Causes of population change in a long-distance migratory passerine, the willow warbler

(*Phylloscopus trochilus)*

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Contents

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Abstract

Over the past 40 years there have been large declines in the abundance of many migratory bird species which breed in Europe and winter in Africa. As potential causes of these declines exist across both the breeding and non-breeding seasons, identifying the key drivers of these population changes is complex. In this thesis, national-scale surveys of bird abundance and demography collected by the British Trust for Ornithology are used to explore the causes of these population changes. Using data from the Breeding Bird Survey, I show that, within Britain, there is strong evidence for geographic variation in the rate of population change of most long-distance migrant species, and particularly in one of Europe's most abundant summer passerine migrants, the willow warbler, *Phylloscopus trochilus.* Since the mid-1990s, willow warbler populations have experienced rapid declines in abundance in the south-east of Britain while slightly increasing in the north-west. Using data from the Nest Record Scheme, I show that willow warbler productivity has also declined in the south-east, but remained stable in the north-west and may therefore have contributed to the differing patterns of population change. However, these patterns of population change could also be influenced by changes in environmental conditions during the non-breeding season. Significant variation in the stable isotope ratios of winter-grown feathers of willow warblers from different parts of Britain may indicate that birds from different parts of Britain also use different locations or resources within Africa, and may thus experience different environmental conditions. Using data from the Constant Effort Site (CES) scheme, I show that the survival rates of adult willow warblers are also significantly lower in the south-east than the north-west of Britain, and lower in females than males, but adult survival has not changed significantly in recent decades. However, the sex ratio of willow warblers caught in CES sites has become significantly more male-biased in both regions, suggesting possible increases in female mortality prior to adulthood. Thus, for willow warblers in south-east Britain, productivity has declined, juvenile female survival may have declined and adult survival rates are lower than those in north-west Britain. These findings highlight the likely importance of interactions between breeding and non-breeding season processes for the population dynamics of migratory species, and emphasize the need for a greater understanding of the processes influencing the survival of migrants in their first year of life.

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Introduction

Understanding the demographic drivers of population change

The demographic rates of animal populations carry an integrated signal of the environmental conditions experienced by individuals throughout the course of their lives. Unravelling the relative role of different demographic processes in determining population size is therefore a fundamental step in understanding species responses to environmental change. Within-species variation in demographic rates can arise through differences in the local environmental conditions experienced by individuals, such as resource availability, competition and predation rates (Newton 2004). Consequently, whether the overall abundance of a species increases, decreases or remains stable, depends on both the distribution and density of the population relative to environmental gradients in both space and time.

Changes in the birth and death rates of a population can be driven by changes in the environmental conditions experienced by individuals at any point during their annual cycle. Environmental conditions may affect population size through both density-independent (e.g. extreme weather influencing mortality rates; Robinson *et al.* 2007, Frederiksen *et al.* 2008) and density-dependent (e.g. competition for resources; Rodenhouse *et al.* 2003, Mallord *et al.* 2007) processes. In addition, the strength of density-dependent influences on the demographic rates of a population in one season may be regulated by conditions in the previous season (Ratikainen *et al.* 2008). For example, if harsher over-wintering conditions lead to increased mortality, lower densities in the subsequent breeding season may reduce competition for resources, leading to increased breeding success of surviving individuals. Such seasonal compensation effects can make detecting the link between environmental and demographic change complex (Harrison *et al.* 2011). Additionally density-dependent processes can cause large population changes with only small and temporary changes in demography (Green 1999). Consequently, correlations of annual changes in environmental conditions, demographic rates and population size may not always prove successful in revealing the drivers of population change.

Population demography may also be affected by non-lethal processes that occur during one season and influence individual fitness in the following season, termed carry-over effects (Marra *et al.* 1998, Gill *et al.* 2001, Bearhop *et al.* 2004, Gunnarsson *et al.* 2005). For example, individuals that winter in poor quality habitats may be in poorer body condition during the subsequent breeding season, and may thus have lower breeding success than those that wintered in higher quality habitats (Marra *et al.* 1998, Gunnarsson *et al.* 2005). Understanding the effect of conditions in one season on individual fitness in the next becomes particularly complex when species are migratory, as these species can span multiple locations across huge geographical areas.

As environmental processes can operate across multiple scales, one way to begin to understand the processes governing species population dynamics is to explore the degree and spatial pattern of variation around population trends. For example, large-scale processes (e.g. changing climatic conditions) may create spatial gradients of population trends, while locally variable population trends are likely to be the result of small-scale variation in habitat quality (Figure 1 A & C). In migratory populations, the scale over which environmental processes operate can vary across both breeding and non-breeding ranges, consequently the strength of migratory connectivity (whether individuals from different breeding locations also winter in geographically distinct areas) can also influence the patterns of population change on breeding grounds, with conditions in winter potentially either exacerbating or buffering those in summer (Figure 1 B & D). The strength of processes influencing population change can also vary over time (Nevoux *et al.* 2008). Consideration of mean demographic rates across entire periods of change may therefore mask important shorter-term changes in demography (Green 1999). Exploration of the variation in demographic rates during periods of contrasting population trends can greatly help to highlight the drivers of population trends (Siriwardena *et al.* 1998, Fewster *et al.* 2000, Robinson *et al.* 2004).

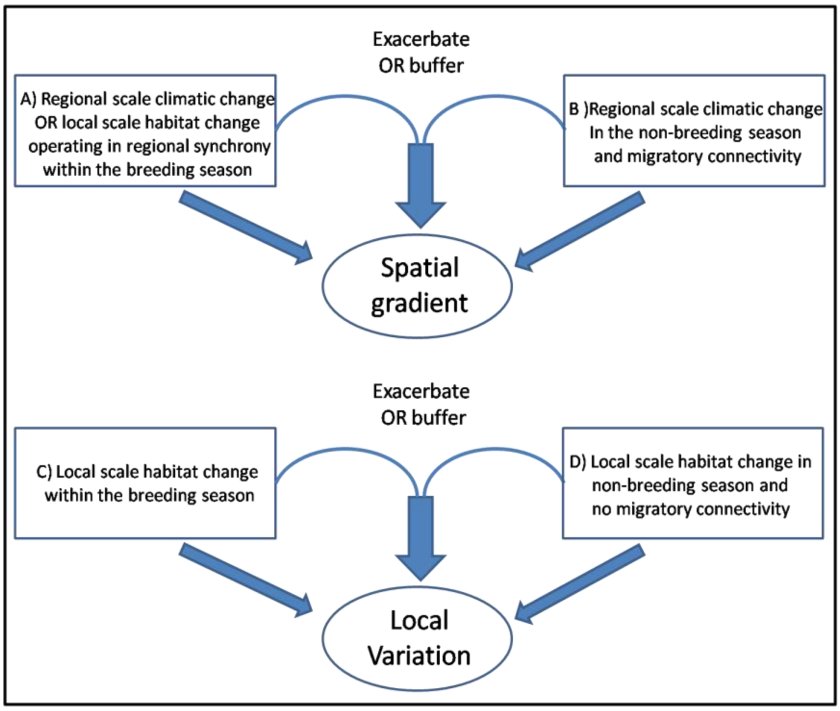

Figure 1: Schematic representation of the potential outcome (ovals) of different drivers (rectangles) of population change in migratory species. Drivers operating in both the breeding and non-breeding season could lead to either large-scale spatial gradients or local-scale variability (with no larger-scale gradient) in population trends. Large arrows indicate the potential for breeding and non-breeding season drivers to operate either in synergy to exacerbate population declines, or in opposition such that one driver may buffer the effects of the other.

Recent population change in European breeding birds

Since the late 1970s, large changes in the abundance and distribution of many European breeding bird species have been recorded (Gregory *et al.* 2005, Sanderson *et al.* 2006, Hewson & Noble, 2009, Thaxter *et al.* 2010). In the UK, long-term monitoring of breeding abundance has highlighted declines in the abundance of farmland and woodland specialists (Sheehan *et al.* 2010). In some species, declines in abundance have been linked to changes in breeding performance (Shrubb 1990, Green & Stowe 1993, Brickle *et al.* 2000) and/or survival of adult or first-year birds (Peach *et al.* 1999, Robinson *et al.* 2004), and this detailed understanding of the demographic mechanisms underlying population declines has helped in the design of appropriate conservation actions (Vickery *et al.* 2004). More recently, studies have highlighted severe declines in populations of Afro-Palaearctic migrants which, as a group, declined at significantly faster rates than short-distance European migrants and resident species from 1970 to 2000 (Sanderson *et al.* 2006, Thaxter *et al.* 2010). Consequently, the majority of work has focused on understanding the impact of changes in conditions during the non-breeding season on survival of migrants (Møller 1989, Peach *et al.* 1991, Szep 1995, Robinson *et al.* 2008). However, it is also likely that many migratory species are experiencing similar deteriorations in the quality of breeding grounds as resident species (e.g. Browne & Aebischer 2001). Therefore there is an urgent the need to produce an integrated picture of the processes governing the demography and abundance of migratory species throughout their annual cycle.

The Palaearctic-Afrotropical migration system

About one quarter of all bird species breeding in Europe spend the greater part of their lives in sub-Saharan Africa, migrating north to breed during the summer months. Overall, this equates to 1300-2600 million pairs of ~125 species (Zwarts *et al.* 2009). Southward migration from European breeding grounds takes place between August and November (Newton 2008). One of the greatest obstacles to Afro-Palaearctic species during this migration is the Sahara desert, the crossing of which can mean a journey of up to 2000 km in hot and dry conditions, with little access to food and water (Jenni-Eiermann *et al.* 2011). It is therefore likely that, for the majority of species, mortality during this crossing is high (Zwarts *et al.* 2009). Once across the Sahara, migrants enter the Sahel zone, a semi-arid savannah belt which runs parallel to the southern edge of the desert. Migrants typically reach this zone at the end of the wet season when resources are plentiful, and it provides important resources for species to refuel before they continue their southwards migration, as well as hosting a number of species during the entire non-breeding season (Newton 2008).

The movements and distribution of migrant species within Africa are greatly influenced by the movements of the Inter-tropical Convergence Zone (ITCZ) (Newton 2008, Zwarts *et al.* 2009). This tropical rain belt moves northward across the equator during the northern summer before retreating southwards in the autumn. The length of the wet season is therefore shortest at the northern edge of the Sahara, and it gradually increases moving south. Consequently, over a 500 km area of West Africa, annual rainfall can vary from 100 mm in the north to more than 2000 mm in the south (Zwarts *et al.* 2009). This rainfall gradient greatly influences the vegetation of West Africa, and creates latitudinal habitat bands running from the northerly grasslands and open savannahs just south of the Sahara, to the woody savannas and forests of the southern coast. This also means that, for species wintering north of the equator, conditions gradually become drier over the course of the non-breeding season. Therefore while some species of migrant spend their entire non-breeding season in dry season conditions in northern Sahel, others may winter entirely in the wet season conditions in the southern tropics (Newton *et al.* 2008). In general, each species is thought to seek out those African habitats that most closely resemble their principle breeding habitats (Moreau 1972, Newton 2008), with the high densities of migrant passerines often found in seasonal savannahs, within scrubby or reedy areas (Newton 2008).

Northward migration begins in early spring, with males typically arriving on breeding grounds by early April (BirdTrack, 2011). In the south and east of the UK, the highest densities of Afro-Palaearctic migrant species such as nightingale, *Luscinia megarhynchos*, garden warbler, *Sylvia borin*, blackcap, *Sylvia atricapilla*, chiffchaff, *Phylloscopus collybita,* and willow warbler, *Phylloscopus trochilus,* typically occur in lowland woodlands with areas of early and middle succession growth (Fuller & Crick 1992). By contrast, in the north and west, species such as redstart, *Phoenicurus phoenicurus,* wood warbler, *Phylloscopus sibilatrix,* and pied flycatcher, *Ficedula hypoleuca,* are often found at high densities in upland woods (Fuller & Crick 1992).

Potential drivers of population change in Afro-Palaearctic migrants

Population declines in Afro-Palaearctic migrants first became evident in the 1970s, when sharp reductions in the survival and abundance of species such as whitethroat, *Sylvia communis*, sand martin, *Riparia riparia*, and sedge warbler, *Acrocephalus schoenobaenus* were linked to declines in Sahel rainfall during this decade (Møller 1989, Peach *et al.* 1991, Szep 1995). However, since then, the rate of decline in these species has slowed and species wintering further south in the humid West African forest and savannah have begun to decline (Hewson & Noble 2009, Thaxter *et al.* 2010). While concern over the impact of increasing human populations and associated land use change (e.g. increased grazing, fuel-wood consumption, infrastructure extension, conversion of woodland to intensive agriculture and use of pesticides) on the non-breeding season environment of these species has been raised (Mullie & Keith 1993, Jones 1995, Hewson & Noble 2009, Norris *et al.* 2010), our current knowledge of non-breeding season distribution of migrant species in relation to these changes is poor. Consequently, the relative impact of environmental change in the humid zone on species demography and abundance remains largely unexplored. In addition, degradation of stop-over sites may be causing increased competition for resources, resulting in longer stopover periods or causing migrants to leave with lower fat reserves, which may reduce the distance they can travel before the next stop (Newton 2004, Wilson & Cresswell 2006). Such degradation may also restrict the ability of long-distance migrants to advance arrival dates in order to respond to changes on the breeding grounds (Both *et al.* 2010).

Across Europe, changing environmental conditions on breeding grounds are also likely to be impacting the success of migratory species. Over the past 20 years, increasing spring temperatures have led to changes in phenology across many taxa (Parmesan & Yohe 2003, Thackery *et al.* 2010). In birds breeding at temperate latitudes, advancement of laying dates has been widely recorded (Crick *et al.* 1997, McCleery *et al.* 1998, Parmesan & Yohe 2003, Thackery *et al.* 2010), with variation in the extent of these shifts linked to local rates of temperature change (Both *et al.* 2004, Both & Marvelde 2007). However, in some species differences in the rate of change of laying dates and timing of emergence of insect prey may lead to the main chick-rearing period no longer coinciding with the main peak of prey abundance and declines in individual productivity (Both *et al.* 2006, Visser *et al.* 2006). Additionally, the breeding habitats of migrants have experienced similar degradation as those of resident species, through processes such as agricultural intensification and overgrazing of woodland understory (Browne & Aebischer 2004, Gill & Fuller 2007, Holt *et al.* 2010). Consequently, variation in the breeding success of migrant species is likely to depend on both larger-scale climatic processes and smaller-scale habitat change (Figure 1).

Willow warblers, Phylloscopus trochilus

The willow warbler is one of Europe’s most abundant summer passerine migrants, and ~2.6 million of Europe’s 56 million pairs breeding within the UK (Burfield & van Bommel 2004, Newson *et al.* 2008). From late-March to mid-July, willow warblers are on their breeding grounds throughout Europe. Willow warblers breed in a diverse array of habitat types, but scrub, second growth and young woodland rich in species such as birch *Betula* spp., alder *Alnus glutinosa* or willow *Salix* spp. are thought to provide the best breeding conditions and the most accessible insect food resources (Cramp 1992, Gillings *et al.* 1998 & 2000). Willow warblers are ground-nesting birds, relying on dense understory to provide nesting habitat

(Fuller 1982), and consequently they tend to occupy areas with relatively open canopies (Bellamy *et al.* 2009). They mainly feed on insects and spiders but will take berries in the autumn, obtaining their food by picking from leaves, twigs and branches but also flycatching (Cramp 1992). Additionally the proportion of juvenile willow warblers in wet scrub has been found to be higher than in dry scrub (Fuller 1982), suggesting that the presence of water in the environment may also be important for this species, possibly due to higher abundances of their insect prey.

Willow warblers depart their breeding grounds in late summer, with southward movement beginning in late July. They start to appear in the northern Sahel from August onward, tending to stay in this zone for 1-2 months before travelling south in late October (Salewski *et al.* 2002, Newton 2008). The limited evidence available from reports of ringed birds suggests that British-breeding willow warblers winter in the Gulf of Guinea, principally around the Ivory Coast and Ghana (Norman & Norman 2002). In the Ivory Coast, willow warblers were found most frequently in structurally diverse isolated forest fragments (Salewski & Jones 2006), however, they are also found in wooded savannas and dry evergreen forests (Cramp 1992). Willow warblers are not territorial on their non-breeding grounds and have been found to form mixed species flocks with resident warblers (Salewski & Jones 2006, also see Gatter 1997).

Willow warblers are unusual among migratory passerines in completing a full body moult twice a year, on both breeding and wintering grounds (Underhill *et al.* 1992, Weber *et al.* 2005 & 2010). On their African wintering grounds, willow warblers in moult have been found from December to March, with the majority moulting in January and February (Underhill *et al.* 1992, Salewski *et al.* 2004). Within Europe, the timing of post-nuptial moult varies with latitude, with southerly populations completing moult directly after breeding, while at more northerly breeding latitudes seasonal time constraints may mean that moult often begins during the breeding period (Underhill *et al.* 1992), a strategy which may be particularly energetically expensive. However, as the feathers of willow warblers have been shown to be less fatigue resistant than those of chiffchaffs, which only moult once per year, it is likely that they are of lower quality and consequently the costs of producing them may also be less (Weber *et al.* 2005).

Recent changes in willow warbler populations

Since the 1990s, the abundance of willow warblers within Europe has declined by ~30%, with the majority of losses occurring in the UK, Sweden, Finland, Germany and France (PECBMS 2010). The monitoring of willow warbler populations in the UK has been carried out by BTO volunteers within two long-term surveys; the Countryside Bird Census (CBC) running from the 1962 to 1993 and the Breeding Bird Survey (BBS) from 1994 onwards. Under the CBC, bird territories are mapped from observations made on seven to ten site visits per year (Marchant *et al.* 1990). However, plots were mainly farmland or woodland sites and biased in favour of southern and eastern areas of the UK where observer density is greatest (Gregory *et al.* 2000). In order to address these biases, the CBC was replaced in 1994 by the BBS, in which squares were randomly allocated within regions of the UK in proportion to the number of potential volunteers. Squares are only visited three times a year and the greater simplicity of the BBS means that coverage is much higher and representative of a broader range of habitats (Freeman *et al.* 2007). Consequently trends are more likely to be representative of the wider countryside.

In the UK, declines in the abundance of willow warblers have been evident since the mid-1970s (Bailie *et al.* 2010). However, examination of geographical variation in the rate of willow warbler population change has also highlighted periods of regional divergence in willow warbler population trends between Scotland and England (Figure 2), suggesting that the strength of demographic and environmental drivers may also vary between these countries. From 1966 to the early 1980s, the abundance of willow warblers breeding in both Scotland and England fluctuated but showed no overall clear trend. Between the 1980s and early 1990s, there were steep population declines of ~25% and ~40% in Scotland and England, respectively (Figure 2). Since the early 1990s, populations of willow warblers breeding in Scotland have recovered to about 65% of the numbers present during the 1960s, while populations in England continued to decline to about 30% of their population size when monitoring began (Figure 2). Recent data from the BBS (1994 – 2006) indicate that the density of willow warblers also varies greatly across the UK, with the highest numbers in the north and west of the country (mean number of willow warblers per BBS plot = ~4.5). Consequently willow warblers have experienced the largest declines in the southern regions where densities are lowest (mean number of willow warblers per BBS plot = ~1.5, Figure 2). Examination of demographic trends within areas of contrasting population trends may therefore help explain both the differences in the abundance and the rate of population change of willow warblers breeding within the UK.

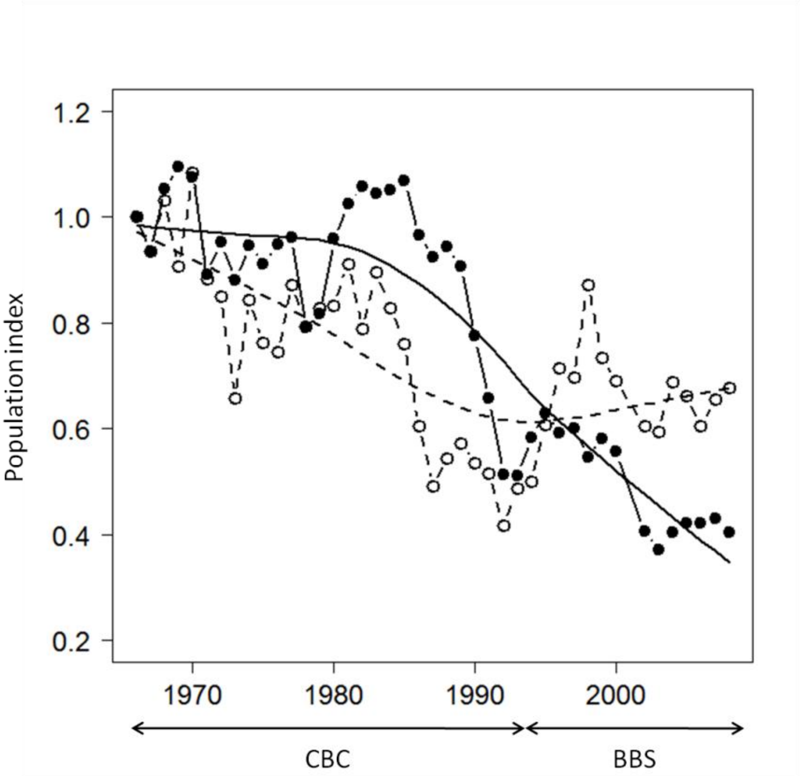

Figure 2: Temporal trends in the population index of willow warblers breeding in Scotland (open circles) and England (filled circles). Arrows indicate the Countryside Bird Census (CBC) monitoring period and the Breeding Bird Survey monitoring period (BBS). Lines are smoothed trends fitted with the lowess function in R (R 2.12.0).

