philopatry in the willow warblers at other locations.

The results of the comparison of return rates showed that philopatry differed between males and females and between our three study sites. At Tovetorp return rates of male willow warblers was 36.1% (13 of 36) and unknown among females, as these were not colour-banded at this site. On Gotland, return rates of male willow warblers was 31.4% (17 of 54) and of females 18.7% (3 of 16). As previously stated, no breeding philopatry was observed at Abisko not among banded males (N=74), nor among banded females (N=21). When searching through available literature, we found 21 individual, published scientific papers documenting return rates in willow warblers. These studies had been conducted all over the willow warbler's range in Europe, and none mentioned reoccurring, complete absence of philopatry.

Figure 18. Kristaps Sokolovskis above the field site in Abisko, 2013, photo: Sven Jakobsson.

If all known nests with eggs were considered, the average number of fledged young per nest for Gotland was 3.4 ($N_{known\ nests}$= 47) and for Abisko3.8 ($N_{known\ nests}$=41), i.e. presenting no difference (W=1114.5, p = 0.187). When only successful nests were considered, i.e. only nests where young had survived and fledged, the average number of fledged young per nest for Abisko was 6.3 ($N_{\text{succ. nests}}$=25) and for Gotland 5.8 ($N_{\text{succ. nests}}$=21); statistically higher in Abisko (Wilcoxon Ranked Sum Test, W = 454.5, p-value = 0.025). When comparing nest predation between Abisko and Gotland, there was no difference between the sites (Fisher's Exact Test, p=0.677). The average percentage of nest predated was 41.1% (21 of 52) on Gotland and 36.3% (18 of 48) in Abisko. Data on breeding success and nest predation was not available for Tovetorp.

Average breeding density on Gotland was 110 pairs/ km^2, 106 pairs/ km^2 at Tovetorp, and 49-71 pairs/ km^2 in Abisko. Population index trends for the wider area of the three sites was provided by The Swedish Bird Survey (www.fageltaxering. lu.se) and showed no temporal change between 1998-2013 at Tovetorp and Gotland. In the region surrounding Abisko however, the index displayed a statistically significant ($p<0.001$) yearly decline of 6.5%, amounting to a 55% decrease in population size during the period between 2002-2013.

The absence of returning willow warblers to Abisko made this site unique, not only in comparison to our two other study sites where return rates were within the norm, but also in comparison to all previous records of this species. We hypothesised that a site exhibiting low levels of site fidelity also would have low breeding success, high nest predation and low breeding density. However, it was demonstrated that there was no difference in nest predation between Abisko and Gotland and breeding success was actually higher in Abisko than on Gotland. The only parameter that tended to display a variation that agreed with our prediction was breeding density, which was lower in Abisko. We discarded high mortality rates as the main cause of the low philopatry, predominantly because, for the level of philopatry to go from the species-usual of 25-30% for males to 0%, mortality had to be extraordinarily high. Instead, we proposed that the absence of philopatry was a consequence of range expansion and an influx of individuals dispersing rapidly north employing a more nomadic breeding strategy.

Paper IV

Spatio-temporal perspectives on the effects of land-use change on two common bird species: the past, present and future.

In Scandinavia, the most dramatic changes in land cover and land-use have happened during the 20th century. Before these changes, Sweden was a heterogenous, rural landscape, where farming was mostly self-sustaining, wood- and grasslands kept open by grazing (**fig. 19**) and the forests used for firewood and charcoal pits (Nilsson 1990; Eriksson *et al.* 2002; Kumm 2003; Cousins *et al.* 2015). Beginning in the early 1900s and escalating dramatically by the 1950s, farms were abandoned and grazed forests transformed into dense stands of coniferous sylvicultures. Thus, forestry is the land-use that dominates Sweden today and about 60% of the country's surface is forest (Swedish Statistics 2015, **fig.7**).

Identifying how the extensive transition of the landscape may have affected the distribution of species is a difficult endeavour when past landscapes are long gone. Historic maps can be utilize for this purpose and at a local scale, knowledge on past shifts in land-use are quite good. However, at a regional scale, the progression of landscape change has only just recently been evaluated and the studies are few and have mainly focused on impacts on plant diversity (Hooftman & Bullock 2012; Cousins *et al.* 2015).

Figure 19.. Photos of grazed forests in Sweden. To the left: goats and cows grazing in a forest in Ångermanland, northern Sweden 1930 (photo: Olof Eneroth). To the right: man standing in a forest pasture in Skåne, southern Sweden 1930 (photo: Olof Eneroth). Source: Skogsbiblioteket, SLU

It is well known that land-use change has affected bird species, but typically, investigation into how the transition of the historic landscape has changed bird habitat availability has focused on farmland species and only reach back as far as the 1950s (e.g. Chamberlain *et al.* 2000b; Kujawa 2002; Brambilla *et al.* 2010; Green *et al.* 2012). This is because there are few detailed maps describing land-uses over larger areas dating from earlier periods. However, Sweden presents as a unique exception to this limitation: precise and detailed maps are available from as far back as the 17th century.

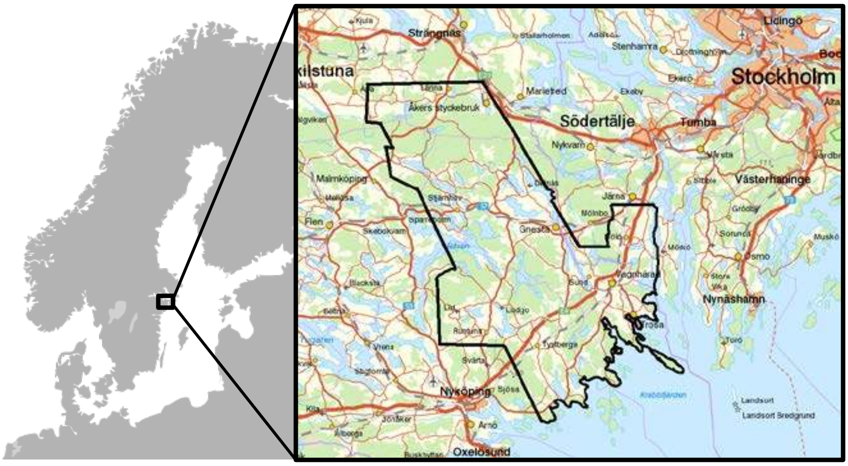


Figure 20. The location of the study area in Sweden marked with a black line, situated south of the capitol Stockholm.

In this paper we evaluated the landscape changes that have occurred during the last 100 years, focusing on habitats favoured by willow warblers and chaffinches (see **Methods** for species descriptions), and assessed the impacts of the changes on the two bird species. We conducted the study in an area situated in south-eastern Sweden, covering 165200 ha (midpoint 59°00’N, 17°11’E, **fig.20**). One historic, cadastral map developed between1899-1901 (“the 1900 map”) was compared in terms of seven land cover types to several present-day maps (collectively termed “the 2013 map”). The seven land cover types were: coniferous forest, deciduous forest, logged forest, grazed forest, edge zone, open pasture and powerline corridor (PLC). In addition, a predicted change in forestry for the year 2100 developed by the Swedish Forest Agency (SFA & SLU 2008) was applied to the 2013 map to acquire estimates for land cover of a future landscape.

Inventory of bird occurrence in the different land cover types was conducted during one week in the spring of 2014, during which 10-11 sample sites/ land cover type were inventoried for singing males of the two species. Specifically, we addressed the following three questions; has availability of potential bird territories changed over time because of i) land-cover change ii) landscape heterogeneity? And, iii) how can predicted change in forest structure and cover in 100 years from now affect availability of potential bird territories?