Thesis structure

Since the start of the ringing scheme in the early 1900s, the British Trust for Ornithology has been collecting data on the abundance, distribution and demography of birds breeding within the British Isles. Consequently, their databases can provide a hugely valuable resource for large-scale, longitudinal studies of population demography. In this thesis, a range of BTO datasets are used to explore levels of spatial and temporal variation in abundance of British breeding birds and, for willow warblers, to explore the evidence for changes in demography contributing to changing patterns of abundance and distribution.

The processes influencing population size and trends can differ greatly across countries, and exploration of the extent of geographic variation in population trends may help to reveal factors influencing population changes. In **chapter one,** data from the Breeding Bird Survey (BBS) are used to explore differences in the rate of population change in Scotland and England of 74 species. Differences in species population trends between Scotland and England are particularly evident in long-distance migrants, with species wintering in the arid zone of West Africa increasing at a much faster rate in Scotland than England, while the majority of species wintering in the humid zone of West Africa are increasing in Scotland while declining in England. Consequently, within England but not Scotland, species wintering in the humid zone are declining at a significantly faster rate than those wintering in the arid zone. This finding suggests that seasonal interactions between breeding and non-breeding season processes may be important in influencing the abundance of migratory populations in the UK.

Within the UK, comparison of population trends across national boundaries may capture variation across latitudinal but not longitudinal gradients. In **chapter two** we use national survey data from Britain (BBS) and Ireland (Countryside Bird Survey (CBS)) to explore the variation in patterns of willow warbler population trends across multiple spatial and temporal scales. Willow warbler population trends follow a large-scale spatial gradient, from sharp declines in the south and east of England to shallow declines and/or slight increases in parts of north and west England, across Scotland and Ireland. Reducing the spatial scale of analysis reveals local-scale variation in both the rate and extent of population, and the potential drivers and mechanisms underlying these patterns and the challenges in diagnosing the drivers of population declines in migratory species are discussed.

In order to explore the influence of changes in productivity on population trends, long-term surveys of nesting success across multiple sites are required. In the UK, the annual breeding performance of a wide range of bird species has been monitored by the BTO Nest Record Scheme (NRS) since 1939. Under this scheme, volunteers locate nests and record information on their success. This allows the calculation of laying dates and the success of individual nesting attempts. In **chapter three,** following the patterns presented in chapter two, we explore variation in the number of fledglings per breeding attempt for willow warblers within two broad regions of Britain with divergent population trajectories; the north-west and south-east. These analyses show that since the early 1980s, declines in productivity have occurred in the south-east but not the north-west of Britain, and may therefore be contributing to population declines in this region. In recent years, advances in the onset of breeding have occurred in many European breeding bird species. At temperate latitudes where productivity typically declines across the breeding season, such advances might be expected to benefit productivity. We therefore explore the impact of changes in timing of breeding and the pattern of seasonal decline in productivity on the trends in productivity in both the north-west and south-east regions.

The declines in productivity in the south-east of Britain could be a consequence of reductions in willow warbler clutch size and/or increases in failure rates at the egg and/or chick stages. Consequently, declines in productivity may arise through a range of different mechanisms. In **chapter four** we use the Nest Record Scheme (NRS) dataset to explore the seasonal and temporal variation in each of these components of productivity, in order to identify the potential drivers of the changes in willow warbler demography and population size. As willow warblers are ground-nesting insectivores, their breeding success may be particularly vulnerable to changes in both the temperature and rainfall experienced during the breeding season, particularly as climatic conditions in Britain vary over similar spatial scales as willow warbler productivity and population trends. In chapter four, national-level climatic datasets are therefore also used to link the success of individual nesting attempts to weather conditions during the nesting period.

The divergent patterns of population change in willow warblers breeding in different areas of Britain could result from differences in the conditions experienced by individuals from those regions on migration or in Africa. In **chapter five** we look for evidence that the feathers of willow warbler from different parts of the breeding range vary in stable isotope composition, which may reflect differences in their distribution, their timing of moult and/or their use of resources during the pre-nuptial moult. We find significant variation in the $\delta^{15}N$ and $\delta^{13}C$ values of willow warbler feathers grown during the non-breeding season and collected from different areas of Britain, and the possible reasons for this variation are explored.

In order to estimate variation in survival rates of British breeding birds, BTO volunteers have been carrying out standardised mist netting under the Constant Effort Site scheme since 1983. **Chapter six** uses ringing and recapture data from Constant Effort Scheme (CES) sites to explore the influence of adult survival on the regional variation in population trends in British willow warblers. Between 1986 and 2008, we found evidence of lower survival of adult willow warblers in the south-east than the north-west of Britain and lower annual survival in adult females than males. However, there was no evidence that survival rates have changed significantly in either sex or region. The implications of these differences in survival rates of adult willow warblers for the regionally divergent population trends are considered.

In **chapter seven,** the consequences of sex-biased mortality for population sex ratio and productivity are explored, using data from the Constant Effort Scheme (CES). These analyses suggest that, in both the north-west and south-east of Britain, the willow warbler population is becoming increasingly male-biased, suggesting possible declines in the survival of first-year females in addition to low survival rates of adult females. This is likely to be limiting the number of breeding opportunities available to males, and consequently the number of unpaired males singing later in the breeding season may be high. We discuss the implications of this finding for the monitoring of populations carried out mainly through records of male song.

Finally, the **General Conclusions** provides a synthesis of the demographic variables explored throughout the thesis, their implications for the temporal and regional variation in willow warbler population trends and the potential role of demographic rates for which there are not sufficient data to explore trends.

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Chapter one

Geographic variation in population trends of breeding birds in Great Britain

Abstract

1. In many countries, national indices are used to assess the population status of breeding birds, determine species listings and establish priorities for conservation effort. However, the processes influencing population status and trend may vary geographically within countries. Exploration of the nature and extent of geographic variation in population trends may help to reveal factors influencing population changes and to prioritise conservation actions.

2. Since 1994, the abundance and distribution of common breeding birds throughout the UK has been monitored through the BTO/RSPB/JNCC Breeding Bird Survey (BBS). In addition to providing UK-wide indices of population change for many species, separate population trends are also produced for Scotland and England, allowing geographic variation in population trends within the UK to be explored. Here we investigate the extent of variation in population trends between Scotland and England for 74 species, and how this varies among resident and migratory species with differing patterns of breeding and non-breeding season habitat use.

3. Between 1994 and 2007, mean annual rates of population change in Scotland and England were similar for 38 resident and 21 short-distance migrant species but, for 15 long-distance migrant species, mean rates of population change differed significantly between Scotland and England, with most species declining at a faster rate or increasing at a slower rate in England than Scotland.

4. Of the six long-distance migrant species that spend the non-breeding season in the arid zone of Africa, five are increasing in abundance in both countries. In contrast, the seven species wintering in the humid zone of West Africa are all declining in England, but only two are also declining in Scotland. Consequently, within England but not Scotland, the population trends of species wintering in the arid and humid zone differ significantly, with those in the arid zone increasing and those in the humid zone declining.

5. In long-distance migrants, latitudinal gradients of population change exist in both the breeding season and non-breeding season, such that populations which both breed in England and winter in the humid zone in Africa are declining at faster rates than populations of species which either winter in the arid zone or breed in Scotland. This pattern highlights the likely importance of seasonal interactions in the population dynamics of these migratory species,

with the effects of environmental conditions in one season potentially being either exacerbated or buffered by the quality of conditions in the other season.

Introduction

Biodiversity monitoring schemes designed to assess population status and abundance typically operate at national scales. However, as environmental conditions at individual sites are likely to vary, interpretation of the impact of these conditions on species may depend on the spatial resolution of analysis of monitoring schemes (Wiens 1989). In the UK, it is common practice to produce UK-wide population indices, which are subsequently used to classify species listings (Sheehan *et al.* 2010) and prioritise conservation effort (Gregory *et al.* 2005). In a number of cases, a combination of long-term monitoring programs and targeted localised fieldwork has been highly successful in identifying the demographic and environmental drivers of population changes (Siriwardena *et al.* 1998, Fuller *et al.* 1995, Peach *et al.* 2004, Robinson *et al.* 2004, Siriwardena & Stevens 2004), and subsequent research has resulted in government policies directly aimed at enhancing the conservation status of these species (Vickery *et al.* 2004). However, there are still numerous cases where the drivers of population declines are less well understood, and therefore the priorities for conservation efforts are less clear (Sanderson *et al.* 2006, Hewson & Noble 2009, Thaxter *et al.* 2010). In these cases, exploration of variation in rates of population change at smaller spatial scales may help to reveal the key processes influencing those changes.

Across Europe, changes in species abundance have been linked to changes in a number of different environmental conditions (Fuller *et al.* 1995, Peach *et al.* 2004, Browne & Aebischer 2001, Beale *et al.* 2006, Gregory *et al.* 2007, Pearce-Higgins *et al.* 2010, Wright *et al.* 2009). Land-use changes as a result of agricultural intensification have influenced both the productivity and survival of many species of agricultural habitats (Fuller *et al.* 1995, Siriwardena *et al.* 1998 & 2000, Browne & Aebischer 2001, McCracken & Tallowin 2004, Peach *et al.* 2004, Gregory *et al.* 2005), while changes in the structure and complexity of British woodlands have also been implicated in recent declines in the abundance of several woodland bird species (Hewson *et al.* 2009, Holt *et al.* 2010 & 2011). Additionally, changes in climatic conditions have been linked to changes in the demography of some species (e.g. Frederiksen *et al*. 2008), while warmer springs have been linked to declines in the availability of breeding season food resources for several bird species (Visser *et al.* 1998, Both *et al.* 2006, Pearce-Higgins *et al.* 2010).

Population trajectories have also been shown to vary between species with different migratory strategies (Sanderson *et al.* 2006, Hewson & Noble, 2009, Thaxter *et al.* 2010). In particular, many of the species which spend the boreal winter in sub-Saharan Africa have undergone large population declines in recent years, while populations of resident and short-distance migrant species have generally been stable or shown slight increases (Sanderson *et al.* 2006, Thaxter *et al.* 2010). Between 1967 and 1976, the greatest population declines in Afro-Palaearctic migrants occurred in species over-wintering in the arid savannah zone of Africa and, for several species wintering in this zone, strong correlations were found between the frequency of Sahel drought conditions and both survival and abundance (Møller 1989, Peach *et al.* 1991, Szep *et al.* 1995). However, despite the increases in Sahel rainfall since the late 1980s, declines in many Afro-Palaearctic migrant species have continued, with the greatest losses currently occurring in those species which winter in humid West African forest and savannah (Hewson & Noble 2009, Thaxter *et al.* 2010).

Understanding the drivers of population change in migratory species poses a particular challenge, as it may require knowledge of the relative effects of processes acting on populations during breeding, migration and non-breeding periods (Sutherland & Dolman 1994, Marra *et al.* 1998, Gill *et al.* 2001, Gunnarsson *et al.* 2005, Norris & Marra 2007). Integrating the relative effects of pressures facing any one species throughout its annual cycle can therefore be extremely complex, particularly for Afro-Palaearctic migrants which are often monitored in the breeding season, but for which very little is known of their distribution or movements in the non-breeding season (Bensch *et al.* 2006, Salewski & Jones 2006, Wilson & Cresswell 2006).

Since 1994, the abundance of common breeding bird species within the UK has been monitored as part of the British Trust for Ornithology (BTO)/Royal Society for Protection of birds (RSPB)/Joint Nature Conservation Committee (JNCC) Breeding Bird Survey (BBS) (Risely *et al.* 2011, Newson *et al.* 2008). The BBS is a national population monitoring survey, however, as the UK consists of different countries, separate indices are also produced for Scotland, England, Wales and Northern Ireland. Here we compare population indices of species breeding in England and Scotland; the two largest UK countries with the most comprehensive BBS coverage. Among resident bird species, variation in the rate of population change between these two countries could suggest differences in the influence of local environmental pressures operating within Britain. However, in migratory birds, spatial variation in population trends is also likely to depend on processes occurring outwith the breeding grounds, and on the strength of carry-over effects and migratory connectivity, which may exacerbate or buffer processes occurring during the breeding season (chapter 2, Harrison *et al.* 2011). Exploring geographical variation in population trends may therefore help to highlight the relative influence of processes operating during both the breeding and non-breeding season on the population changes occurring in birds breeding within the UK. In this study we therefore use the BBS population indices for England and for Scotland to explore the degree of geographic variation in species population trends. Focusing on long-distance migrants, we then explore the degree to which population trends in Scotland and England vary with aspects of their winter and breeding ecology.

Methods

Data collection

An index of the abundance of widespread bird species in the UK has been provided by the BBS since 1994. In the BBS, 1 km^2 survey sites are allocated to volunteers following a stratified random sampling procedure and coverage is representative of habitats throughout the UK. Within each of 83 regions (roughly equating to UK counties), the number of BBS sites reflects the number of potential volunteers in the region while the location of individual sites within a region is selected at random. Between 1994 and 2007, the BBS covered an average of 2178 sites each year, ranging from 1569 in 1994 to 3604 in 2007, providing comprehensive coverage of the majority of the UK. Coverage is greatest in lowland areas and the south-east of England and lower in the north of Scotland.

BBS surveyors visit each 1 km square three times a year. In the first visit, two parallel 1 km transects lines are identified and the habitats of each 200 m section along both transects are recorded using a hierarchical coding system (details in Crick 1992). Two subsequent surveys of bird abundance along these transects are then carried out, a minimum of four weeks apart; the first between early-April and mid-May and the second between mid-May and late-June. Bird transect surveys typically start between 6am and 7am, and last around 90 mins; days with poor weather are avoided as this can influence the number of birds recorded. Observers record all birds seen or heard within 100 m of the transect line, excluding birds identified as juveniles, for each 200 m transect section.

Calculation of population indices

In order to quantify the rates of population change in species breeding in Scotland and England, separate annual population indices are calculated for each country, as described in Risely *et al.* (2011). Variation in annual counts are modelled with Poisson generalised linear models, a function of year and site effects, weighted to account for differences in sampling effort across the UK, with standard errors adjusted for overdispersion. Indices provide a measure of population size on an arithmetic scale relative to an arbitrary value of 100 in 1994. If an index value increases from 100 to 200, the population has doubled; if it declines from 100 to 50, it has halved. Over 200 species have been recorded on BBS survey squares but, in this study, we included only the 74 species for which the annual mean number of BBS squares on which they were recorded between 1994 and 2007 was greater than five in both Scotland and England (Appendix 1).

Investigating correlates of population change

A recent study of patterns of population change among breeding birds in England used information in Wernham *et al.* (2002) to identify species primary wintering areas (Thaxter *et al.* 2010). We used this classification to separate species into long-distance (Afro-tropical) migrants (n=15), Short-distance (European migrants) (n=21) and resident species, which over-winter in the UK (n=38). Following Hewson and Noble (2009) and Thaxter *et al.* (2010), we included chiffchaff, *Phylloscopus collybita*, as a long-distance migrant. However, blackcap, *Sylvia atricapilla*, was included as a short-distance migrant due to lack of evidence that it crosses the Sahara (Wernham *et al.* 2002).

We investigated ecological correlates of geographic variation in population change for long-distance migrants only. A recent study by Ockendon & Atkinson (in prep) identified, for a range of Afro-Palaearctic migrant species, the bioclimatic zone in which the majority of the UK population is thought to spend most of the winter, from information reported in Cramp (1977 – 1994), Curry-Lindahl (1981) and Wernham *et al.* (2002). Using this classification, the wintering areas of long-distance migrant species were divided into arid (6 species) (combining the Sahelian *Acacia* savanna and West Sudanian savanna, Olson *et al.* 2001), humid (7 species) (combining the Guinean Forest-Savanna mosaic and Guinean Moist forest) and south (2 species) (Southern and Central Africa) ecoregions. In addition, the primary breeding habitat of these species was classified into three broad categories: farm (n=6), wood (n=7) and wetland (n=2), following Ockendon & Atkinson (in prep) and Cramp (1977 – 1994). Finally, following Thaxter *et al.* (2010), we also classified long-distance migrant species by their nesting location: open nesters (n=8) and cavity or hole nesters (n=7).

We use Pearson correlations to explore the association between the rate of population change in England and Scotland, and paired t-tests in R (2.12.0, R core development team,

2011) to explore regional differences in the population trends of resident, short-distance migrants and long-distance migrant species separately. For long-distance migrant species only, we used paired t-tests to explore differences between the population trends in England and Scotland within each wintering bioclimatic zone, breeding habitat and nesting location. We then used a one-way ANOVA to explore variation in population trends between wintering bioclimatic zones within each country (Scotland and England).

Results

Regional variation in population trends

From 1994 – 2007, there was a significant positive correlation between the rate of population change of 74 species breeding in England and in Scotland (Figure 1, r = 0.51, p<0.001). Of these species, 45 had the same direction of population trend; 36 increasing (Figure 1, upper right quadrant) and 10 declining (Figure 1, lower left quadrant) in both regions, but 28 species had opposing trends in England and Scotland; nine increasing in England while declining in Scotland (Figure 1, upper left quadrant) and 19 declining in England while increasing in Scotland (Figure 1, lower right quadrant). Overall, population trends were increasing at a significantly faster rate in Scotland than in England (mean population change in England: 17.7 (± 6.4 SE) and Scotland: 44. 1 (± 10.7 SE), paired t-test, t = -2.8, df = 73, p=0.006).

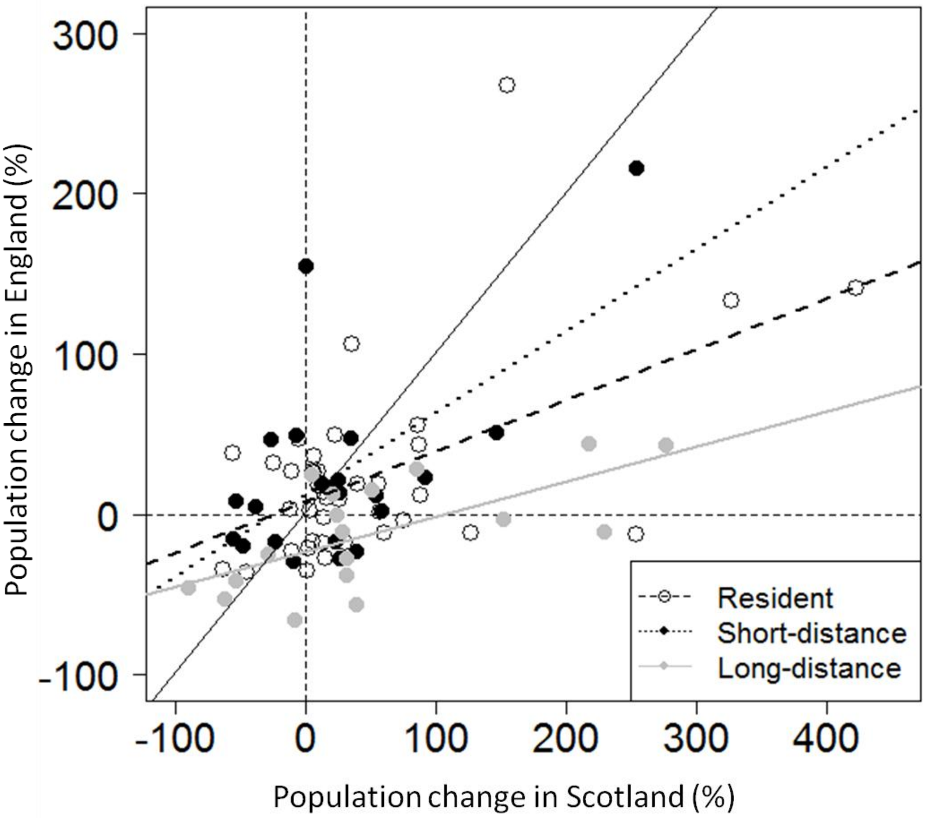

Figure 1: Correlations between changes in the population size of species breeding in England and Scotland for resident (dashed line, r = 0.64, n = 38, p = 0.01), short-distance (dotted line, r = 0.61, n = 21, p = 0.003) and long-distance (grey line, r = 0.56, n = 15, p < 0.001) migratory bird species between 1994 and 2007. The solid black line is the line of unity.

Migratory status and regional variation in population trends

There was no significant difference between the population trends in England and Scotland of resident species (paired t-test, t = -1.64, df = 37, p = 0.11, Figure 2) or short-distance migrant species (paired t-test, t = 0.04, df = 20, p = 0.97, Figure 2). However, the mean population trends of long-distance migrant species differed significantly between Scotland than England, with populations in Scotland increasing significantly while most populations in England were in decline (paired t-test, t = -3.39, df = 14, p = 0.004, Figure 2).

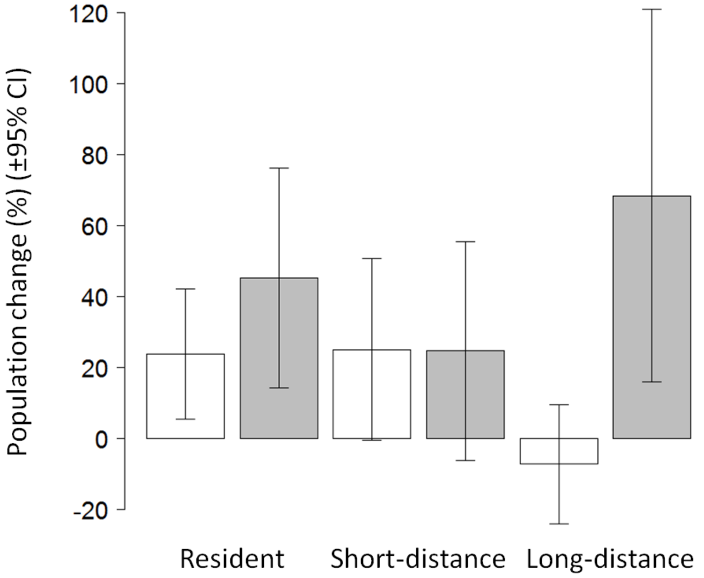

Figure 2: Changes in the population size, of resident (n = 38), short-distance (n=21) and long-distance (n=15) migratory species breeding in England (white bars) and Scotland (grey bars) between 1994 and 2007. Only species for which BBS indices could be calculated for both Scotland and England are included.

Long-distance migrants and regional variation in population trends

Among the 15 long-distance migrant bird species, strong population increases are only seen in Scotland (redstart, *Phoenicurus phoenicurus,* chiffchaff, *Phylloscopus collybita,* house martin, *Delichon urbica*, and garden warbler, *Sylvia borin*) (Figure 3a). All of the seven long-distance migrants which spend the non-breeding season in the humid zone of West Africa have negative population trends in England while five of these species are increasing in Scotland (Figure 3b). Consequently there is a significant difference between the mean population change in Scotland and England of species wintering within this zone (mean population change in Scotland = 56.0% ± 38.4 SE, England = -30.4% ± 7.5 SE, paired t-test: $t = -2.59$, $df = 6$, $p = 0.04$, Figure 3b). Of the six long-distance migrants spending the non-breeding season in the arid zone of West Africa, five species have positive population trends in England while all six species have positive population trends in Scotland. As the magnitude of increase in population abundance in these species is much higher in Scotland than England, there is also a significant difference between the mean population change in Scotland and England of species wintering within this zone (mean population change in Scotland = 113.5% ± 43.7 SE, mean population change in England = 19.8% ± 9.2 SE, paired t-test: t = -2.62, df = 5, p = 0.04, Figure 3b).

Of the six long-distance migrant species which breed on farmland, two species declined in both Scotland and England (whinchat, *Saxicola rubetra,* and swift, *Apus apus*), while three species increased more in Scotland than England (wheatear, *Oenanthe oenanthe*, house martin and whitethroat, *Sylvia communis*) and one species increased more in England than Scotland (swallow) (Figure 3c). Overall farmland species have higher population trends in Scotland than England (paired t-test: t = -3.31, df = 4, p =0.03, Figure 3c). Seven of the 15 long-distance migrants breed in woodland, of these species only one (spotted flycatcher, *Muscicapa striata*) is declining in both Scotland and England (Figure 3c). Of the remaining six species, all are increasing in Scotland, while only two are increasing in England (chiffchaff and redstart) but at a slower rate than in Scotland, and the remaining five are declining in England (Figure 3c). Woodland species are therefore also increasing at a faster rate in Scotland than England (paired t-test: t = -2.63, df = 5, p-value = 0.04, Figure 3c).

There are eight long-distance migrants that have open nest structures, of these one is declining in both Scotland and England (whinchat). The remaining seven are all increasing in Scotland, and two of these are also increasing in England (whitethroat and chiffchaff) but the rest are declining in England (Figure 3d). Overall, populations of open nesting species are increasing significantly faster in Scotland than England, where most are in decline (t = -3.27, df = 7, p-value = 0.01, Figure 3d). The remaining seven long-distant migrants are cavity nesters and, of these, two are decreasing in both Scotland and England (swift and spotted flycatcher), four are increasing in both regions while one species (house martin) is slightly declining in England while greatly increasing in Scotland (Figure 3d). There was no significant difference between the population trends of cavity nesting species breeding in Scotland and England (paired t-test: t = -1.57, df = 6, p-value = 0.17).

Population trends of migrants breeding within England also varied significantly depending on their wintering zone, with species wintering in the humid zone declining significantly and those in the arid zone increasing significantly, on average (t = 4.22, df = 10.1, p < 0.001, Figure 4). By contrast, within Scotland, population trends of arid and humid zone species did not differ significantly, and were mostly positive (t = 0.98, df = 10.5, p = 0.35, Figure 4). However, in neither country did population trends vary significantly among species with different breeding habitats (England: t = 0.58, df = 10.3, p = 0.57; Scotland: t = -1.35, df = 9.8, p

= 0.21) or nesting locations (England: t = 0.56, df = 12.6, p = 0.58; Scotland: t = -0.45, df = 11.3, p = 0.69).

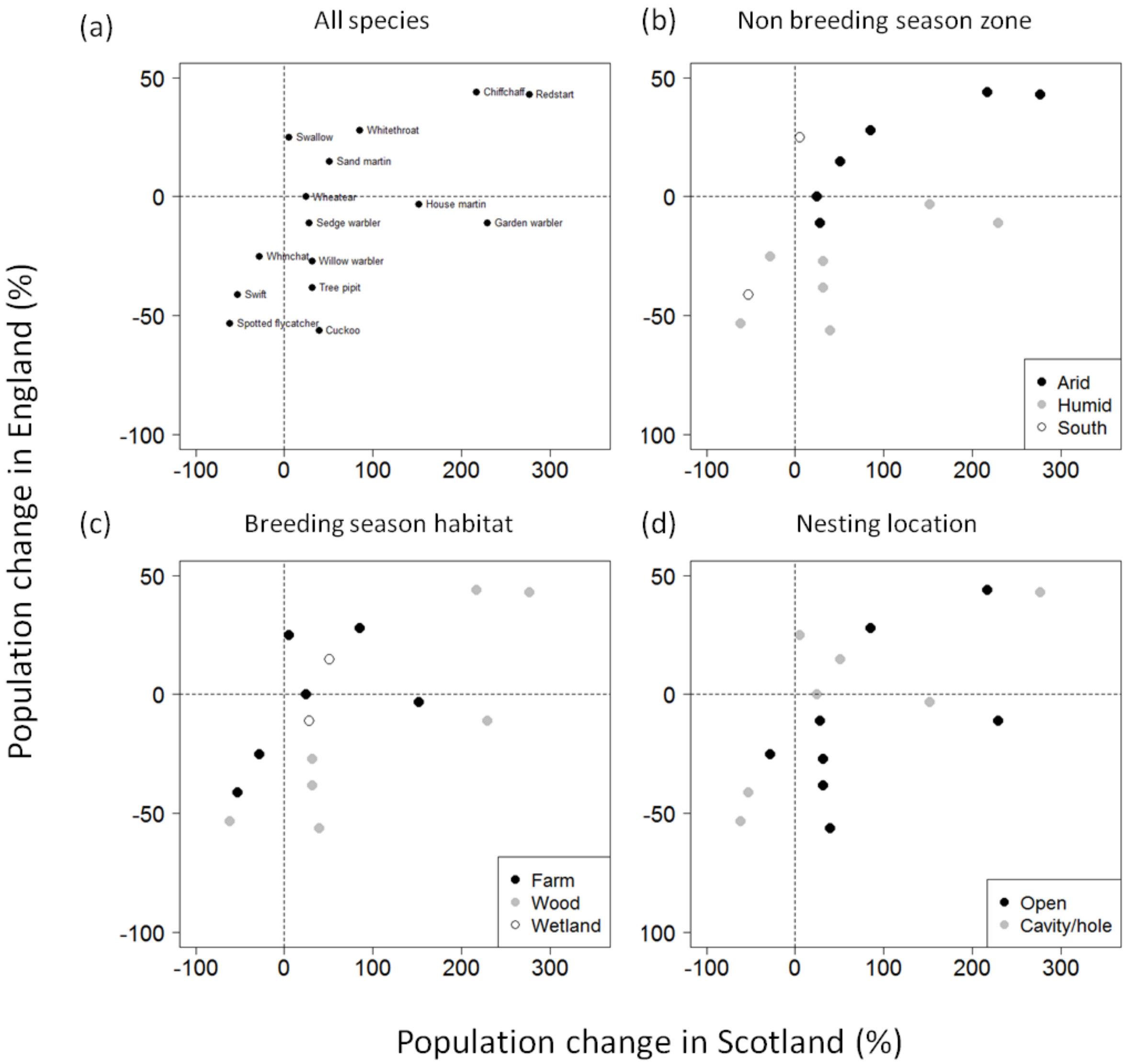

Figure 3: Regional variation in population change between 1994 and 2007 of (a) 15 long-distance migratory species, and those species grouped by (b) non-breeding season bioclimatic zone, (c) breeding season habitat and d) nesting location.

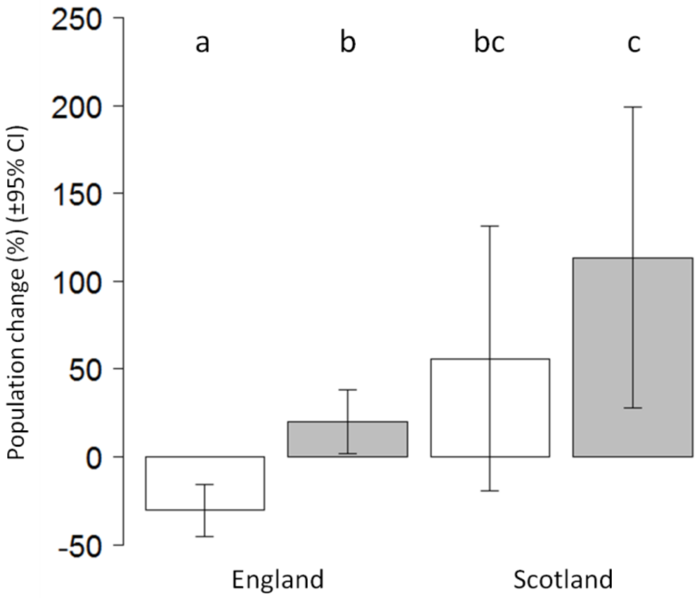

Figure 4: Changes in the population size between 1994 and 2007 of species breeding in England and Scotland wintering in the humid (white bars, n = 7) and arid (grey bars, n = 6) zones in West Africa. Only species for which BBS indices could be calculated for both Scotland and England are included. Letters indicate significant differences ($p < 0.05$) from unpaired (within-country and zone) and paired (between-country and zone) t-tests.

Discussion

Of the 74 species examined here, 40% have regionally divergent population trends, with 26% increasing in Scotland while declining in England, and 14% declining in Scotland but increasing in England. Significant differences between population trends in Scotland and England were apparent among long-distance migrants but not residents or short-distance migrants, suggesting that non-breeding season factors are important in these patterns. The largest population declines have occurred in English-breeding populations of species wintering in the humid zone of Africa, and population trends of species from the arid zone of Africa are also increasing faster in Scotland than in England. This highlights the likely importance of interactions between processes operating in each season, and suggests that the consequences of changes in environmental conditions in one season can potentially be buffered or exacerbated by conditions occurring in the other season (Marra *et al.* 1998, Bearhop *et al.* 2004, Gunnarsson *et al.* 2005, Norris & Marra 2007).

Geographical variation in population trends of resident and short-distance migrant species

In both resident and short-distance migrant species, there was no significant difference between rates of population change in Scotland and England. However, there are several resident and short-distance migrant species for which spatial variation in population trends does exist, with 10 of the 38 resident species and 3 of the 21 short-distance migrants increasing in Scotland but declining in England while 5 of the 38 resident and 4 of the 21 short-distance migrants were increasing in England but declining in Scotland. For example, green woodpecker, *Picus viridis,* and collared dove, *Streptopelia decaocto*, have declined in Scotland while increasing in England, while the abundance of jays, *Garrulus glandarius*, has increased rapidly in Scotland but slightly declined in England. There are a number of both short-distance and resident farmland species which are declining in England and increasing in Scotland e.g. linnet, *Carduelis cannabina*, yellowhammer, *Emberiza citrinella*, skylark, *Alauda arvensis*, and starling, *Sturnus vulgaris*. Declines in farmland birds such as these have been closely linked to agricultural intensification (Fuller *et al*. 1995, Siriwardena *et al.* 1998, Donald *et al.* 2001) and thus the geographic variation in these trends may reflect differences in land-use practices between Scotland and England.

Drivers of variation in population change in long-distance migrants

We found clear differences in the population trends of long-distance migratory species associated with different bioclimatic zones of Africa. However, we also found that the extent of these differences varied across the breeding grounds. Of the six long-distant migrant species wintering in the arid region of West Africa, all are increasing in Scotland and only sedge warblers, *Acrocephalus schoenobaenus,* are declining in England. During the late 1960s and early 1970s, many of these species experienced high rates of population decline (Thaxter *et al.* 2010), which have been linked to declines in survival associated with droughts in the Sahel (Møller 1989, Peach *et al.* 1991, Szep *et al.* 1995). In recent years, however, there have been several years of higher rainfall in this region (Nevoux *et al.* 2008), which may have led to increased survival and population recovery in both countries. However as geographical differences in the population trends of these species are largely due to the much higher rates of increase in Scottish than English populations (e.g. redstart, chiffchaff, whitethroat), this may suggest that Scottish populations may potentially have benefitted more from improved over-winter conditions than English populations.

In addition to the effect of winter rainfall, increasing human populations and the associated increases in grazing pressure, fuel-wood consumption, conversion of woodland to intensive agriculture, and use of pesticides in sub-Saharan Africa (Jones 1995, Mullie & Keith 1993, Norris *et al.* 2010) may also be impacting migrants. Previous studies have highlighted the potential role of conditions in the humid zone of West Africa in recent species declines, which is likely to be associated with habitat loss and degradation in this area (Hewson & Noble 2009, Thaxter *et al.* 2010). However, while the abundance of all seven species wintering in this zone have declined in England, all but two (whinchat and spotted flycatcher) have increased in Scotland. In particular, garden warblers, and house martins, have declined slightly in England and increased greatly in Scotland, while cuckoos, *Cuculus canorus,* and willow warblers, *Phylloscopus trochilus,* have declined greatly in England while slightly increasing in Scotland.

Differences in Scottish and English population trends of species wintering in both the arid and humid zones of Africa could be due to these populations wintering in geographically distinct parts of these zones, and thus experiencing different environmental conditions. However, recovery rates of ringed individuals of these species in Africa is typically very low and therefore there is limited evidence with which to explore regional differences in wintering areas (Wernham *et al.* 2002). Three of the species which are declining in England but not in Scotland (willow warbler, tree pipit, *Anthus trivialis,* and garden warbler), are considered to be itinerant during the non-breeding season and can move over large areas (Salewski & Jones 2006, Newton 2008). This strategy may mean that the impact of localised changes in environmental conditions on population trends of these species is relatively weak. However, if local-scale changes in environmental conditions are occurring throughout the wintering grounds, then their impact on itinerant and sedentary species may be similar.

Occupation of lower quality non-breeding areas has been associated with poorer subsequent breeding performance in some species (Marra *et al.* 1998, Gunnarsson *et al.* 2005). However, the consequences of such carry-over effects may vary with the quality of breeding season conditions. For example, higher quality breeding conditions may mean that the impact of negative carry-over effects (e.g. later arrival or arrival in lower body condition) on individual breeding success is reduced. The overall pattern of population trends of both humid and arid zone long-distance migrants being more positive in Scotland than England may be an indication of differences in the quality of breeding season conditions (e.g. lower rates of predation, greater food availability). Additionally, however, the declines in humid zone species in England but not Scotland suggests that conditions in Scotland may potentially be buffering the impact of conditions in the non-breeding season while, in England, lower quality breeding season conditions could potentially exacerbate the effects of non-breeding season conditions.

The arid and humid zones of Africa also differ in their distance from the breeding grounds. Previous studies have shown that species which winter further away from breeding grounds have advanced their timing of arrival on breeding grounds less than species wintering closer (Møller *et al.* 2008). For one long-distance migrant, the pied flycatcher, there is evidence that this has led to asynchrony between the chick rearing period and peak insect abundance (Both *et al.* 2001 & 2006), which can result in declines in breeding success (e.g. Visser *et al.* 1998 & 2006). However, as changes in the as the phenology of the breeding season are unlikely to be uniform across breeding grounds, the consequences of later arrival on breeding grounds may also vary geographically (Both *et al.* 2004 & 2010). Therefore if humid zone species have not advanced their arrival times as much as arid zone species, the consequences may differ between Scotland and England.

Conclusions

Within Britain, the population trends of many breeding birds are highly regionally variable. This pattern is particularly strong in long-distance migrants, in which Scottish populations have increased more than English populations over the last two decades (Figure 2). Critically, however, the population trends of migrants breeding in England but not Scotland also significantly differed, with the majority of those in the arid zone increasing and those in the humid zone declining. This highlights the strong importance of seasonal interactions in the population dynamics of migratory species. Further exploration of geographic variation in survival and productivity is needed in order to understand the demographic processes driving these patterns.

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Chapter two

Spatial and temporal variation in population trends in a long-distance migratory bird

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Abstract

Aim Over the past three decades, evidence has been growing that many Afro-Palaearctic migratory bird populations have suffered sustained and severe declines. As causes of these declines exist across both the breeding and non-breeding season, identifying potential drivers of population change is complex. In order to explore the roles of changes in regional and local environmental conditions on population change, we examine spatial and temporal variation in population trajectories of one of Europe's most abundant Afro-Palaearctic summer migrants, the willow warbler, *Phylloscopus trochilus*.

Location Britain and Ireland

Methods We use national survey data from Britain & Ireland (BBS: BTO/RSPB/JNCC Breeding Bird Survey and CBS: BWI/NPWS/Heritage Council Countryside Bird Survey) from 1994 to 2006 to model the spatial and temporal variation in willow warbler population trends.

Results Across Britain & Ireland, population trends follow a gradient from sharp declines in the south and east of England to shallow declines and/or slight increases in parts of north and west England, across Scotland and Ireland. Decreasing the spatial scale of analysis reveals variation in both the rate and spatial extent of population change within central England and the majority of Scotland. The rates of population change also vary temporally; declines in the south of England are shallower now than at the start of the time series, whereas populations further north in Britain have undergone periods of increase and decline.

Main conclusion These patterns suggest that regional-scale drivers, such as changing climatic conditions, and local-scale processes, such as habitat change, are interacting to produce spatially variable population trends. We discuss the potential mechanisms underlying these interactions and the challenges in addressing such changes at scales relevant to migratory species.

Keywords population dynamics, habitat change, migratory connectivity, sub-Saharan Africa, willow warbler.