The occurrence of the willow warbler differed markedly between land cover types (Poisson Regression, χ^2=31.43, df=6, p<0.001, **fig. 15**), with the highest density of territories in logged forest and power line corridors but entirely absent from open pasture and very rare in mixed, coniferous forest. The chaffinch was present in all seven land cover types and territory densities were very similar (Poisson Regression, χ^2=13.33, df=6, p=0.038, **fig. 21**). The highest density of territories was found in logged forest, edge zones, deciduous forest and power line corridors. The chaffinch was however very rare in open pastures.

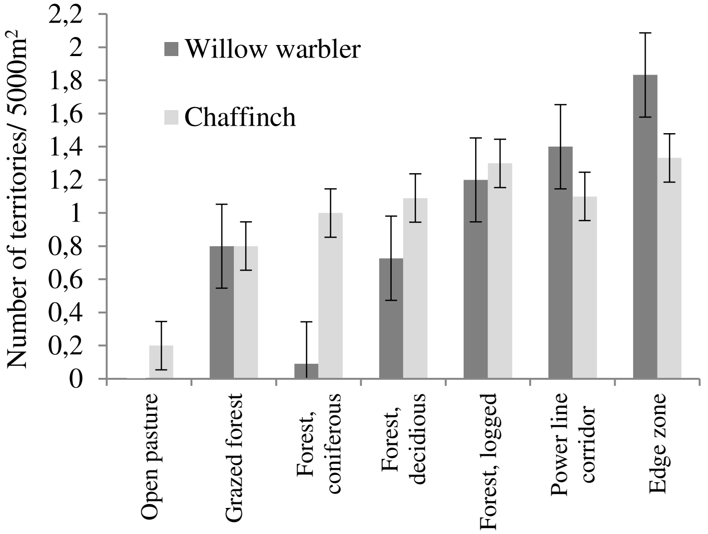


Figure 21. Average number of territorial male willow warblers and chaffinches observed per 5000m^2 land cover type, i.e. territory density per land cover type. The average is based on observations made in 10-11 randomly selected study sites per land cover type and the bars show the standard error.

Table 3. Calculation on coverage (ha) of different land cover types as present in the landscape according to the 1900 map, the 2013 map and a future scenario, and the subsequent availability of potential territories for the bird species under study based on these surface areas; willow warbler (ww) and chaffinch (cha). Land cover types listed do not represent all land cover types present, but are selected based on their importance for the two bird species and representation in the landscape. All calculations are made for our study area in Södermanland county, south-eastern Sweden.

Land use types	1900 map			2013 map			Year 2100		
	ha	# ww	# cha	ha	# ww	# cha	ha	# ww	# cha
Forest, deciduous	356	518	776	758	1 103	1 654	758	1 103	1 653
Forest, coniferous	26 739	4 862	53 78	88 686	16 030	177 021	67 779	12 200	135 558
Grazed forest	65 820	105 311	105 311	175	280	280	175	280	280
Forest, logged	0	0	0	11 317	27 161	29 425	35 007	84 107	91 018
Power line corridor	0	0	0	472	1 320	1 037	0	0	0
Pasture, open	203	0	81	5 501	0	2 201	5 501	0	2 200
Total number of potential territories		**110 689**	**159 565**		**45 957**	**211 818**		**97 600**	**230 710**

Question i). When summarized, the total number of potential territories made available by the landscape composition had decreased for willow warblers (45 957 today vs. 110 689 at the turn of the 19th century, **table 3**) but increased for chaffinches (211 818 today vs 159 165 at the turn of the 19th century, **table 3**).

Question ii). Heterogeneity decreased in the landscape between the 1900 map and the 2013 map(Wilcoxon Ranked Sum Test, $p<0.001$, $W= 81.5$) and when total forest perimeter length in 100 randomly distributed sample circles was compared between the maps, it could also be showed that this had decreased, suggesting a decline in edge zone availability (Wilcoxon Ranked Sum Test, $p<0.001$, $W=781$).

Question iii). In the estimations of the future scenario, based on predictions where 7% arable land was to be converted into production forest, logged and early succession areas to increase in percentage to 34% and power line corridors to become absent, availability of potential territories increased for both bird species (**table 3**).