Introduction

Across Europe, population declines are currently being reported in a wide range of Afro-Palaearctic bird species (Burfield & van Bommel, 2004; Møller, *et al.,* 2008). While the causes of these declines are not yet fully understood, the impact appears to be greater in long-distance (particularly sub-Saharan) than short-distance migrants (Sanderson *et al*., 2006; Hewson & Noble, 2009). Consequently, attention has focussed on changes occurring on winter and passage sites or in timing of migration, including changing patterns of rainfall over the Sahel (Møller, 1989; Peach *et al*., 1991; Szep *et al*., 1995; Robinson, *et al*., 2003) and the loss and degradation of key winter habitats through expansion of human populations (Newton, 2008). However, recent changes in breeding numbers and fecundity of migratory species have also been linked to habitat changes on breeding areas (Browne & Aebischer, 2001), and larger-scale factors such as climate change (Both & Visser, 2001; Huppop & Huppop, 2002). Identifying the causes of population change in migratory birds is thus likely to require an unravelling of the effects and relative importance of local- and regional-scale processes and the potentially complex manner in which they may interact (Mustin *et al*., 2007).

In general, regional-scale processes operating in the breeding season, such as large-scale variation in climatic conditions, may be expected to lead to large-scale spatial gradients of population change, whereas local-scale environmental processes, such as habitat change, may tend to create spatially variable population trends. Local-scale changes operating in regional synchrony (e.g. the spread of a new pathogen or predator) could also result in a large-scale spatial gradient of population change. In migratory birds, however, connectivity between breeding grounds and wintering grounds can potentially result in drivers in one season influencing population trends in another season (Marra *et al*., 1998; Gill *et al*., 2001, Gunnarsson *et al*., 2005). When migratory connectivity is strong, such that individuals from different breeding locations also winter in geographically distinct areas, changes within the wintering grounds have the potential to result in large-scale spatial gradients of population change in the breeding grounds. However, when there is weak or no migratory connectivity, non-breeding season environmental changes could result in small-scale variation in breeding season population trends, for example as reduced survival on passage or in winter results in fewer birds returning across the breeding range. The extent to which conditions in the non-breeding season influence population trends will also depend on their interaction with processes operating during the breeding season. Synergistic interactions (e.g. through individuals experiencing either the best or the worst conditions in both seasons, termed seasonal matching by Gunnarsson *et al*., 2005), could exacerbate population declines, while opposing interactions (individuals experiencing good conditions in one season and poor conditions in the other) could buffer population declines. Exploring patterns of spatial variation in population trends can therefore highlight the most likely sources of environmental changes driving these patterns.

One long-distance Afro-Palaearctic migrant, the willow warbler (*Phylloscopus trochilus*), provides an opportunity to explore many of these issues. The willow warbler is one of Europe's most abundant summer migrants, with population levels estimated at more than 56 million pairs (Burfield & Van Bommel, 2004), of which the UK population comprises 2.6 million pairs (Newson *et al*., 2008). From late-March to mid-July, willow warblers are on their breeding grounds throughout Europe, most frequently in scrub and woodland (Cramp 1992). Willow warblers depart from their breeding grounds in the latter part of the summer to arrive in Africa in late August and September. Within Africa, willow warblers tend to stay in the Sahel-Sudan zone, just south of the Sahara desert, for 1-2 months before travelling further south in late October or November (Salewski *et al*., 2002; Newton, 2008). The limited evidence available from reports of ringed birds suggests that British-breeding willow warblers winter in the Gulf of Guinea, principally around the Ivory Coast and Ghana (Norman & Norman, 2002). Evidence of geographic variation in population trends of breeding willow warblers first became apparent in the 1990s, when numbers in farmland and woodland Common Bird Census (CBC) plots in Britain suggested a decline in southern Britain which appeared to coincide with declining survival rates (Peach *et al*., 1995). By contrast, no evidence for any changes in population size or survival in the north of Britain was apparent at that time.

Since 1994 in the UK, and 1998 in the Republic of Ireland, willow warbler abundance has been monitored as part of the British Trust for Ornithology (BTO)/Royal Society for Protection of birds (RSPB)/Joint Nature Conservation Committee (JNCC) Breeding Bird Survey (BBS) and the Bird Watch Ireland (BWI)/National Parks and Wildlife Service (NPWS)/Heritage Council Countryside Bird Survey (CBS) respectively (Risely *et al*., 2009 and Coombes *et al*., 2006). We use these large-scale datasets to present a comprehensive account of (1) large-and small-scale spatial variation in willow warbler population trends in Britain and Ireland over the last thirteen years, (2) the extent to which these spatial trends vary across different time periods. We discuss these findings in the context of the variety of ecological drivers and interactions which may underlie the observed patterns.

Methods

Data collection

An index of the abundance of widespread bird species has been provided by the BBS since 1994 and by the CBS since 1998. In the BBS, 1 km^2 survey sites are allocated to volunteers following a stratified random sampling procedure and coverage is representative of habitats throughout the UK. Within each of 83 regions (roughly equating to UK counties), the number of BBS sites reflects the number of potential volunteers in the region while the location of sites is selected at random. Between 1994 and 2006, the BBS covered an average of 2178 sites each year, ranging from 1569 in 1994 to 3287 in 2006, providing comprehensive coverage of the majority of Britain & Northern Ireland. Coverage is greatest in lowland areas and in the south-east of England and lower in the north of Scotland. Consequently confidence in population trends estimated across the Highlands and Islands of Scotland, where fewer sampling points are available, is likely to be lower than in areas of greater coverage. Overall, willow warblers were detected in 2400 BBS squares over this time period (Figure 1).

In the CBS, the Republic of Ireland is divided into eight regions within which 10 km squares are randomly selected and allocated to volunteers in sequence. In order to ensure sufficient spatial coverage, the 1 km square at the extreme southwest corner of each 10 km of square is surveyed. Between 1998 and 2006, an average of 300 sites was surveyed each year, with coverage being greatest in the north and east of the country and less frequent in the south-west. Overall, willow warblers were detected in 328 CBS squares over this time period (Figure 1).

BBS and CBS use very similar methodologies. Each 1 km square is visited three times a year. In the first visit, two parallel 1 km transects lines are chosen and the habitats of each 200 m section along both transects are recorded using an hierarchical coding system (Crick 1992). Two subsequent early morning visits to the square are then carried out, a minimum of four weeks apart; the first between early-April and mid-May and the second between mid-May and late-June. Transect counts typically start between 6am and 7am, and bird count visits last around 90 mins; days with poor weather are avoided as this can influence the number of birds recorded. Observers record all birds seen or heard within 100m of the transect line, excluding birds that can be identified as juveniles, separately for each 200m transect section.

Figure 1: The distribution of all BBS and CBS sites in which willow warblers were recorded between 1994 and 2006, with the 50 km grid overlain.

Estimation of population trends

Using the maximum of the two counts (early and late breeding season), the total number of willow warblers detected across all transect sections within each 1 km square was calculated for each year. In addition, the majority habitat of each survey square was defined as the most frequent primary habitat across all transect sections within each square. Habitats were grouped into one of six broad categories; grass, mixed, scrub, human, wood and wetland (see Crick 1992 for details of habitats).

In order to examine the variation in willow warbler abundance over time across Britain & Ireland, survey data were aggregated over 50 km grid squares and a Poisson general linear model with a log link was fitted in SAS 9.1 (SAS Inc. 2003). To explore the influence of spatial scale on this variation, counts were summed over three spatial scales (100 km^2, 50 km^2 and 10 km^2). While patterns of population trends at the larger spatial scales (100 km^2 and 50 km^2) may indicate broad regional shifts in population trajectories, aggregating the data at these scales may also mask important and informative local variability in population trends. In particular, large-scale patterns within areas where data are sparse or not available may be heavily influenced by trends in surrounding squares. The survey data were therefore also aggregated within 10 km grid squares. In order to explore the effect of the location of the boundaries of data aggregation on estimated population trends, we carried out an additional analysis at the 50 km scale with the 50 km grid offset by 25 km both latitudinally and longitudinally.

At each scale, Poisson general linear mixed models with a log link were fitted to describe changes in abundance over time. Counts were modelled as a function of year*site, with site as a random effect nested within habitat type. This allowed sites with the same habitat types to be treated as more similar by the model, thus accounting for some of the variation introduced by habitat differences. The model was also offset by the number of squares in each spatial unit per year to account for differences in survey effort. Squares with fewer than two observations were excluded from all analyses. For the 100 km and 50 km analyses, all squares encompassing fewer than five BBS or CBS sites were removed, as these were unlikely to cover enough of the square to give a true representation of population trend over the whole area.

Using these predicted rates of change for survey squares at all three spatial levels, kriging was then applied to produce smoothed prediction surfaces of annual population change across the whole of Britain & Ireland. Suitability of this technique for use with BBS data is discussed in Newson & Noble (2008). To explore temporal variation in these spatial patterns, the trends were calculated for three equal time periods (1994-1997, 1998-2001, 2002-2006) at the 50 km scale.

Results

The direction and magnitude of abundance trends varies greatly with geographical location (Table 1). Across Britain & Ireland, there was significant latitudinal and longitudinal variation in population trends, from negative trends in the south and east to more positive trends in the north and west. There was also a significant interaction between latitude and longitude, indicating that populations in the east of the country are declining faster than average for their latitude, while trends in the west tend to be higher than average for their latitude (Table 1).

Table 1: Parameter estimates from a general linear model of variation in willow warbler population trends in Britain & Ireland between 1994 and 2006, in relation to latitude and longitude of the 157 50 km squares containing BBS and CBS data (see Figure 1 for distribution of squares). Also given are the Wald χ^2 values and associated significance values for each term.

Variable	Estimate (SE)	χ^2	p-value
Latitude	0.020 (0.006)	11.29	0.0008
Longitude	-0.227 (0.074)	9.46	0.0021
Latitude*Longitude	0.004 (0.001)	8.48	0.0036

The spatial variation in population trends at the 100 km scale highlights the broad patterns of latitudinal and longitudinal variation in abundance trends, with both north/south and east/west gradients of population change apparent (Figure 2). The greatest declines in willow warbler abundance have occurred in the south-east of England, from which a gradient of population change is apparent in zones running from the south-east to the north-west throughout England, Wales and into Scotland. A zone in which willow warblers have slightly increased in number is apparent in the north-west of Scotland. Slight population increases are also apparent across the majority of the Republic of Ireland at the 100 km scale (Figure 2a). When the trends are aggregated within 50 km grid squares, trends throughout much of Ireland, England and southern Scotland are similar to the 100 km scale, but zones of apparent increase in Wales and north-west England are indicated, and the location of the increasing populations in Scotland appears to be more easterly (Figure 2b). When the 50 km grid was offset by 25 km latitudinally and longitudinally, population trends were found to be consistent in areas with high coverage (e.g. south-east England) and there were only slight changes in the estimated population trends in areas with lower coverage (e.g. north-west Scotland).

At the 10 km scale, more spatial variability is apparent but, across the majority of England, the overall pattern of widespread declines is consistent with the larger-scales (Figure 2c). In both Scotland and Ireland, however, aggregating the data at the 10 km scale suggests the presence of local patches of declines and increases. In Scotland, patches of decline in the far-north coincide with areas of relatively sparse data (Figure 1) which may cause over-estimation of the true spatial extent of these declines.

The patterns of spatial variation in willow warbler population trends across the UK have not been consistent throughout the 13 years over which they have been recorded by the

BBS. In the south and east of England, populations experienced slight declines from 1994 to 1997, followed by sharp declines in 1998-2001 and relative stability in 2002-2006, with patches of both slight declines and increases across the region (Figure 3). These trends represent a decline from already relatively small population sizes below 54º N at the start of the survey period, to extremely low numbers which, from 2001 onwards, fluctuate around 1.0 to 1.2 willow warblers per 1 km^2 survey plot (Figure 4). Above 54º N, willow warbler abundance is higher (Figure 4). In central England and southern Scotland, from 54º to 56º N, population trends are similar across all temporal periods with wide widespread slight increases in abundance across the region (Figures 3 & 4). Above 56º N, willow warbler abundance is high (Figure 4) and there were increases across much of the region from 1994-1997 (Figure 3). As in the south of England, this is by followed a period of decline from 1998-2001, with areas of modest increase and decrease apparent from 2002-2006 (Figure 3). This stability is, however, at a much higher level of abundance than in the south (Figure 4).

Impact of distribution of habitat types on population trends

An array of habitat types were covered by the BBS squares that contained willow warblers. However, throughout Britain & Ireland, the coverage of different habitat types is relatively even, with c. 70-90% of all squares containing willow warblers comprising grass, which encompasses all semi-natural grasslands and marsh habitats. It is therefore unlikely that patterns of population change are a result of uneven habitat distribution within the BBS and CBS, though this does not mean that the population trends are not influenced by changes in habitat quality or availability.

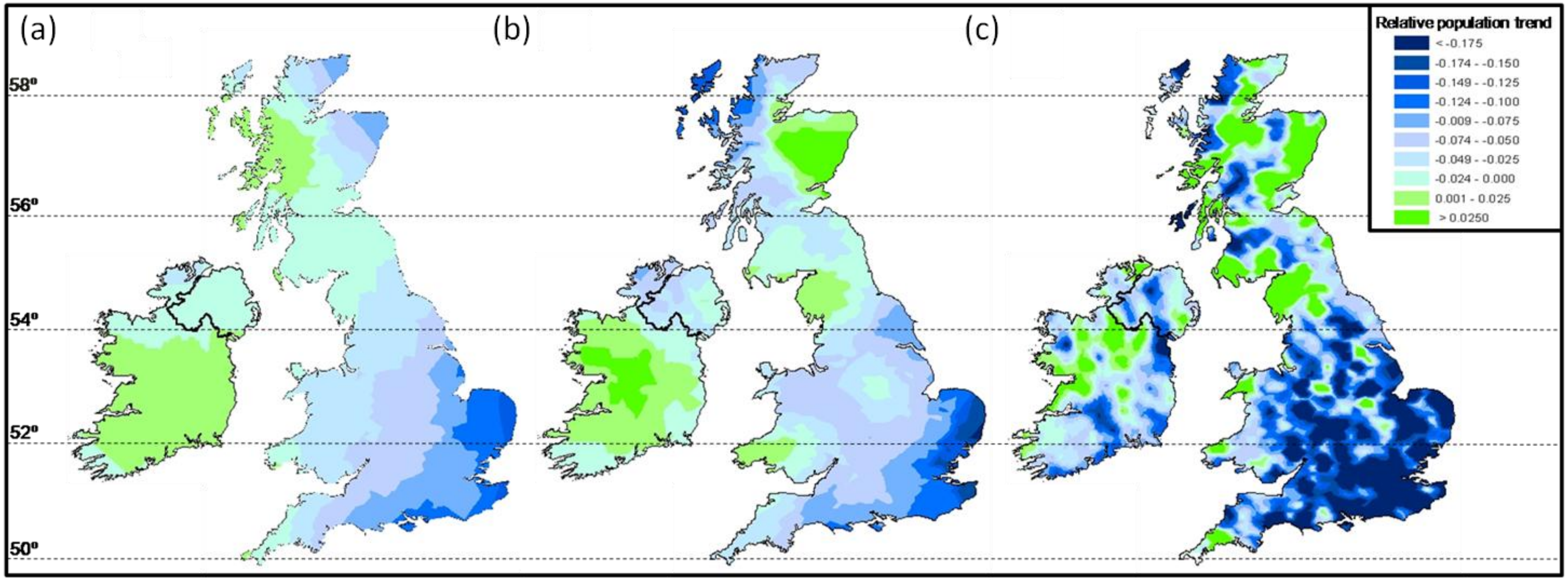

Figure 2: Spatial variation in the relative change in number of British and Irish willow warblers in 1 km^2 BBS and CBS survey plots between 1994 and 2006 (UK) and 1998 and 2006 (Republic of Ireland) aggregated at (a) 100 km^2 (b) 50 km^2 (c) 10 km^2.

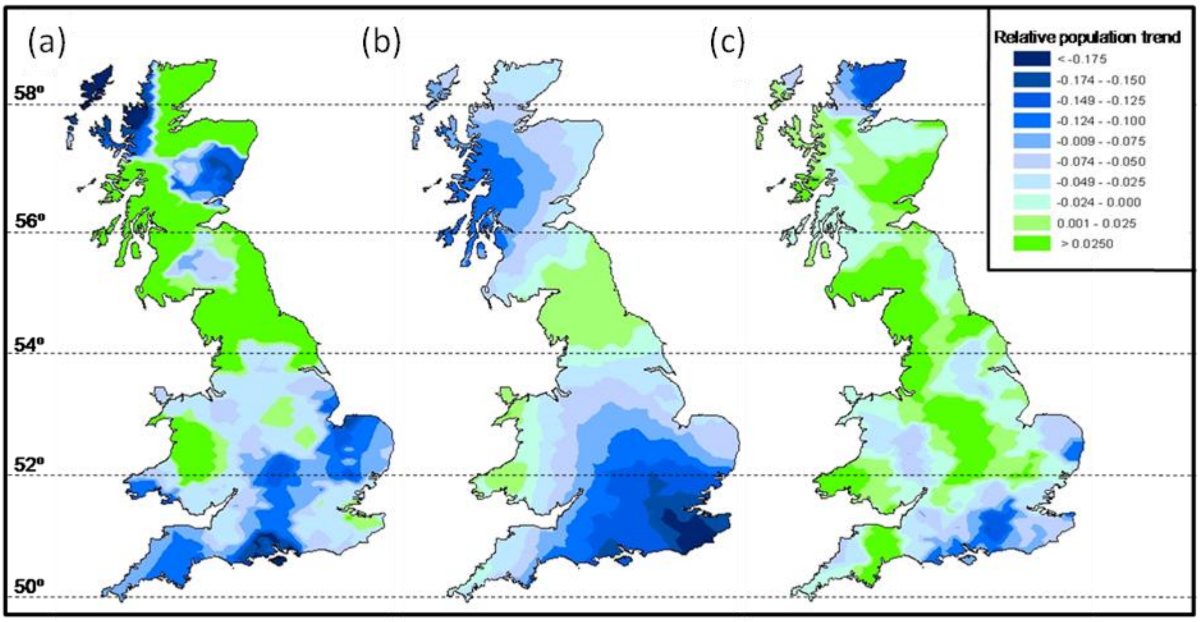

Figure 3: Spatial variation in the relative change in number of UK willow warblers in 1 km^2 BBS sites between (a) 1994 - 1997 (b) 1998 - 2001 (c) 2002 - 2006. Data are aggregated to the 50 km scale.

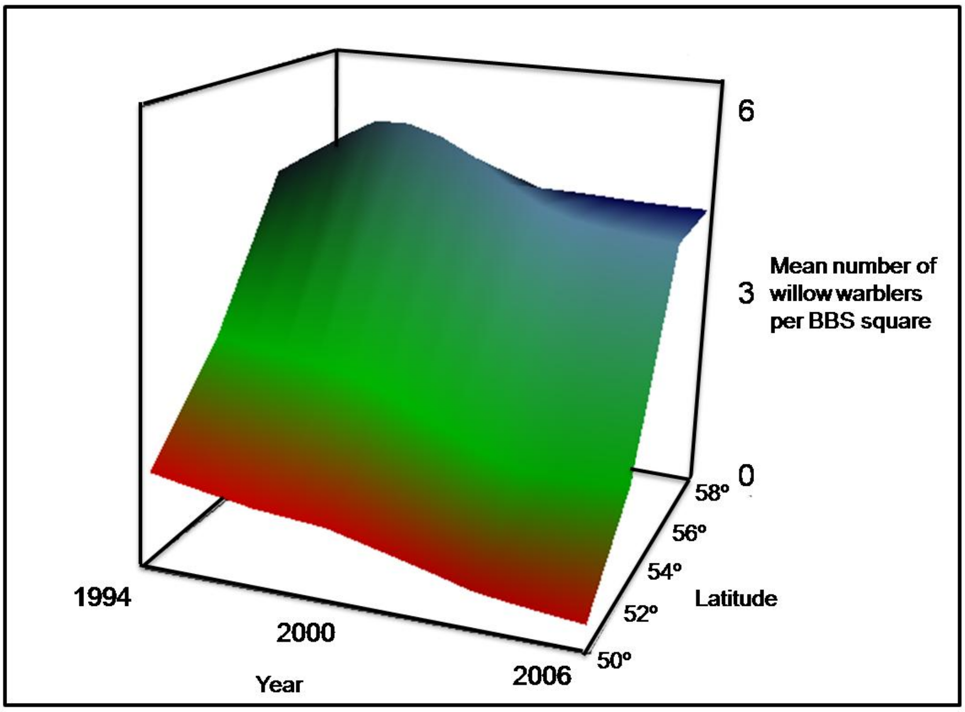

Figure 4: Latitudinal variation in the number of willow warblers per 1 km^2 in Britain between 1994 and 2006.

Discussion

Willow warbler population trends are highly spatially variable across Britain & Ireland, with the sharp declines in the south and east of England, gradually increasing to shallow declines and slight increases in areas of north and west England, Scotland and Ireland. In addition to this large-scale gradient, there are also patches of small-scale variation in areas of central England and much of Scotland. While declines in the south-east of England have been continuous throughout the survey period, reducing the population from ~1.94 (± 0.09 SE) to ~1.2 (± 0.04 SE) willow warblers per 1 km survey square, populations in the north of Britain have experienced periods of both increase and decrease in abundance, with abundance now estimated at ~4.6 (± 0.24 SE) willow warblers per 1 km survey square. The extent of spatial variation in population trends and their consistency across different spatial scales help to highlight possible drivers of population change, and suggest an influence of both regional-scale drivers, such as changing climatic conditions, and local-scale processes, such as habitat change.

Comparisons of spatial and temporal scales of measurement

In the south of England, BBS coverage is high and widespread declines in the populations of willow warblers are evident across the region at all three spatial scales (100 km, 50 km and 10 km). Willow warbler populations in the south of England have been declining since the mid 1980s (Peach *et al.*, 1995), thus the BBS survey captures the end of a sustained and widespread period of decline across this region, with many areas being reduced to one or fewer willow warbler pairs per km^2. In the south-east of England, the rate of population change is also consistent across spatial scales, which suggests the influence of either a regional-scale environmental driver or local-scale drivers occurring synchronously throughout the region. However population abundance in these areas is now so low that detecting population responses to current drivers could prove difficult. By contrast, from central England northwards through Scotland and Ireland, the maximum rate of decline increases with decreasing spatial scale, which may suggest that the influence of local-scale drivers of change are masked at the larger spatial scales by less severe changes in neighbouring squares. However, in the far north and west of both Britain & Ireland, inconsistencies between the three spatial scales (100 km, 50 km and 10 km) may also reflect data limitations. The smaller number of survey points in these areas can result in the precise location of the boundaries of data aggregation exerting a strong influence on the spatial patterns. Thus, while zones of population increase in the north and west of Britain & Ireland were clearly present during this time period, the boundaries of these zones of increase are not clear.

Potential drivers of spatial variation in population trends

The clear large-scale spatial gradient in willow warbler population trends may suggest the involvement of regional-scale drivers operating within the breeding season, such as regional-scale spatial variation in changes in mean spring temperatures and the seasonality of rainfall. Mean spring temperatures in the south and east of Britain are increasing faster than in the north and west (Perry, 2006). Such advancement of spring temperatures has been directly linked to advancements in the period of peak insect abundance (Visser *et al*., 2005; Both *et al*., 2006). As well as rising spring temperatures, some areas in the south of the UK are also experiencing a greater volume of rainfall over shorter time periods (Perry, 2006). High levels of rainfall can influence the ability of birds to provide food for chicks (Keller & van Nordwijk, 1994). Thus, in the south of the UK, rising temperatures may increase the likelihood of mismatches with key resources and increasing rainfall may reduce the success of breeding attempts. By contrast, in the north and west of Britain & Ireland the increases in rainfall have primarily occurred during winter months (Perry, 2006) and therefore the risk of rainfall increasing nest failure rates may be lower.

Regional-scale variation in breeding season population trends could also result from local-scale changes that are occurring throughout these regions (2c). For example, increases in the abundance and range of roe (*Capreolus capreolus*) and muntjac (*Muntiacus reevesi*) deer in the south-east of England (Corbet & Harris, 2008; Ward, 2005) have been linked directly to the loss of woodland understory and declines of breeding songbirds (Gill & Fuller, 2007). Although this habitat loss operates at a small-scale, the rapid range expansion of muntjac, in particular, may mean that these changes are occurring in synchrony across large areas, and could thus cause the type of large-scale population gradient observed in willow warbler breeding trends. Conversely, in the British uplands, there is potential for recent changes in management practices to actively promote extensive scrub and woodland regeneration (Gillings *et al*., 1998; 2000). The rate and extent of this regeneration is, however, likely to be limited, restricting its benefit to localised patches. This is therefore an example of a process likely to result in high levels of local variation in population trends such as those observed in the north and west of Britain & Ireland.

The spatial structure of population trends in the breeding season can also be greatly impacted by processes occurring during the non-breeding season, depending on the extent of migratory connectivity. On the wintering grounds in Africa, willow warblers are relatively mobile and exploit a wide range of habitats (Norman & Norman, 2002; Salewski, 2006;

Newton, 2008), suggesting that any migratory connectivity between the locations of breeding grounds and wintering grounds is likely to be relatively weak. In Africa, the effects of the recent increase in the frequency of drought conditions in the Sahel region on migrant species have been exacerbated by the substantial ecological impacts of increasing human populations and associated farming practices (Hein, 2006; Hein & Ridder, 2006). Overgrazing causes reductions in the quality of grasslands, removal of trees and shrubs and the loss and degradation of wetlands which, coupled with the increasing use of pesticides on farmlands (Mullie & Keith, 1993) has limited the availability of passage areas and the food resources of long-distance migrants (Newton, 2008). In systems without strong migratory connectivity, this type of widespread habitat degradation would be expected to result in a high level of local variation in breeding season population trends, but not a large-scale spatial gradient in trends. However, if willow warblers from the north of Britain & Ireland tend to either migrate at different times, use different passage sites or use the same sites for differing periods of time, or winter in different areas than those from the south of England, environmental changes in Africa could lead to the regional-scale variation in breeding season population trends.

Conclusions

The regional-scale gradient in breeding season population trends of willow warblers in Britain & Ireland suggests regional-scale drivers, such as changing climatic conditions, across different parts of Britain & Ireland. However, if there is migratory connectivity or variation in the timing of passage of birds from different parts of Britain & Ireland, then regional-scale environmental changes in Africa could also be creating these patterns. In addition, the high level of local-scale variation in the north and west suggests a potential interaction between regional-scale drivers and spatially fragmented local-scale drivers, although relatively low coverage in this part of the UK could also influence these patterns. Thus, unravelling the drivers requires the quantification of levels of migratory connectivity and differences in timing of migration, and identification of the extent to which local-scale habitat change and regional-scale climatic change overlap with the spatial distribution of population change.

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Chapter three

Changes in productivity and timing of breeding of willow warblers, *Phylloscopus trochilus*, in regions with divergent population trends

Abstract

1. In recent decades, the abundance of many long-distance Afro-Palaearctic migratory bird species has rapidly declined. While deterioration of environmental conditions in the non-breeding season have been linked to lowered adult survival in some species, the impact of changes during the breeding season on population declines has been less well explored.

2. Advances in the seasonal onset of breeding have become increasingly apparent in many temperate breeding bird species in recent years and, among migratory bird species, long-distance migrants appear to have advanced less than short-distance migrants. Constraints on the capacity of long-distance migrants to alter timing of migration and breeding in response to changing environmental conditions have therefore been implicated in their population declines. However, the impact of advances in timing of breeding on overall productivity will depend on both the seasonal variation in productivity and the distribution of nesting dates throughout the season.

3. Since the mid 1990s, there has been strong spatial variation in the population trajectories of one of Europe’s most abundant Afro-Palaearctic summer migrants, the willow warbler, *Phylloscopus trochilus*. Within Britain, willow warbler populations breeding in the south-east have declined sharply while populations in the north-west have been relatively stable. Using long-term survey data from the British Trust for Ornithology (BTO) Nest Record Scheme, we quantify levels of productivity, timing of breeding and seasonal variation in productivity in each region, in order to explore their potential contribution to the divergent population trajectories.

4. Between 1965 and 1985, willow warbler productivity averaged ~3.5 - 4 fledglings per breeding attempt in both the north-west and south-east regions, however productivity has subsequently declined in the south-east region and remained stable in the north-west, consistent with the regional variation in population trends. Productivity in the south-east has declined at all stages of the season but late-season nests have experienced the greatest declines in productivity in recent years.

5. Productivity in each region declines seasonally, but advances in the timing of breeding have reduced the proportion of late-season nests, which could potentially compensate for environmental impacts on overall productivity. However, modelling of productivity throughout

the season in the absence of changes in laying dates indicates that these advances are unlikely to have influenced the overall trends in productivity.

6. The decline in willow warbler productivity in the south-east region of Britain is likely to have contributed to the rapid population declines in this area, and the small advance in timing of breeding is unlikely to have made a substantial difference to overall productivity. Changes in conditions for breeding may therefore be a key component of population declines in the south-east.

Introduction

Over the past four decades there have been large declines in the abundance of many of the long-distance Afro-Palaearctic migrants that breed in Western Europe (Burfield & van Bommel 2004, Sanderson *et al*. 2006, Hewson & Noble 2009, Thaxter *et al*. 2010). Although changing environmental conditions in the non-breeding season have been linked to lowered overwinter survival for some of these species (Møller 1989, Peach *et al*. 1991, Szep 1995, Robinson *et al*. 2008), changes in productivity may also be implicated in their population declines (Browne & Aebischer 2004), as variation in population trends across the breeding range is apparent in some species (chapter 1, Morrison *et al*. 2010).

Changing environmental conditions during the breeding season have been implicated in recent declines in the productivity and abundance of a wide range of bird populations in western Europe (Fuller *et al.* 1995, Browne & Aebischer 2001, Peach *et al*. 2004, Beale *et al.* 2006, Gregory *et al*. 2007, Pearce-Higgins *et al*. 2010, Wright *et al*. 2010). Extensive degradation of important breeding habitats, through processes such as agricultural intensification and overgrazing of woodland understory, have been linked to declines in productivity in several Afro-Palaearctic migratory bird species (Browne & Aebischer 2004, Gill & Fuller 2007, Holt *et al*. 2010). In addition, changing weather conditions have been shown to influence the abundance and availability of prey resources for several species (Both *et al*. 2006, Pearce-Higgins *et al*. 2010), and these effects may be exacerbated in degraded habitats (Browne & Aebischer 2004, Peach *et al*. 2004).

The impact of changing environmental conditions on the breeding grounds may be influenced by shifts in the timing of breeding (Both *et al.* 2004, Visser *et al.* 2006). Since the 1960s, advances in timing of breeding have been apparent in several migratory bird species (Crick *et al*. 1997, Both *et al.* 2001, Sparks *et al*. 2007). However, the rate of these advances can vary both between and within species, and positive correlations between population trends and the magnitude of these advances have been identified among local breeding populations (e.g. pied flycatchers *Ficedula hypoleuca*; Both *et al*. 2006) and among species (Sparks *et al*. 2007, Møller *et al.* 2008). In seasonal environments, the influence of advances in timing of breeding on overall productivity may therefore be an important contributor to current population trends (Both *et al*. 2006 & 2010).

For species breeding at temperate latitudes, productivity can vary greatly across the breeding season (Price *et al*. 1988), with declines in breeding success towards the end of the season tending to reflect declines in resource availability and/or the suitability of environmental conditions (Visser *et al.* 1998, Przblyo *et al.* 2000, Sheldon *et al.* 2003). Consequently, the overall productivity of a population will be influenced by the proportion of individual nesting attempts occurring at different points in the season. Changes in the relative timing of breeding and/or the strength of seasonal variation in environmental conditions can therefore strongly influence overall productivity (Visser *et al*. 2004).

Population trends in the willow warbler, a long-distance Afro-Palaearctic migratory bird species, vary throughout Britain. Populations breeding in the south and east of the Britain are declining at faster rates than in the north and west, where populations are relatively stable (Morrison *et al*. 2010). In the early 1990s, there was some evidence that changes in survival rates may have contributed to this variation, with survival of willow warblers in the south of Britain declining from 45% to 24% from 1987-1988 to 1991-1992 while survival in the north during this period did not change (Peach *et al.* 1995). However, since 1992, despite a recovery in survival, overall declines in the British breeding population have continued (Morrison *et al*. 2010). This suggests that other factors, such as changes in productivity could also be influencing these population declines. We use national-scale datasets from the British Trust for Ornithology (BTO) Nest Record Scheme (NRS) to explore 1 – trends in productivity in the two regions of the UK currently experiencing contrasting population trends, 2 – the extent of changes in laying dates of willow warblers breeding across the whole breeding season in the two regions, 3- the potential influence of shifts in timing of breeding on the temporal trends in productivity.

Methods

Data collection: the Nest Record Scheme (NRS)

Since 1939, the annual breeding performance of a wide range of bird species across Great Britain has been monitored through the BTO NRS (for full details see Crick *et al*. (2003)). In the NRS, volunteer observers locate nests and record information including species, location, dates of each visit, numbers of eggs or young, the developmental stage of nests, eggs and young and the outcome of the nest (fledged or failed). This information allows calculation of laying dates and the daily probability of failure for those nests that are followed until the breeding attempt is completed.

Quantifying components of willow warbler productivity from the Nest Record Scheme

Estimating laying dates

For 6971 willow warbler nests surveyed between 1965 and 2007, we used the methods described by Crick *et al*. (2003) to estimate the date of the onset of laying (first egg dates) for each nest, as the mid-point between the earliest possible nesting date (visit date – (incubation period + laying period) and the latest possible nesting date (visit date – laying period). The accuracy of these estimates of first egg date can be refined over subsequent visits and is therefore higher in nests which are found towards the start of egg-laying. Nests where the difference between the earliest and latest possible first egg dates was greater than 20 days were excluded from these estimates.

Estimating willow warbler productivity

We estimated willow warbler productivity in each region and time period as the mean number of fledglings per breeding attempt (FPBA) using the following equation:

Equation 1: $FPBA = BS(1-DFI)^{IT}(1-DFN)^{NT}$

where BS = brood size (maximum number of chicks known to have hatched), DFI and DFN = daily nest failure rates during the incubation period and the nestling period, respectively, and IT and NT = the length of the incubation period and the nestling period (both in days), respectively. Values for the last two parameters were taken as 14 days and 15 days respectively, from Ferguson-Lees *et al.* (2011).

Brood size and daily nest failure rates for each region and time period were estimated using generalised linear models in the GENMOD procedure of SAS (SAS Inc. 2003). Brood size was estimated using a normal error distribution, while daily nest failure rates were estimated using a formulation of Mayfield’s (1961, 1975) method as a logistic model with a binomial error term, in which success or failure over a given number of days (as a binary variable) was modelled with the number of days over which the nest was exposed during the egg (pre-hatching) or chick (post-hatching and pre-fledging) period as the binomial denominator (Johnson 1979, Hensler & Nichols 1981, Aebischer 1999). The numbers of exposure days during the egg and chick stage periods were calculated as the mid-points between the maximum and minimum possible number of exposure days, given the timing of nest visits recorded on each nest record card. Following Siriwardena *et al*. (2000), we calculated CIs for FPBA by combining the variances for the individual reproductive parameters using the formula outlined by Hensler (1985). Statistical significance was indicated by non-overlap in 95% confidence intervals.

Trends in willow warbler productivity in Britain

Individual nest records were divided into the two broad geographical regions of Britain with contrasting willow warbler population trends from the mid-90s onwards (declining in the south-east and stable or slightly increasing in the north-west (Morrison *et al*. 2010) (Figure 1). The nest record data are spatially referenced to the county level and consequently this is the finest spatial scale at which these data can be analysed. Division of the dataset up into the two regions was based on the analysis in chapter 2 (Figure 2). This showed areas of stable or increasing population abundance (relative population change > 0) throughout the north and west of Scotland, the north-west of England and the north-west of Wales. Consequently these were grouped as one region while populations in the south-west, south-east and north-east mainly showed population declines and were consequently grouped as the other region. Although there were patches of increase in the south-west of England and decrease in the north-east of Scotland this division was the most appropriate way of capturing the larger scale spatial gradient of population change. Preceding the period of spatial variation in population trends (mid-90s onwards), there were rapid declines in the abundance of willow warblers across the whole of the UK (introduction, Figure 2). In order to explore the role of changes in productivity in these declines, nest records from before the 1990s were also included in the analyses. However, prior to 1965, very few willow warbler nesting attempts were recorded, thus we only considered records from 1965 onwards in the analyses. Due to the sparsity of data in some years, nests were grouped into 5 year time periods, with the exception of 2000 – 2007, to examine temporal trends in productivity and into two broad time periods from 1965-1989 and 1990-2007, to examine changes in the seasonality of productivity over the breeding season.

For each geographical region we used equation 1 to estimate mean FBPA across all nests recorded within each 5 year time period from 1965 - 2007, with the exception of the last time period which ran from 2000 to 2007. Seasonal variation in productivity within each region was explored by calculating mean FBPA within three time periods specific to that region (Table 1). In order to avoid problems of low sample sizes (which can result in highly variable estimates of FPBA), we estimated seasonal variation in FPBA within two broad time periods; 1965 – 1989 (n = 4863 nests) and 1990 – 2007 (n = 2108 nests), which also encompassed the period during and after the decline in willow warbler abundance in the south-east.

Figure 1: Areas of Britain included within north-west (pale grey) region in which willow warbler populations are stable or increasing and south-east (dark grey) region in which willow warbler populations are declining (Morrison *et al*. 2010).

Table 1: Seasonal grouping of nests into early (nests laid before the 25% quartile of first egg dates), mid-season (nests laid between the 25th and 75th quartile of first egg dates) and late (nests laid after the 75th quartile of first egg dates) periods in the north-west and south-east of Britain.

	North-west	**South-east**
Early	April 10th - May 13th	April 10th – May 8th
Mid	May 14th – June 26th	May 9th – June 20th
Late	June 27th – July 30th	June 21st – July 30th

Estimating shifts in timing of breeding

To calculate the rate of change in timing of breeding (estimated first egg dates of individual nesting attempts) between 1965 and 2007, we used generalised linear mixed models within the lmer library in R 2.12.0 (R core development team, 2011). First egg dates were modelled as a function of year, region and year*region fitted as fixed effects, and year was also fitted as a categorical random effect to account for possible non-independence of observations between years. To examine changes in the seasonal distribution of willow warbler first egg dates, we used the density function in R 2.12.0 to produce smoothed density estimates of first egg dates in both regions during 1965 – 1989 and 1990 – 2007.

Quantifying the impact of shifts in timing of breeding on overall productivity

In order to explore the influence on overall productivity of changes in the proportion of individuals breeding at each point in the season, we used equation 2 to calculate weighted mean productivity (FPBA) estimates for each region.

Equation 2: $FPBA_{WM} = \Sigma\ (fpba_{\ seasonal} * Prop_{\ seasonal})$

Where $FPBA_{WM}$ = weighted mean no. of fledglings per breeding attempt, $fpba_{\ seasonal}$ = mean no. of fledglings per breeding attempt for early, mid and late season nests (see earlier for dates), $Prop_{\ seasonal}$ = proportion of willow warblers nests laid during the early, mid and late seasons (see Table 1).

To explore the potential consequences of changes in the timing of breeding and the strength of the seasonal decline in productivity, we calculated weighted mean productivity estimates for the two time periods. Productivity varied both because the seasonal onset of breeding changed (nesting attempts tended to start earlier) and because the seasonal pattern in nesting success changed; in order to separate these we first estimated productivity (equation 2) in each region using $fpba_{\ seasonal}$ and $Prop_{\ seasonal}$ from 1965 – 1989 and from 1990 - 2007. We then explored the consequence of (1) no change in timing of breeding, by calculating productivity using $fpba_{\ seasonal}$ from 1990 - 2007 and $Prop_{\ seasonal}$ from 1965 – 1989 and (2) no change in the seasonal productivity pattern, by calculating productivity using $fpba_{\ seasonal}$ from 1965 - 1989 and $Prop_{\ seasonal}$ from 1990 – 2007.

Results

Regional and temporal variation in willow warbler productivity in Britain

Since 1965, willow warbler productivity has tended to be lower in the south-east (estimated mean number of fledglings per breeding attempt = 3.2 ± 0.14 SE) than in the north-west (3.7 ± 0.10 SE, Figure 2) of Britain. Willow warbler productivity has also declined significantly in the south-east over the last four decades (by ~1 fledgling per breeding attempt) while remaining stable in the north-west (Spearman's rank correlation: north-west: r=-0.81,p=0.02, south-east: r=-0.24,p=0.58, Figure 2).