The most important result of this study was how the availability of potential territories for both bird species altered because of the conversion of the old semi-natural forest into the current production forest. In addition, we could show how the forest of the present-day landscape had the potential to shift the conditions for the birds yet again, i.e. if the future entailed increased fiber and timber demands and climate-accelerated tree maturation.

The answer to our first question was yes: land-use change had altered the availability of potential territories for the willow warbler and the chaffinch, but differently depending on the species. The willow warbler was disfavored by the abolishment of forest grazing, whereas the chaffinch benefitted by the increase in production forest that replaced the grazed forest.

The answer to our second question was also yes: the landscape of the 1900 map was more differentiated than the landscape of the 2013 map, and as edge zones and other habitats with stratified plant composition were found to be the most preferred habitats by the two bird species, the heterogeneity of the past should have favored both species extensively.

Our third question regarded a possible future scenario and we estimated an increase in forest cover as a result of higher timber demands and climate-induced accelerated tree maturation. As faster growing trees can be harvested at an earlier age, the proportion of logged areas and early succession areas would increase, which would have a positive effect on the availability of potential territories for both species.

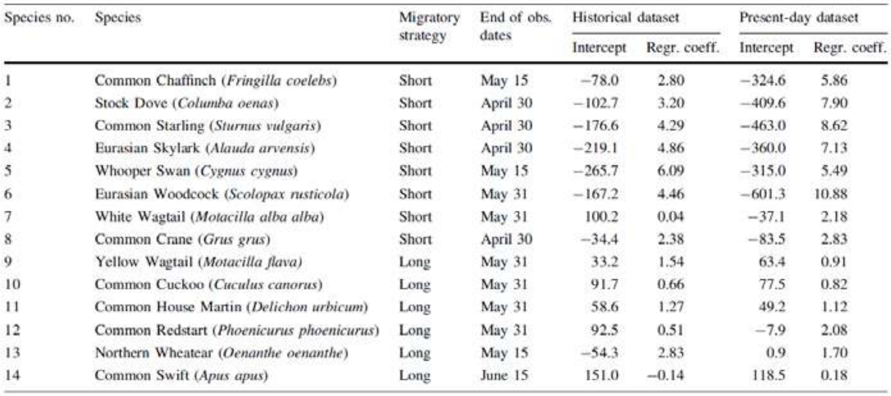
Paper V

Change in spring arrival of migratory birds under an era of climate change, Swedish data from the last 140 years

In this paper, we had the opportunity to utilize records on spring arrival in migratory birds collected before the onset of global climate change. These records, collected by volunteers in a government led initiative in southern and middle Sweden, covered the period 1873-1917 and included first arrival dates of six long-distance migrants and eight short-distance migrants. In order to evaluate possible changes over time, another citizen science data set collected during 1984–2013 on the same species was included in the analysis, and compared to the historical data in terms of relative difference at different latitudes. In addition, we also investigated whether there were differences in latitudinal effect over time depending on migratory strategy by comparing data from migrants employing different migratory strategies. In order to associate our migratory data with climate change effects, average temperature per month and year were obtained for the two study periods at three sites in central Sweden and three sites in southern Sweden.

The calculated arrival dates of the two records cannot be compare directly as they have been collected differently, using different methods. Therefore, the arrival dates of the models and statistical analyses only represent relative differences. For both records, a linear mixed model was used to calculate the relation between arrival day and the factors: latitude, altitude, and distance to large water bodies. The intercept and coefficient for each species from the two records were then used to compute arrival date at specific latitudes (southern and central Sweden) and applied to reveal patterns of change depending on migratory strategy (**Table 4, fig. 22**).