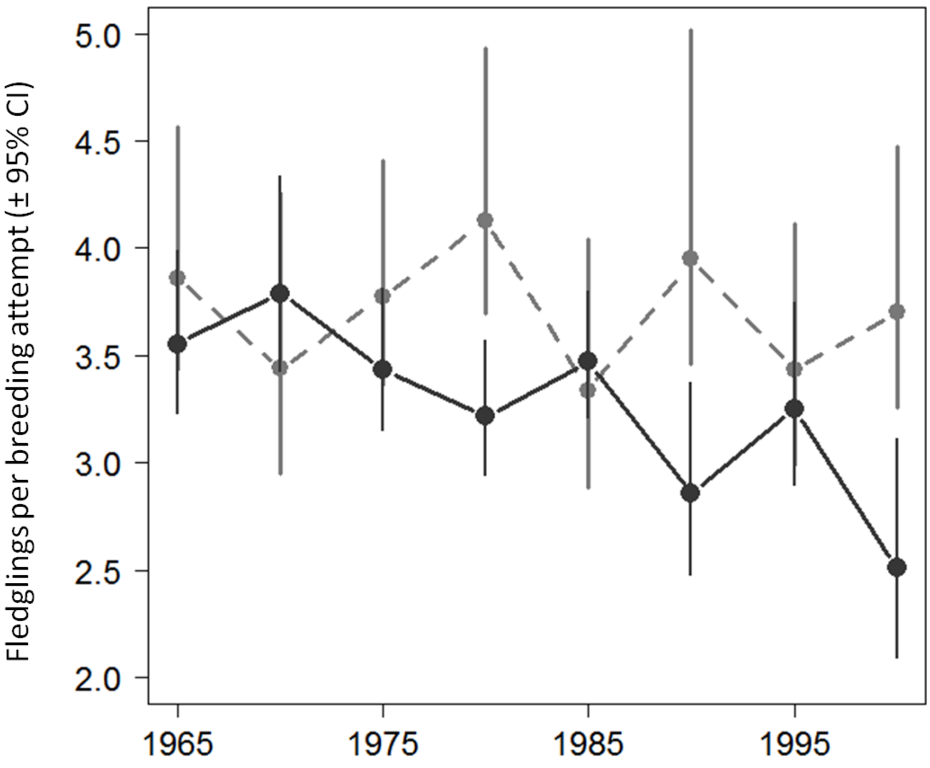

Figure 2: Temporal trends in productivity in five year time periods of willow warblers breeding in south-east (solid lines) and north-west (dashed lines) regions of Britain.

Regional and seasonal variation in willow warbler productivity in Britain

Seasonal declines in willow warbler productivity occur throughout Britain, but the pattern of these declines varies between the two regions and over time. Between 1965 and 1989, sharp seasonal declines in willow warbler productivity from early May to late June were apparent in both the north-west and the south-east (Figure 3a), with the largest difference in productivity between the two regions occurring in early May (Figure 3a). By 1990 - 2007, the seasonal declines in productivity in the north-west were less apparent, primarily because of a reduction in mean productivity of early season nests, and a slight increase in productivity of late season nests (Figure 3a). By contrast, productivity at all stages of the season in the south-east had declined by 1990 – 2007, with the greatest declines occurring in late season nests (Figure 3a).

Thus, the magnitude of the seasonal decline in productivity appears to have decreased in the north-west but increased in the south-east, and the penalties of late-season nesting are now particularly severe in the south-east (Figure 3a).

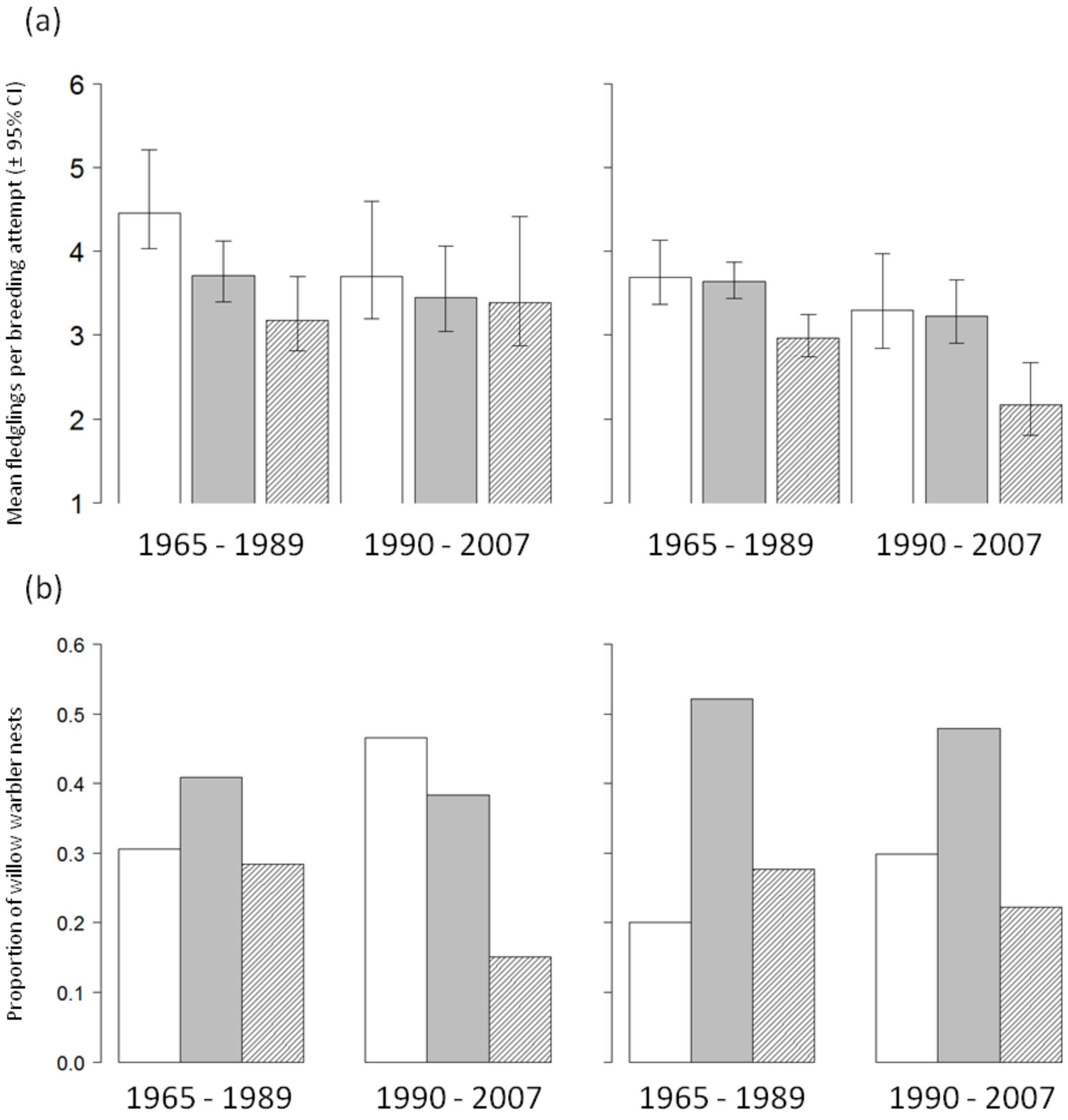

Figure 3: Changes in the seasonal variation in (a) willow warbler productivity and (b) the proportion of willow warblers nesting in north-west (left column, n = 2282) and south-east (right column, n = 4689) regions of Britain through the breeding season. Open bars = early, filled = mid and hatched = late season (see figure 1 and text for details of regions and seasons).

Regional and temporal variation in timing of breeding of willow warblers in Britain

The impact of the changing seasonal pattern of breeding success on overall productivity will depend upon the proportion of birds nesting at different points in the season. Between 1965-89 and 1990-2007, the timing of breeding of willow warblers advanced by ~6 days (~0.14 days/year) in the north-west and ~4 days (~0.09 days/year) in the south-east (Figure 4, Table 2). In both regions, the changes in timing of breeding have resulted in an increase in the proportion of early-nesting willow warblers and declines in the proportion of mid- and late-season nests (north-west: χ^2 =78.03, df = 2, p<0.001, south-east: χ^2 =52.80, df = 2, p<0.001) (Figure 3b), although the decline in the proportion of late-season nests is greater in the north-west than the south-east (Figure 3b).

Table 2: Parameter estimates from a general linear mixed model of annual and regional variation in timing of breeding (estimated mean first egg dates) of willow warblers in the north-west and south-east of Britain.

Independent variable	Estimate (SE)	df	t-value	Pr (>|t|)
Intercept	138.46 (0.85)	6637	167.76	<0.001
Year	-0.14 (0.03)	41	-4.15	<0.001
Region	5.35 (0.62)	6637	8.68	<0.001
Year*Region	-0.05 (0.03)	6637	-2.14	0.0326

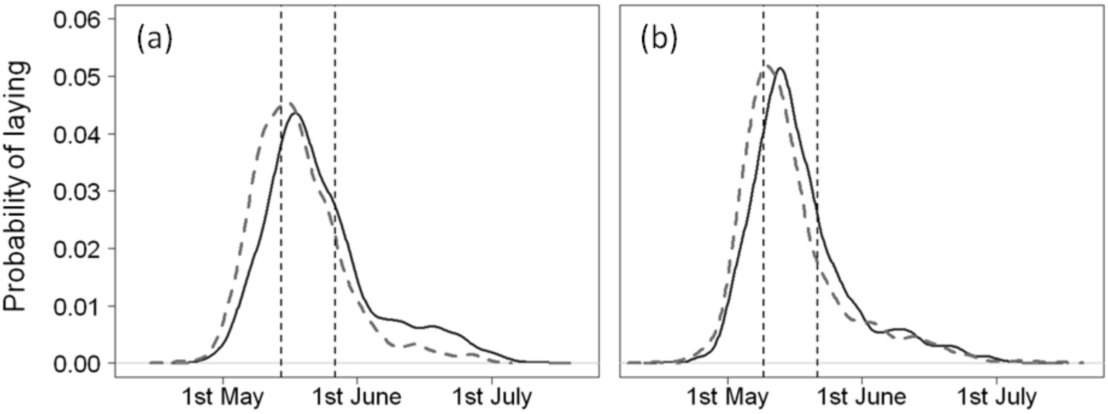

Figure 4: Smoothed distribution of first egg dates of willow warblers nests in 1965-1989 (solid lines) and 1990-2007 (dashed lines)) in (a) north-west and (b) south-east regions of Britain.

Seasonal interactions between productivity and timing of breeding

As the seasonal decline in productivity has weakened in the north-west but strengthened in the south-east (Figure 3a), the shift in laying dates (Figure 4) may have contributed to the differing regional trends in productivity (Figure 2). The weighted mean productivity of willow warblers declined between 1965-89 and 1990-2007 in both regions, but the decline was far more substantial in the south-east than in the north-west (Figure 5). However, in the absence of any change in the distribution of laying dates between 1965-89 and 1990-2007, the estimated weighted mean productivity would have declined slightly, but not significantly, more in both regions (Figure 5, hatched bars). The advance in laying dates in 1990-2007 would also have had little impact even if early, mid and late-season productivity had not changed from that in 1965-89, as the estimated weighted mean productivity does not differ significantly from the weighted mean productivity in 1965-89 in either region (Figure 5, filled bars). The shift in the distribution of laying dates therefore appears to have had very little impact on the change in overall productivity of willow warblers in Britain.

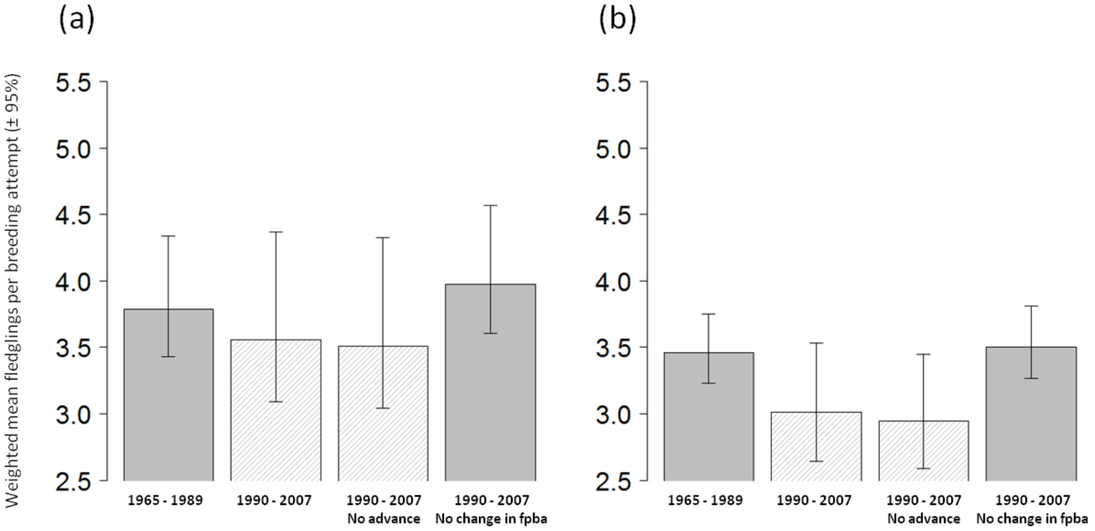

Figure 5: Estimated mean willow warbler productivity in (a) north-west and (b) south-east regions of Britain in 1965 – 1989 and 1990 – 2007, and the predicted mean productivity in 1990 – 2007 with the distribution of laying dates from 1965-89 (no advance) and the productivity levels and seasonal pattern from 1965-89 (no change in productivity). Shading denotes statistical comparisons (see text).

Discussion

During the 1980s there were large declines in the abundance of willow warblers in both the north-west and south-east of Britain (general introduction, Figure 2). However, during this time declines in fledglings per breeding attempt were only evident in the south-east. Given the similarity of the population declines in Scotland and England at this time, it therefore seems unlikely that fledglings per breeding attempt have been the sole driver of the early population declines in the south-east. Since the mid 1990s, however there has been strong spatial variation in the population trajectories of willow warblers breeding in Britain, with steep declines in the south-east and relative stability in the north-west (Morrison *et al*. 2010). From 1965 – 1985, willow warbler productivity was similar in both the north-west and south-east regions, fluctuating around ~3.5 - 4 fledglings per breeding attempt (Figure 2). However, since 1985, willow warbler productivity in the south-east region has declined in line with the population trend in this region, while both productivity and the regional population trend have remained stable in the north-west. Changes in productivity may therefore be an important component of the spatial variation in population trends, and it is therefore important to understand the factors influencing the changes in productivity. Willow warbler laying dates have advanced throughout Britain over this time period, and the advances have been slightly greater in the north-west region. As willow warblers that breed at the start of the season have higher productivity than those breeding towards the end, advancing timing of breeding could lead to increased productivity, particularly in the north-west region where the advance has been greater and the average productivity of early nests is greatest (Figure 3). However, we have shown that the observed shifts in timing of breeding are unlikely to have contributed substantially to changes in overall productivity, probably because the magnitude of the shift is relatively small, and because the increase in frequency of early-nesting events has been accompanied by a decline in early-season productivity in both regions.

Previous studies have identified positive correlations between advances in timing of breeding and population trends, both within and between species (Both *et al*. 2006, Møller *et al*. 2008), suggesting potentially strong benefits of advancing timing of breeding. In willow warblers breeding in the Britain, we also find slightly greater advances in the timing of breeding (~0.14 days/year from 1965 - 2007) in the north-west region where the population is stable than in the declining south-east population (~0.09 days/year from 1965 - 2007). However, these shifts in timing of breeding do not appear to have been sufficient to significantly influence productivity in these populations. Shifts in timing of breeding may be the consequence of changes in timing of arrival and/or a reduction in the interval between arrival and the start of laying (Both *et al*. 2006), and may therefore be sensitive to changes in environmental conditions on wintering, passage and/or breeding sites (Visser *et al*. 1998, Both *et al*. 2004, Saino *et al*. 2004, Gordo & Sanz 2008). Willow warblers from Britain winter in West Africa (Norman & Norman 2002), where they exploit a wide range of seasonally available habitats (Norman & Norman 2002, Salewski & Jones 2006, Newton 2008). Although there is no strong evidence that the wintering locations of willow warblers breeding in the north-west and south-east regions of the Britain are distinct (but see chapter 4), if birds breeding in these two regions differ in their timing of spring migration from Africa, differences in the conditions experienced on migration could potentially influence timing of arrival in Britain (chapter 4, Both *et al*. 2006, Both & te Marvelde 2007, Both 2010) and/or condition for breeding on arrival. Alternatively, laying dates may advance irrespective of any change in arrival dates, if the gap between arrival and laying is simply shortening. In several bird species, shifts in laying dates have been shown to be strongly correlated with changes in spring temperatures (Visser *et al.* 1998, Both & Visser 2001, Gienapp *et al.* 2010). However, in Britain, the greatest increases in spring temperatures have been in the south-east (Perry 2006), where willow warblers have shown a slightly smaller shift in timing of breeding.

Willow warblers are ground-nesting insectivorous birds that feed their young on a wide range of soft-bodied invertebrates (Cramp 1992). Willow warbler breeding success may therefore be influenced by factors such as changes in habitat quality, local weather conditions and predator abundance and activity. For example, changes in rainfall could influence the ability of provisioning adults to provide food for chicks (Keller & van Nordwijk 1994) or chick mortality may increase if the ground on which the nest is constructed becomes too wet. In other species, changes in the seasonality of temperature have been related to shifts in the timing of food availability, and a mismatch between timing of breeding and insect food peaks (Both *et al*. 2006, Visser *et al*. 2006). However these effects are greatest in woodland species where there is strong seasonality in the availability of food (Both *et al.* 2010). The primary willow warbler breeding habitat is scrub and young woodland, however, they have also been found to nest in gardens, orchards, hedges, pasture (Cramp 1955). Therefore the extent of mismatch on productivity may vary not just with the rate of temperature change on breeding grounds but also between breeding habitats, depending on the extent of changes in the seasonal patterns of food availability. The abundance of invertebrates may also be greater later in the summer in wetter habitats (Bailie *et al.* 2010), and therefore the frequency of wet features in the landscape may be an important driver of food availability during the chick rearing and post-fledging periods. In degraded environments, such as the drier arable landscape of the south-east, declines in rainfall may therefore be more limiting to productivity, than in areas where water is more readily available, such as such as in reed beds or river verges.

Changes in the suitability of environmental conditions may be reflected in changes in willow warbler productivity across the breeding season, but their impact on overall productivity will depend on the proportion of nests laid at different points in the season. For example, in the north-west, the largest change in productivity has been a decline in those nests laid before 13th May. However, prior to 1990, only ~30% of nests were laid before 13 May, and this has subsequently increased to ~47%, therefore the impact of this decline on overall productivity is likely to have been relatively small. Similarly, while the large decline in productivity in nests laid after 21st June in the south-east might suggest declining environmental conditions towards the end of the breeding season, the decline in the proportion of late-season nests means that the weaker declines in productivity in early and mid-season nests may have had much more of an impact on overall productivity.

Both the changes in timing of breeding and the changes in breeding success at any point in the season may also be influenced by changes in the relative quality of individuals breeding at that time. In one Swedish willow warbler population, the early arriving males were generally in better condition than late arriving males (Arvidsson & Neergaard 1991). If the overall decline in willow warbler populations disproportionately affects poorer quality individuals and/or the probability of poorer quality breeding sites being occupied, advances in timing of breeding might be a consequence of a proportionately higher number of ‘good quality’ (i.e. early) birds in the population and in the absence of any environmental change would lead to overall higher early and lower later productivity. Conversely however, if the proportion of willow warblers failing early on in their first breeding attempt increases, the number of second breeding attempts in the population could increase, which may influence the observed mid-season productivity, also influencing the extent of the seasonal declines in productivity.

Conclusions

The declines in willow warbler productivity in the south-east are likely to have contributed to the rapid declines in abundance in this region, while the higher productivity in the north-west may be playing a key role in preventing population declines in this area, even potentially buffering against changes on the wintering grounds or on passage. We found no evidence to suggest that the slightly greater shift in timing of breeding in the north-west is likely to have influenced the different trends in productivity in these regions. As the increase in the proportion of early nesting birds has been accompanied by a reduction in the average success of these nesting attempts in both regions, changes in the environmental conditions during the breeding season such as changing rates of predation (e.g Evans 2004, Zanette *et al.* 2011), changes in the abundance and availability of suitable food supplies for chicks (e.g. Pearce-Higgins *et al.* 2010) and changes in weather conditions (e.g. Wright *et al.* 2009) such as more frequent extreme rainfall leading to nests being washed out, are likely to be a more important driver of the regional differences in productivity trends. However, as the greatest declines have been at the end of the breeding season in the south-east, changes in the environmental conditions experienced by breeding willow warblers here may provide a strong clue about the processes influencing the declines in willow warbler abundance in this region.

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Chapter four

Causes of geographic variation in productivity of willow warblers across Britain

Abstract

1. Recent population declines in many Afro-Palaearctic migratory bird species have been widely linked to deteriorating conditions in sub-Saharan Africa. However, there is growing evidence to suggest that changes in productivity may also be contributing to these declines, although the causes of these changes are currently not well understood.

2. Since the mid 1990s, the abundance of willow warblers, an Afro-Palaearctic migrant species, has greatly declined in the south-east of Britain while slightly increasing in the north-west. Over a similar time period, the mean productivity of willow warblers has declined in the south-east, particularly among late-season nests, but remained stable in the north-west. Local variation in breeding season conditions may therefore be an important component of the divergent trends in these populations. Here we use estimates of willow warbler productivity from the UK-wide Nest Record Scheme (NRS) to explore the extent to which changes in clutch size, hatching success and fledging success reflect the regional trends in willow warbler productivity, in order to try and identify potential drivers of these divergent trends.

3. From 1965 to 2007, there was no significant temporal trend in clutch size or hatching success in either region. However, fledging success was significantly lower in the south-east than the north-west of Britain. Fledging success also declined significantly over this period in the south-east region, but not in the north-west.

4. Fledging success of willow warbler nests was particularly low when regional weather conditions were hot and dry during the chick-brooding period, and these conditions were particularly prevalent at the end of the breeding season in the south-east region. However, so few nesting attempts occur in this region at this time of the season that it is unlikely that changes in the frequency of these weather conditions have contributed substantially to decline in fledging success in the south-east.

Introduction

In recent decades, large-scale changes in the structure and complexity of European landscapes have lead to widespread changes the distribution and abundance of biodiversity (e.g. Robinson & Sutherland 2002). In particular, processes such as agricultural intensification (Fuller *et al.* 1995, Browne & Aebischer 2001, McCracken & Tallowin 2004, Peach *et al.* 2004), wetland drainage (Wakeham-Dawson and Smith, 2000) and overgrazing of woodland understory (Gill and Fuller 2007, Holt *et al.* 2010) have been implicated in the declines of many bird species across their breeding grounds. In addition, changing weather patterns have been shown to influence the phenology and abundance of invertebrate prey (Visser *et al.* 1998, Both *et al.* 2006, Pearce-Higgins *et al.* 2010), which may limit the availability of breeding season food resources for such species. Recently, some of the largest population declines in European breeding birds have occurred in species wintering in sub-Saharan Africa (Sanderson *et al.* 2006, Hewson & Noble 2009). As these declines have been more severe than in most short-distance migrant or resident bird species, changes in overwinter survival as a consequence of increasing frequency of droughts in the Sahel have been implicated as a major driver of these losses (Møller 1989, Peach *et al.* 1991, Szep 1995). However, not all long-distance migratory species are declining (chapter 1), and population trends within a species range have been shown to vary over large geographic scales (chapter 2), suggesting that changes in breeding season processes could also be contributing to population changes for these species (e.g. Browne & Aebischer 2001).

Changes in the condition of breeding areas could influence the dynamics of migratory populations by altering the availability of suitable breeding areas, and thus the number of individuals in the population able to breed (e.g. changes in woodland structure). However, reductions in the quality of breeding areas, such as changes in the availability of nesting locations, nest materials, shelter, proximity and abundance of predators, abundance of food and water and increases in the frequency of extreme weather conditions, may also lead to reductions in the success of those breeding attempts that do take place (Brickle *et al.* 2000, Wright *et al.* 2009, Pearce-Higgins *et al.* 2010). Ultimately such gradual deterioration of habitat may lead to habitat loss and population declines (Fuller & Ausden 2008).

Since the mid 1990s, the abundance of one of Europe's most abundant Afro-Palaearctic migrants, the willow warbler, *Phylloscopus trochilus,* has declined by ~30% in the south-east but increased by ~21% in the north-west of Britain (Risely *et al.* 2011, Morrison *et* *al.* 2010). Over a similar time period there has also been a ~20% decline in the number of chicks fledged per breeding attempt in the south-east but no change in the north-west (chapter 3), suggesting that changes in productivity may be playing a role in these divergent population trends. Willow warblers are on their breeding grounds throughout Europe from late-March to mid-July, most frequently nesting in scrub and young woodland (Cramp 1992, Ferguson-Lees *et al.* 2011). Analyses of the timing of nesting of willow warblers in Britain over the last four decades (chapter 3) have shown advances in mean laying dates of ~4 days in the south-east and ~6 days in the north-west (chapter 3, Crick *et al.* 1999). As the success of breeding attempts declines over the course of the breeding season, an increase in the proportion of early breeders might be expected to lead to higher productivity. However, due to a reduction in the average success of early nesting attempts, the change in timing of breeding appears to have had very little impact on productivity in either region (chapter 3). The causes of the observed decline in productivity in south-east Britain may therefore be related to changes in the environmental conditions during the breeding season, particularly at the end of the breeding season when the declines in productivity have been most apparent (chapter 3).

The regional variation in the trends in willow warbler productivity could be influenced by differences in clutch size and/or failure rates at the egg and/or chick stages. Changes in the number of fledglings per breeding attempt could therefore arise from a range of mechanisms, including changes in predation rates, resource availability and weather (Visser *et al.* 1998, Both *et al.* 2004, Wright *et al.* 2009, Newson *et al.* 2010, Dunn *et al.* 2011). Understanding the relative role of each of these components of productivity in driving the seasonal and temporal trends in each region may therefore help to pinpoint potential drivers of the changes in willow warbler demography and population size.

As willow warblers are ground-nesting insectivores, they may be particularly vulnerable to changes in both the temperature and rainfall experienced during the breeding season. For example, intense or prolonged periods of rainfall may lead to flooding of nests or chilling of chicks, while periods of drought may greatly limit prey availability. In Britain, climatic conditions vary over a similar spatial scale as willow warbler population trends, with the north and west of the country typically experiencing cooler and wetter conditions than the drier and hotter south and east (Appendix 1: Map 1 & 7 in Perry 2006). Over the last few decades there has also been regional variation in the rate at which climatic conditions are changing within the breeding season, with the south-east becoming generally warmer and drier in spring and summer than the north-west, where summer temperatures have increased only slightly (Perry 2006). It is therefore possible that regional and seasonal variation in the rate of change in temperature and/or rainfall experienced during the course of breeding attempts are playing a role in the regional variation in changes in willow warbler productivity.

Here we use national-scale datasets from the British Trust for Ornithology (BTO) Nest Record Scheme (NRS) (Crick *et al.* 2003) to explore the extent of regional, temporal and seasonal variation in willow warbler clutch size, hatching success (daily nest failure rates at egg stage) and fledging success (daily nest failure rates at chick stage) between 1965 and 2007. Using regional-scale weather data, we then explore the association between weather conditions and willow warbler productivity by relating the mean daily temperature and rainfall in each region during each nesting attempt to the success of those attempts. These analyses are then used to explore the potential influence of changes in weather conditions on willow warbler productivity in Britain.

Methods

Data collection: the Nest Record Scheme (NRS)

Since 1939, the annual breeding performance of a wide range of bird species in Britain has been monitored through the BTO Nest Record Scheme (NRS; for full details see Crick *et al.* (2003)). In the NRS, volunteer observers locate nests and record information including species, location, dates of each visit, numbers of eggs or young, the developmental stage of nests, eggs and young and the outcome of the nesting attempt. This information allows the calculation of a number of metrics of breeding success for those nests that are followed until the breeding attempt is completed and the outcome is known.

Quantifying components of willow warbler productivity from the Nest Record Scheme

Estimating laying dates

We used the methods described by Crick *et al*. (2003) to estimate the date of the onset of laying (first egg dates) for each nest as the mid-point between the earliest possible nesting date (visit date – (incubation period + laying period) and the latest possible nesting date (visit date – laying period). The accuracy of these estimates of first egg date can be refined over subsequent visits and is generally higher in nests which are found towards the start of egg-laying. Nests where the difference between the earliest and latest possible first egg dates was greater than 20 days were excluded from these estimates.

Estimating clutch size and nest failure rates

Information from the NRS was used to determine willow warbler clutch size and daily egg and chick stage failure rates. In analyses of hatching and fledging success, we included only nests with known outcomes (success = at least one egg hatched/chick fledged, failure = no eggs hatched/chick fledged). Clutch size (maximum egg count) was only determined for nests that had been visited more than once during the egg stage, and any nests for which the maximum number of chicks exceeded the maximum number of eggs were excluded. Daily probability of nest failure was calculated for egg and chick stages separately, and included only those nests that were followed until the breeding attempt was completed.

We used generalised linear models in the glm function of R (2.12.0, R Development Core Team, 2011) to estimate variation in willow warbler clutch size and daily nest failure rates. All analyses of clutch size were constructed with Poisson errors and a log link function. Daily nest failure rates were estimated using a formulation of Mayfield's (1961, 1975) method as a logistic model with binomial errors, in which nest success or failure (as a binary variable) was modelled with the number of exposure days during the egg or chick period as the binomial denominator (Johnson 1979, Hensler & Nichols 1981, Aebischer 1999). The numbers of exposure days during the egg and chick stages of each nesting attempt were calculated as the mid-points between the maximum and minimum possible number of exposure days, given the timing of nest visits recorded on each nest record card. The survival rate over the duration of the nesting period can then be calculated using the following equation from Crick *et al.* 2003:

Equation 1: $J = (1-m)^J$

Where J is the duration of the nesting attempt (14 and 15 days for egg and chick stage, respectively; Ferguson-Lees *et al.* 2011) and m is the daily nest failure rate at egg or chick stage.

Regional variation in trends in willow warbler productivity in Britain

Nest records were divided into north-west and south-east regions of Britain (Figure 1), where there are contrasting willow warbler population trends from the mid-90s onwards (Morrison *et al.* 2010). Preceding the period of spatial variation in population trends (mid-90s onwards), there were rapid declines in the abundance of willow warblers across the whole of the UK (introduction, Figure 2). In order to explore the role of changes in productivity in these declines, nest records from before the 1990s were also included in the analyses. However, prior to 1965 very few willow warbler nesting attempts were recorded by the NRS, thus we only considered records from 1965 onwards in the analyses. In order to explore changes in productivity across Britain, we estimated the difference in clutch size (GLM with Poisson error distribution) and egg and chick stage failure rates (GLMs with binomial error distribution), between the north-west and south-east of Britain using R (2.12.0, R core development team, 2011). Within each region, we then estimated both temporal and seasonal trends in clutch size and nest failure rates (Table 1). Due to the sparsity of data in some years and times of the season, nests were grouped into five year time periods (except for the final time period of 2000-2007 which was seven years in length) and into ten day periods. We then estimated mean clutch size and failure rates across all nests in these time periods.

Figure 1: Areas of Great Britain included within the north-west (pale grey) region in which willow warbler populations are stable and the south-east (dark grey) region in which willow warbler populations are declining (Morrison *et al.* 2010).

Table 1: Number of Nest Records used to estimate willow warbler clutch size and nest failure rates in the north-west and south-east regions of Great Britain in each (a) five-year time period between 1965 and 2007 and (b) 10-day time period (Julian date) from 20 April – 10 July for all nests recorded between 1965 and 2007.

(a)	**Clutch size**		**Daily egg stage failure rate**		**Daily young stage failure rate**	
	North-west	**South-east**	**North-west**	**South-east**	**North-west**	**South-east**
1965 - 1969	102	208	128	267	145	403
1970 - 1974	75	120	100	163	96	294
1975 - 1979	115	199	134	254	176	406
1980 - 1984	60	194	82	271	153	574
1985 - 1989	81	217	116	329	143	650
1990 - 1994	40	104	56	159	103	295
1995 - 1999	72	120	114	150	226	287
2000 - 2007	46	118	78	154	206	202
(b)						
110 – 119	4	22	5	5	7	52
120 – 129	56	329	85	85	196	940
130 – 139	235	526	331	331	556	1339
140 – 149	171	207	236	236	320	429
150 – 159	66	89	129	81	86	177
160 – 169	37	72	81	41	48	110
170 – 179	17	29	38	23	29	55
180 – 189	5	6	6	6	6	9
Total	**591**	**1280**	**808**	**1747**	**1248**	**3111**

Calculation of regional weather conditions during nesting attempts

Four weather metrics were included in this analysis:

- Mean daily temperature from the Met office daily Central England Temperature dataset (Parker et al. 1992).
- Mean daily rainfall from the England & Wales precipitation (EWP) dataset (Alexander & Jones 2000).
- Mean daily temperatures from the Met Office daily Scottish temperature dataset (Jenkins *et al.* 2009).
- Mean daily rainfall from the Scottish precipitation dataset (Alexander & Jones 2001).

Given the broad spatial resolution of the nest record cards, these weather variables were selected to capture the broad-scale climatic differences between the two regions of contrasting population change (north-west and south-east). Using the mean length of the incubation (14 days) and brooding (15 days) periods (Ferguson-Lees *et al.* 2011) for each nesting attempt, we then calculated the mean of the daily temperature and rainfall that occurred in that region during the incubation period (first egg date + incubation period) and the brooding period (first egg date + incubation period + brooding period). These mean lengths of brooding and incubation periods were used regardless of whether nesting attempts were successfully completed, because the actual dates of nest failure are very rarely known.

Calculation of the association between weather conditions and daily nest failure rates

We used GLMs with a binomial error distribution to model daily egg and young stage failure rates as a function of the regional mean daily temperature and rainfall during incubation and brooding during each nesting attempt, respectively. We then used the model predictions to explore the temperature and rainfall conditions that are associated with the highest rates of nest failure.

Results

Regional and temporal variation in components of willow warbler nest success

From 1965 to 2007, mean willow warbler clutch size was similar in the north-west and the south-east of Britain (north-west: 5.94 ± 0.10 SE, south-east: 5.96 ± 0.07 SE, Table 2, Figure 2a), and there was no evidence of any temporal trend in clutch size in either region (Table 3, Figure

2a). However, within both regions there was a significant seasonal trend, with clutch size approximately halving over the course of the breeding season (Table 3, Figure 2d).

Mean daily nest failure rates at the egg stage were also similar in both regions (north-west: 0.011 ±0.001 SE, south-east: 0.011 ± 0.0013 SE, Table 2, Figure 2b), which equates to ~15% of nests failing at the egg stage in both regions. There was no evidence of any temporal trend in daily nest failure rates at the egg stage in either region (Table 3, Figure 2b). However, in the south-east region, there was significant seasonal variation in daily nest failure rates at the egg stage (Table 3b, Figure 2e), with those where eggs were laid in April experiencing the lowest nest success at egg stage (but note that only 5 nests were available for analysis in this time period, Table 1).

Mean daily nest failure rates at the chick stage were consistently and significantly higher in the south-east (0.019 ± 0.001 SE) than the north-west (0.014 ± 0.001 SE) between 1965 and 2007 (Table 2, Figure 2c), with ~25% of nests failing at the chick stage in the south-east and ~20% in the north-west. In addition, mean daily nest failure rates at the chick stage have increased significantly since 1965 in the south-east but not in the north-west (Table 3, Figure 2c). In 1965 in the south-east, ~23% of nests failed at the chick stage which by 2007 had increased to ~35%. Nest failure rates at the chick stage rates in the south-east showed little seasonal variation but, in the north-west, chick failure rates were significantly higher in mid-season nests than at the start or end of the season (Table 3, Figure 2f). In both regions, seasonal trends in nest failure rates at the chick stage rates did not change over time (Table 3).

Table 2: Results of GLMs of regional (south-east versus north-west Britain) variation in clutch size and nest failure rates for willow warblers recorded in the BTO Nest Record Scheme breeding in Great Britain from 1965 to 2007. The estimate for the intercept is the mean value in the south-east and the estimate for the north-west is the mean difference between the south-east and north-west.

		Estimate	Std. Error	z -value	Pr (>|z|)
Clutch size	Intercept	1.79	0.01	155.92	<0.001
	North-west	-0.002	0.02	-0.09	0.93
Daily egg failure rate	Intercept	-4.47	0.08	-59.19	**<0.001**
	North-west	0.008	0.13	0.06	0.96
Daily chick failure rate	Intercept	-3.95	0.05	-76.61	**<0.001**
	North-west	-0.30	0.10	-2.85	**<0.001**

Table 3: Results of GLMs of annual (year) and seasonal (first egg date) variation in clutch size and nest failure rates for willow warblers recorded in the BTO Nest Record Scheme breeding in the (a) north-west and (b) south-east Britain from 1965 to 2007. Interactions between year and first egg date and non-linear seasonal trends (first egg date^2) were explored in all models but are only included when significant.

(a) North-west		Estimate	Std. Error	z-value	Pr (>|z|)
Clutch size	(Intercept)	2.83	0.21	13.90	**<0.001**
	Year	0.0007	0.001	0.45	0.65
	First egg date	-0.007	0.001	-5.15	**<0.001**
Daily nest failure rate at egg stage	(Intercept)	-4.07	1.44	-2.83	**0.004**
	Year	0.01	0.01	1.36	0.17
	First egg date	-0.005	0.01	-0.46	0.68
Daily nest failure rate at chick stage	(Intercept)	-41.55	12.86	-3.230	**<0.001**
	Year	0.01	0.008	1.268	0.20
	First egg date	0.50	0.18	2.816	**0.004**
	First egg date^2	-0.002	0.0006	-2.734	**0.006**
(b) South-east					
Clutch size	(Intercept)	-0.009	1.211	-0.008	0.99
	Year	-0.0003	0.001	-0.31	0.76
	First egg date	0.03	0.02	1.94	0.05
	First egg date^2	-0.0001	0.00006	-2.42	**0.02**
Daily nest failure rate at egg stage	(Intercept)	10.31	6.02	1.71	0.09
	Year	0.01	0.01	1.55	0.12
	First egg date	-0.21	0.08	-2.59	**0.009**
	First egg date^2	0.0008	0.0003	2.68	**0.006**
Daily nest failure rate at chick stage	(Intercept)	-5.21	0.58	-8.929	**<0.001**
	Year	0.01	0.005	2.52	**0.01**
	First egg date	0.007	0.004	1.80	0.07

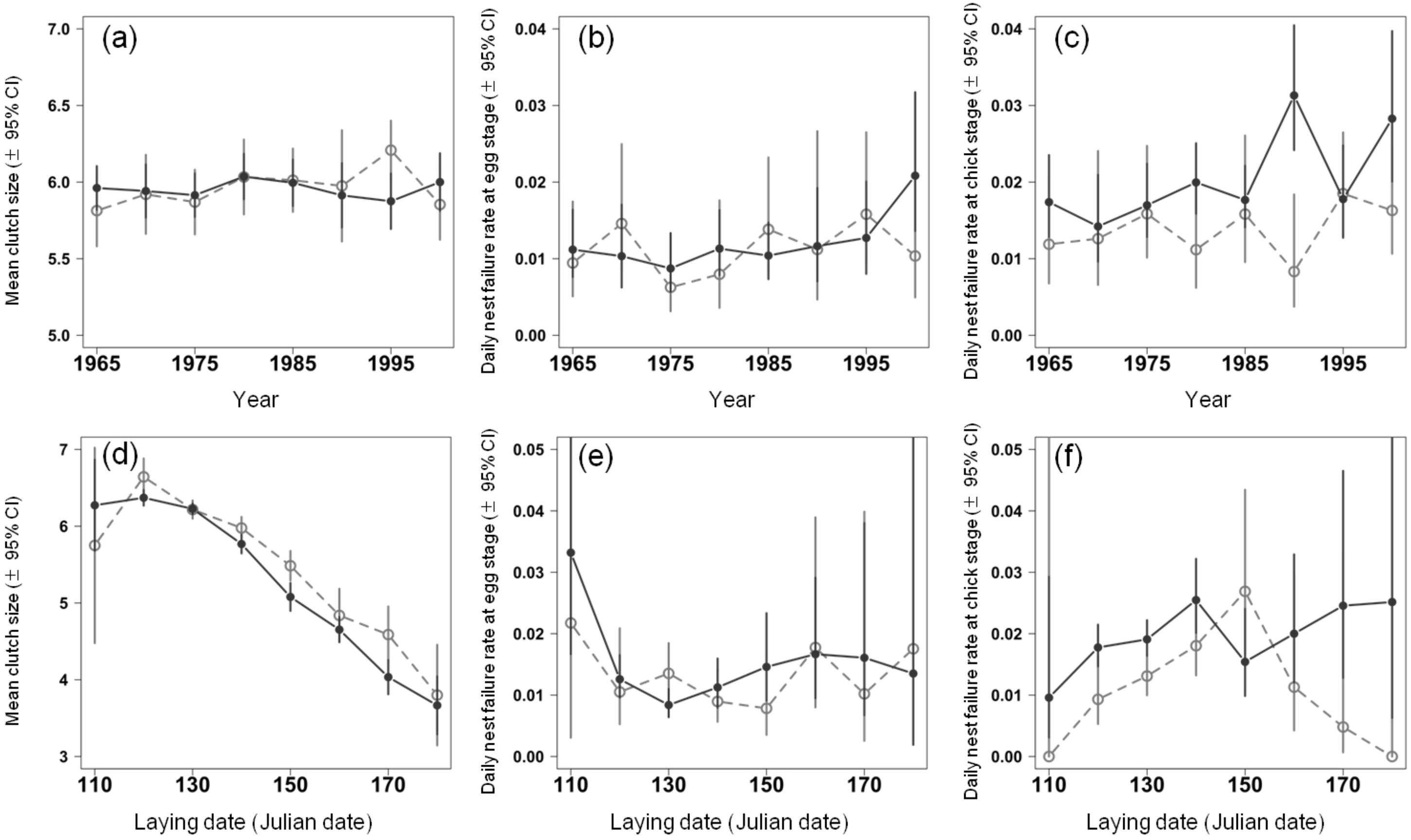

Figure 2: Temporal (top row) and seasonal (bottom row) variation in clutch size (a & d), daily egg failure rate (b & e) and daily chick failure rates (c & f) for willow warblers breeding in south-east (filled points) and north-west (open points) of Britain, recorded in the BTO Nest Record Scheme from 1965-2007.