The calculated relationship between first day of arrival and latitude based on the historical and present-day datasets demonstrated that all bird species arrived earlier today compared to the historical data, both in southern and central Sweden (**fig. 22**). Short-distance migrants arrived earlier than long-distance migrants, but advanced northwards slower than later arriving species (mainly long-distance migrants), both in the historical and in the present day records. In the comparison of relative difference, short-distance migrants had, over time, advanced their arrival to southern Sweden more



Species no.	Species	Migratory strategy	End of obs. dates	Historical dataset		Present-day dataset	
				Intercept	Regr. coeff.	Intercept	Regr. coeff.
1	Common Chaffinch (*Fringilla coelebs*)	Short	May 15	−78.0	2.80	−324.6	5.86
2	Stock Dove (*Columba oenas*)	Short	April 30	−102.7	3.20	−409.6	7.90
3	Common Starling (*Sturnus vulgaris*)	Short	April 30	−176.6	4.29	−463.0	8.62
4	Eurasian Skylark (*Alauda arvensis*)	Short	April 30	−219.1	4.86	−360.0	7.13
5	Whooper Swan (*Cygnus cygnus*)	Short	May 15	−265.7	6.09	−315.0	5.49
6	Eurasian Woodcock (*Scolopax rusticola*)	Short	May 31	−167.2	4.46	−601.3	10.88
7	White Wagtail (*Motacilla alba alba*)	Short	May 31	100.2	0.04	−37.1	2.18
8	Common Crane (*Grus grus*)	Short	April 30	−34.4	2.38	−83.5	2.83
9	Yellow Wagtail (*Motacilla flava*)	Long	May 31	33.2	1.54	63.4	0.91
10	Common Cuckoo (*Cuculus canorus*)	Long	May 31	91.7	0.66	77.5	0.82
11	Common House Martin (*Delichon urbicum*)	Long	May 31	58.6	1.27	49.2	1.12
12	Common Redstart (*Phoenicurus phoenicurus*)	Long	May 31	92.5	0.51	−7.9	2.08
13	Northern Wheatear (*Oenanthe oenanthe*)	Long	May 15	−54.3	2.83	0.9	1.70
14	Common Swift (*Apus apus*)	Long	June 15	151.0	−0.14	118.5	0.18

Table 4. List of migratory species under study, with categorisation of migratory strategy (long-distance migrants pass the Saharan desert, while short-distance migrants winter north of Sahara). Period of included observations/year in present-day dataset starts at January 1 and ends according to the dates in the table (SOF 2002). The table further includes intercept and regression coefficients for the effect of latitude on first arrival date for each species in the historical and present-day records. Values from the historical data model were obtained from a linear mixed model per species, and values from the present day model were derived as mean values from linear quantile regression models for each year and species.

than long-distance migrants (Mann– Whitney U test, N_{short}= 8; N_{long}= 6, z= 2.9, p<0.01). In central Sweden however, no such difference between long- and short-distance migrants was displayed (Mann–Whitney U test, N_{short}= 8, N_{long}= 6, z= 1.3; p = 0.2). Short-distance migrants showed a larger difference in first arrival between the two data sets in southern than in central Sweden (Wilcoxon Matched Pairs Test, n= 8; z= 2.2, p<0.02), but no such distinction could be found among long-distance migrants (Wilcoxon Matched Paird Test, N= 6; z= 0.1, p = 0.9).

The temperature data showed that spring temperature had increased between the historical and present day period. Owing to low sample size, potential differences in the extent of the temperature increase over time between southern and central Sweden could not be analyze, but in the six sampled sites, average increase over time was larger in central than in southern Sweden for all months (south vs. central temperature increase: March: 1.3 vs. 1.8°C, April: 1.4 vs. 1.9 °C and May: 1.4 vs. 1.7 °C)

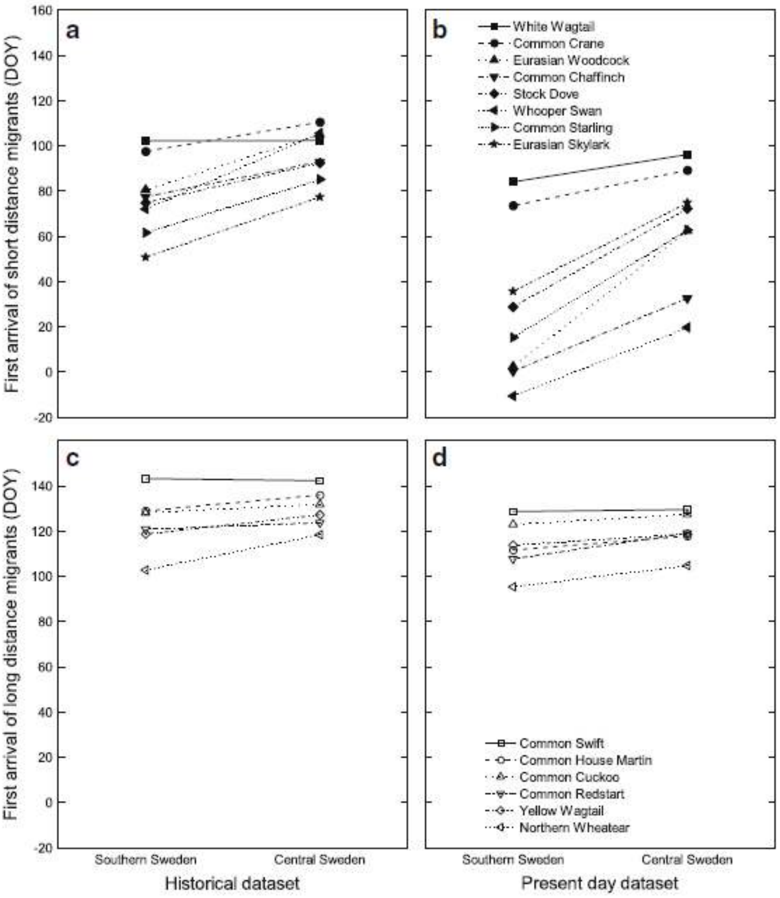


Figure 22. Estimated first arrival day of year (DOY) with regression lines, in relation to latitude for the historical (a, c) and present day (b, d) records in short-distance (a, b) and long-distance (c, d) migrants. Southern Sweden = 55.5°N and central Sweden = 61°N. DOY 50 represents February 19, while DOY 100 represents April 10

We showed in this paper that all 14 migrant species included in the analysis arrived earlier today compared to the historical records, both in southern and central Sweden. The difference is however relative, as the data included were based on different sampling methods, and must be interpreted with this in consideration. That conditions during the two time periods had changed was made clear in our comparisons of spring mean temperatures, which had increased in the two regions when the historical and present day time intervals were compared, with indications of a greater increase in central compared to southern Sweden.

We found that long-distance migrants had advanced arrival to southern Sweden less than short-distance migrant. Interestingly, we could also show that the speed of migration was greater in later arriving species, which mainly were long-distance migrants, than in earlier arriving migrants, which mainly were short-distance migrants. The fact that short-distance migrants had advanced spring arrival more than long-distance migrants is also partly due to that fact that some individuals (especially of the species woodcock, whooper swan and chaffinch) seemed to have included southern Sweden into their wintering range, i.e. to some extent become winter residents.

Concluding remarks

Studying the effects of climate change on wild species is a challenge, it entails trying to understand a phenomenon that is global, but locally divergent, ever dynamic, continuously progressing and interacting with other drivers of change. One aspect that proves paramount is the access to historical records. In the studies included in this thesis, I and my co-authors have had the fortune to apply historical perspectives to not only migration, but also breeding phenology and landscape change.

Specifically, the results of **Paper I** add knowledge through its holistic perspective, an otherwise largely missing approach to phenological responses to climate change. The population scale outcome of a phenological change, or indeed a missing or delayed one, will depend on the relationship between different life-history events and thus it is important to incorporate several phenological steps when evaluating responses to environmental change. Our results, indicating a relationship in terms of interacting timing of several phenological events, has been inferred in other studies where willow warblers have been included: Sokolov *et al.* (1999) demonstrates a positive correlation between breeding and autumn departure at the Courish Spit and also refers to similar results by Ryzhanovsky (1997). In addition, a very recent study on productivity in willow warblers breeding in the UK, could, in concordance with our findings, demonstrate that breeding had advanced and also that productivity had remained constant (Morrison *et al.* 2015). Whether the advancements seen in breeding area phenologies will be sufficient in adjusting willow warblers to ongoing climate change remains to be seen, but the fact that the population studied in **Paper I** is altering phenology suggest that at least the potential exists.

The great contrast in migratory change between willow warblers migrating past SBO and HSBO that was detected in **Paper II**, suggested that a latitudinal difference in adaptation, or at least response, to rapid climatic change may exist within the species. As severe weather events, e.g. sudden drops in temperature, are more common in early than in late spring (Brown

& Brown, 1998, 2000) and also more severe at higher than lower latitudes (e.g. Crawford 2001; Boonstra 2004), this could explain why sensitivity to temperature is less pronounced in northern breeding individuals than in southern breeding individuals. The rate of increase in temperature during spring is also more rapid at higher latitudes (Hurlbert & Liang 2012; Stålhandske *et al.* 2014), meaning that a certain temperature change resembles a longer elapse of time at lower latitudes. Thus, birds at lower latitudes need to be more sensitive to temperature cues in order to sustain the same degree of accuracy in phenological timing as birds at higher latitudes.

Migratory speed is also a critical trait determining birds' ability to assess temperature change (Hurlbert & Liang 2012). In **Paper V**, long-distance migrants are shown to advance arrival to southern Sweden less in relative difference to short distance migrants, and also to constitute the majority of species that move northwards faster. The futher a bird needs to travel, the higher speed it tends to employ, hence long-distance migrants generally migrant at higher speeds than short-distance migrants (e.g. Fransson 1995). Within species, populations may also differ in migration speed depending on breeding latitude, e.g. in kestrels (*Falco tinnuculus*) individuals breeding in northern Sweden travel twice the distance of individuals breeding in southern Sweden but in the same time (Wallin *et al.* 1987). The higher migration speed of long-distance migrants and high latitude breeders is thus an important parameter to consider when differences in phenological response are discussed.

The fact that it was early migrating individuals at SBO, both during arrival in spring and departure in autumn, that were advancing migration and doing so in association with growing season onset and winter index of the NAO, revealed an intriguing demographic aspect to phenological change (**Paper II**). It means that when responses to environmental change occur, it is not necessarily all in a population that responds. Ultimately, **Paper I and II** revealed that individuals were best described when considered in the intersection of several categories; migratory phase, age and sex. It is known from other species that advancement in spring arrival can be caused by the behaviour of newly recruited juveniles and not the result of changed behaviour of adults (Gill *et al.* 2013). Hence, it is possible that the juvenile willow warblers departing earlier in autumn in our data set constitute a large part of the earlier arriving willow warblers in spring. Unfortunately, the re-capture rate of willow warblers is low at bird ringing stations (about 1 in 1000 is caught again), and monitoring the behaviour of individual birds, from hatching through successional breeding seasons, either demands a very large study sample over a large area or a yet unavailable technical solution, e.g. a transmitter of considerable lightness and range.

The absence of philopatry in willow warblers breeding in Abisko is one of the most intriguing findings presented in this thesis. A distinguishing feature in alpine biomes such as Abisko is environmental stochasticity, e.g. sudden shifts in temperature and extreme cold spells. With climate change, the unpredictability of high latitude habitats may come to increase. For example, modelled future scenarios predict a temperature increase exceeding 4°C in Fennoscandia, much higher than what is expected at lower latitudes (Cubasch *et al.* 2001). Specifically for Abisko, changes that already have been documented include; increasingly unpredictable snow cover dynamics (Callaghan 2011), increase in precipitation (Johansson *et al.* 2011), advanced birch leave development (Andrews *et al.* 2011) and rapid range expansion of geometrid moths, which are willow warbler prey species (Hagen *et al.* 2007; Jepsen *et al.* 2008; Post *et al.* 2009; Jepsen *et al.* 2011). When habitat stability is unpredictable, dispersal costs are lowered in birds (Newton 2003; Oro *et al.* 2011). Thus climate induced acceleration of environmental stochasticity may be an additional factor that has rendered nomadic breeding behaviour favourable in Abisko. It is however surprising that the difference between Abisko and other sites is so extreme. As we acknowledge in **Paper III**, several other studies have measured philopatry in willow warblers at high latitudes and found it to be present. But notably, none of these studies conducted in Sweden were published on data collected after 1996 and if measurements of return rates were to be conducted again at these sites, the result may be different. Thus, Abisko may not be so extreme. A long-term study on hole nesters in Abisko also confirms that philopatry continues at normal levels in other bird species in the area, e.g. in the pied flycatcher (Nils Åke Andersson pers. comm.), indicating that it is not extreme local conditions that prevents individual birds from returning but rather something specific to willow warblers.

The willow warbler is a common bird in Sweden, more so than the chaffinch, and both are associated with common habitat types. However, the population trends differ between the species; the willow warbler is declining over most of its range whereas the chaffinch is stable. By tracking landscape changes backwards in time as in **Paper IV**, historical perspectives suggest that in Sweden one cause can be an increase in coverage of habitats that the chaffinch can utilize, and that these habitats to a large extent have replaced a landscape where habitat composition was more varied and favourable to willow warblers. It is perhaps intuitive that commonness may hide quite substantial demographic dynamics but therefore commonness is also a trait that benefits from being studied from a historical viewpoint. Neither the willow warbler nor the chaffinch are common today only because they were predisposed to be so by the landscape a 100 years ago, but by considering the land-use changes that has occurred and the current population status, assumptions about the fate of the species in the future are facilitated.

One of the conclusions of **Paper V** regards the apparent northwards expansion of witnering range/ switch to resident behaviour in certain short-distance migrants. It has been suggested that, since fossil records generally display little corroboration of new phenotypes despite the fact that the Pleistocene experienced greater temperature shifts than what we are currently observing (Parmesan 2006), species are more likely to track preferred environments by shifting their ranges than they are to stay in their changing home and evolve (Maggini *et al.* 2011). Range tracking can also occur temporally, as seen in the short distance migrants converting to resident behaviour. In **Paper V** it is concluded that the effect of climate change is less profound over latitude in long-distance migrants than in short-distance migrants, which also is corroborated by the apparent difference in migratory change between northern and southern willow warblers in **Paper II**. It is apparent, by the results of **Paper V** and the litterature discussed in the **Introduction**, that short-distance migrants are privileged by much phenological flexibility, enabling them to respond to environmental change with greater emphasis than long-distance migrants. Hence it is presumably foremost in long-distance migrants, as the willow warbler, that negative effects of climate change may come to pass, as recent declines in theses species also suggest (Both et al. 2010; Laaksonen & Lehikoinen 2013), whereas it will be in short-distance migrants that the most profound and conspicuous responses will be measured.

Acknowledgments

This is to you, mum, who bought me all those animal books when I was a child and who said that school was a great place to got to, because there you could do science and learn even more about animals. Oh, how I wanted to learn about animals! You are always there to support me. Älskar dig mamma

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References

Artwork on dividers

I. Adapted from an 18th century block-printed Indian pattern on cotton, drawings by Johanna Hedlund

II. Adapted from an antique block-printed cotton, drawings by Johanna Hedlund

III. Adapted from Sidney Farnsworth's illuminated manuscript, drawings by Johanna Hedlund

IV. Adapted from a block-printed cotton designed for the European market in 1780-90, drawings by Johanna Hedlund

V. Adapted from antique Suzani pattern, drawings by Johanna Hedlund

Litterature

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