Variation in hatching and fledgling success in relation to regional weather conditions

In order to explore the effect of variation in weather conditions on the daily failure rates of willow warbler nesting attempts, we calculated the regional mean daily temperature and rainfall that occurred during the incubation and the brooding period of each nesting attempt. We found no significant effect of temperature or rainfall during incubation on daily nest failure rates at egg stage (Table 3) but daily nest failure rates at chick stage increased significantly with regional mean temperature during brooding (Table 3). However, the association between high temperatures and low levels of rainfall means that the highest daily nest failure rates at chick stage (> 0.0225) tended to occur when weather conditions were both hot (mean daily temperature > 15°C) and dry (mean daily rainfall < 4 mm) (Figure 3). On average, ~30% of nests failed at the chick stage under these conditions compared to ~20% failing in all other weather conditions.

Table 3: Results of binomial GLMs of the effect of mean rainfall and temperature in each region during each nesting attempt on daily nest failure rates at egg and chick stages for willow warblers recorded in the BTO Nest Record Scheme from 1965 to 2007. Interactions between mean rainfall and temperature were also explored and are only included when significant.

		Estimate	Std. Error	z-value	Pr (>|z|)
Daily nest failure rate at egg stage	(Intercept)	-5.09	0.41	-12.28	<0.01
	Mean rainfall during incubation	0.09	0.05	1.77	0.077
	Mean temperature during incubation	0.04	0.03	1.17	0.242
Daily nest failure rate at chick stage	(Intercept)	-4.60	0.34	-13.52	<0.001
	Mean rainfall during brooding	-0.06	0.04	-1.50	0.14
	Mean temperature during brooding	0.06	0.02	2.42	**0.02**

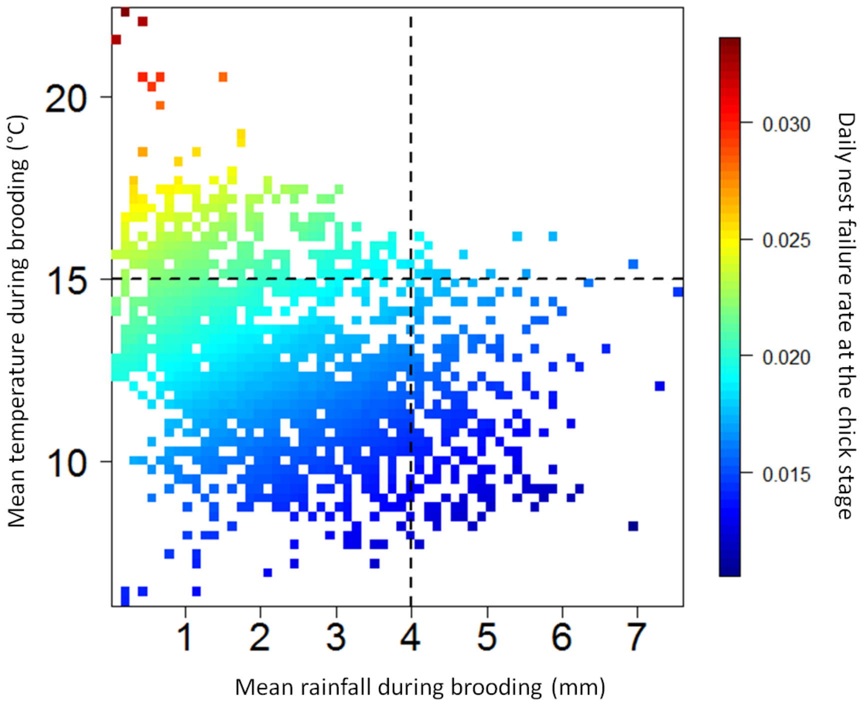

Figure 3: The mean regional rainfall and temperature during chick brooding of willow warbler nests with different daily chick stage failure rates. Dashed lines indicate the conditions (>15 °C temperature and < 4mm rainfall) beyond which chick failure rates are highest (typically exceeding 0.0225).

Association between hot and dry weather conditions and breeding success

As the highest daily chick failure rates occur when regional weather conditions are both dry and hot (Figure 3), the frequency of exposure of nesting attempts to these conditions could potentially influence the regional, temporal and seasonal variation in fledging success. Across Britain, 99% of the nesting attempts in the NRS for which regional mean daily temperatures exceeded 15°C and regional mean daily rainfall was less than 4 mm during the brooding period were in the south-east region (Figure 4a). The proportion of nests with chicks during periods with these hot and dry conditions also varies considerably through the breeding season from, on average, only ~2% of early nests to ~40% of late nests (Figure 4b). The proportion of late-season nests in the south-east region that had chicks during these hot and dry conditions has increased significantly since 1965, from ~24% to ~64% (Table 4, Figure 5), but there was no change in the proportion of early or mid-season nests with chicks during hot and dry conditions (Table 4, Figure 5). However, as late-season nests in this region comprise only ~10%

of the total number of willow warbler nests, there was no significant correlation between the proportion of nests with chicks during hot and dry conditions and the mean daily chick failure rates in the south-east (Spearman rank correlation, r = 0.02, p =0.9). Thus, hot and dry weather conditions tend to be associated with high chick failure rates, but very few nests are active during these weather conditions.

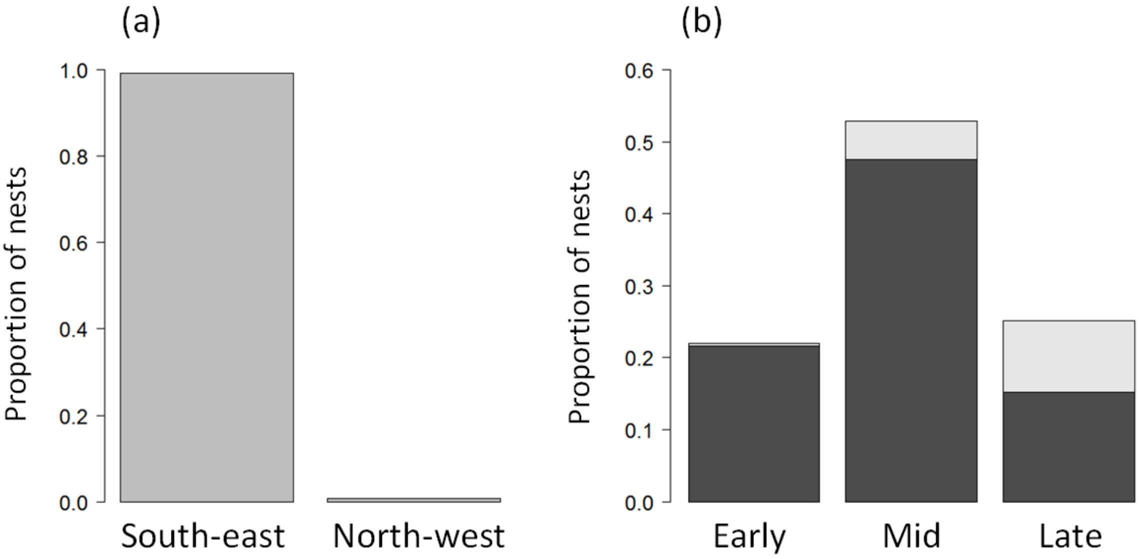

Figure 4: Variation in the proportion of willow warbler nests for which regional mean daily temperatures > 15°C and regional mean daily rainfall < 4 mm during the brooding period in (a) south-east and north-west Britain and (b) early (16 April – 8 May), mid (9 May – 26 May) and late (27 May – 13 July) nests in the south-east region (dark grey = temperatures < 15°C and rainfall > 4 mm, pale grey = temperatures > 15°C and rainfall < 4 mm) between 1965 and 2007.

Table 4: Results of binomial GLM of temporal (year) variation in the frequency of early (16 April – 8 May), mid (9 May – 26 May) and late (27 May – 13 July) season willow warbler nests with chicks during periods of regional mean daily temperatures > 15°C and regional mean daily rainfall < 4 mm, for nests recorded in the BTO Nest Record Scheme in the south-east of England from 1965 to 2007. Seasonal grouping of nests into early (nests laid before the 25% quartile of first egg dates), mid-season (nests laid between the 25th and 75th quartile of first egg dates) and late (nests laid after the 75th quartile of first egg dates) periods in south-east of Britain.

		Estimate	Std. Error	z-value	Pr (>|z|)
Early	(Intercept)	-4.21	0.69	-6.07	<0.001
	Year	0.008	0.03	0.30	0.77
Mid	(Intercept)	-2.27	0.17	-13.23	<0.001
	Year	0.004	0.008	0.48	0.63
Late	(Intercept)	-0.73	0.15	-4.70	<0.01
	Year	0.02	0.007	2.45	**0.02**

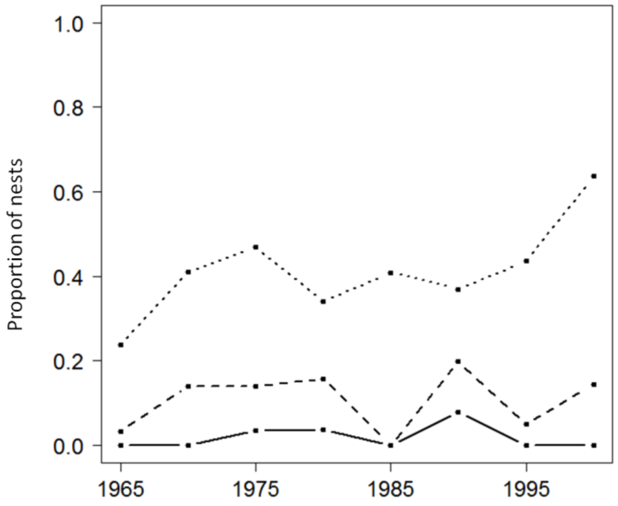

Figure 5: Temporal variation in the proportion of early (16 April – 8 May) (solid line),, mid (9 May – 26 May) (dashed line) and late (27 May – 13 July) (dotted line) season willow warbler nests in the south-east of Britain for which regional mean daily temperatures > 15°C and mean daily rainfall < 4 mm during the brooding period.

Discussion

Since the mid 1990s, willow warblers breeding in Britain have shown regional variation in both abundance and productivity, with declines in the south-east and stability in the north-west (Morrison *et al.* 2010, chapter 3). During this time, willow warblers in both regions have continued to lay and hatch the same number of eggs, however, the probability of these broods successfully fledging has declined significantly in the south-east. We found that lower fledging success in the south-east was associated with hotter and drier weather during brooding, which may indirectly affect food availability and/or vulnerability to predation. However, even though climatic conditions vary over a similar spatial scale and are changing in a similarly region-specific manner, very few nesting attempts took place at the end of the breeding season in the south-east. Therefore while it is possible that increases in the proportion of nests active during hot and dry conditions are leading to increasing fledgling mortality, this is only in a small proportion of nests. Consequently the overall contribution of these nesting attempts to the temporal trend in fledgling mortality is likely to be small.

Typical of many single-brooded species breeding at temperate latitudes, willow warbler clutch sizes decline across the breeding season (Lack 1947, Cramp 1955, Tianinen 1982, Crick *et al.* 1993, Evans *et al.* 2009). In the north-west, the effect of this decline on seasonal variation in fledglings per breeding attempt (chapter 3) may be slightly offset by the increase in fledging success towards the end of the breeding season, however these estimates are based on only a small number of nesting attempts and therefore may not be representative of the wider population (Table 2b). Seasonal declines in clutch size are typically explained as a consequence of trade-offs between clutch size and other components of fitness (Ludvig *et al.* 1995). In pied flycatchers, *Ficedula hypoleuca*, clutch sizes are larger but decline more rapidly within the breeding season in years with earlier peaks in caterpillar abundance (Both *et al.* 2005). This was a result of later breeding birds laying smaller clutch sizes and is believed to be an adaptive response to the timing of food availability. Seasonal variation in clutch sizes may also be related to female body condition, as later breeding birds are often in poorer condition (Gladbach *et al.* 2010), while late-season clutch sizes may also be subject to trade-offs with the time required to moult or prepare for migration (Hussel 1972).

Despite strong seasonal declines, there was very little annual variation in clutch size or nest failure at egg stage in British willow warblers. This suggests that changes in female body condition and conditions during incubation are not driving the declines in fledglings per breeding attempt in the south-east. We also found no evidence of a relationship between weather during incubation and nest failure at the egg stage. It is possible that the lower hatching success at the start of the breeding season is a consequence of high spring rainfall washing out early nesting attempts. However, due to the low probability of finding nests which fail early, these nests are likely to be under-represented in the NRS. While the weather data were selected to capture broad-scale climatic differences between the north-west and south-east of Britain, it is possible that regional-scale temperature and rainfall data may also not be of sufficient resolution to identify their direct associations with nest failures. Ideally collation of weather data at the county scale may clarify these relationships. However, this was beyond the scope of the current study.

The higher chick mortality in times of hot and dry weather may be due to lower food availability as these conditions can influence invertebrate abundance (Peach *et al.* 2004, Pearce-Higgins *et al.* 2010). In the absence of change in both clutch size and hatching success this may have important consequences for chick mortality, as parents will still have the same number of chicks to provide for and consequently starvation rates may increase. Declines in the availability of resources during the breeding season may also impact adult survival and, consequently, the effort individuals put into breeding attempts may be traded off with survival costs. The higher rates of chick failure in the south-east could therefore be the result of regional variation in the availability of resources during the breeding season and differences in the effort adults allocate to reproduction. In the south-east, the only temporal increase in the frequency of nests active during hot and dry conditions was at the end of the breeding season, however, fledging mortality has increased equally across the entire season. Therefore, while increased fledging mortality at the end of the breeding season may be related to the increasing frequency of hot and dry weather, as the frequency of late season nests is so low, they are likely to only be a small component of the overall trend.

Declines in breeding season resources have also been linked to reductions in the ability of adults to compensate for the effect of predation on provisioning rates and consequently chick growth and condition (Dunn *et al.* 2010). Typical nest predators in Britain include carrion crow *Corvus corone*, black-billed magpie *Pica pica*, Eurasian jay *Garrulus glandarius*, great spotted woodpecker *Dendrocopos major* and grey squirrel *Sciurus carolinensis* (Newson *et al.* 2010). However, currently there is no strong evidence to suggest that population changes in these species are affecting the abundance of willow warblers (Thomson *et al.* 1998, Newson *et al.* 2010). In addition to these species, the impact of increases in the abundance and range of roe (*Capreolus capreolus*) and muntjac (*Muntiacus reevesi*) deer in the southeast of England

(Ward 2005, Corbet & Harris 2008) have been linked to the loss of woodland understory and declines of breeding songbirds (Gill & Fuller 2007). While this is mainly thought to operate through nesting habitat loss and fragmentation it is also possible that deer are opportunistically eating eggs and chicks or trampling nests which could be contributing to the recent losses at chick stage in this region.

Conclusions

The declines in willow warbler productivity in the south-east are largely a consequence of declines in chick fledging success, which may be driven by changes in the seasonality and availability of resources and/or increasing predation rates. We found weak evidence of a relationship between the rate of chick failure and temperature during brooding, and the highest chick failure rates are associated with periods of hot and dry weather. However there was no relationship between hot and dry weather conditions and temporal changes in fledging mortality, as increases in the frequency of these conditions occurred mainly at the end of the breeding season where only a low proportion of nesting attempts take place. Therefore while declines in fledgling mortality may be playing an important role in the regionally variable population trends, the processes driving these changes require further investigation.

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Chapter five

Variation in feather stable isotope ratios of breeding willow warblers, *Phylloscopus trochilus*, across the UK.

Abstract

1. While a considerable amount is known about the distributions of Afro-Palaearctic migrants within Europe, our knowledge of the locations and timings of their movements beyond the breeding season far less comprehensive. Exploration of the non-breeding season movements of Afro-Palaearctic migratory species can greatly improve our understanding of the processes influencing their population trajectories within breeding grounds and consequently help to design appropriate conservation actions.

2. In recent years, the development of techniques to study the non-breeding season movements of migratory species remotely have become important tools in investigating the distribution and resource use of migratory populations beyond their breeding grounds. As stable isotope ratios vary naturally across environmental gradients, analysis of feathers collected on breeding grounds but grown during the non-breeding can provide an indication of how conditions experienced during the non-breeding season vary across breeding populations.

3. Since the mid 1990s, there has been strong regional variation in the rates of willow warbler population change, *Phylloscopus trochilus,* breeding within Britain. As willow warblers are Afro-Palaearctic migrants, it is possible that these trends are influenced by processes operating on passage or during winter, if birds from different regions migrate at different times or through different locations. Here we look for evidence of variation in $\delta^{15}N$ and $\delta^{13}C$ values of winter grown feathers from willow warblers breeding in at three populations within this gradient of population change (Southern England, West Wales and North Scotland), which may indicate differences in the location and/or timing of moult within Africa.

4. Willow warblers from N Scotland had significantly higher $\delta^{15}N$ and $\delta^{13}C$ values than those from S England. However there was no difference between $\delta^{15}N$ and $\delta^{13}C$ values of male and female willow warblers. On average, $\delta^{15}N$ and $\delta^{13}C$ values were significantly higher in N Scotland than in E England, and $\delta^{15}N$ but not $\delta^{13}C$ values were significantly greater in willow warblers caught later in the breeding season.

5. The variation in isotope ratios suggests that during the pre-migratory moult period in Africa willow warblers from different parts of Britain may vary in their distribution, their timing of moult and/or their use of resources during moult. Identifying the causes of the variation in

isotope ratios is likely to require ground-truthing of isotope ratio distribution within the winter and passage grounds in Africa.

Introduction

During the course of their lives, migratory species are exposed to conditions across locations that can span continents. Consequently local-scale variation in demography may be influenced by individual differences in the both the location and timing of seasonal movements. Variation in rates of population change in migratory bird species within the breeding range (e.g. chapter 1, Both *et al.* 2006) can therefore be influenced by breeding and/or non-breeding season processes, if individuals from specific areas of the breeding range also use specific locations or resources within the non-breeding range (Marra *et al.* 1998, Bearhop *et al.* 2004, Hobson 2005, Norris & Marra 2007, Gunnarsson *et al.* 2005).

Currently the majority of our knowledge of the distribution and abundance of European long-distance migrants comes from large-scale monitoring programs, carried out during the breeding season (Sanderson *et al.* 2006, Gregory *et al.* 2005). In general, the wintering ranges of European migrants have been identified from reports of ringed birds (recoveries) and a small number of direct observations. However, recovery rates for most migrant passerines are generally extremely low and often focused around areas of human occupation or sites where specific studies of bird populations have taken place (Wernham *et al.* 2002). Consequently our understanding of the full extent of their passage and wintering areas is often incomplete and may be subject to sampling biases (Korner-Nievergelt *et al.* 2010). However, the recent technological developments have greatly advanced understanding of the distribution and habitat use of migratory birds in less accessible parts of the world. Technologies such as geolocators and satellite tags have provided records of movements of individuals throughout migratory ranges (Rodríguez *et al.* 2009, Egevang *et al.* 2010, Tøttrup *et al*. 2011, Vardanis *et al.* 2011), while stable isotopes analysis of body tissue can provide information on within- and between-species variation in distribution and habitat use (Marra *et al.* 1998, Chamberlain *et al.* 2000, Norris *et al.* 2004, Bensch *et al.* 2006).

Stable isotope ratios vary naturally across terrestrial and marine landscapes, between habitats and among trophic levels, and can be used both as markers of large-scale variation in geographic location and environmental conditions (e.g. latitude, precipitation, distance from sea) or smaller-scale variation in local environmental conditions (e.g. habitat, soil type). The isotope ratios in consumers reflect those of their prey; consequently the tissues of animals (e.g. blood, egg shell, feathers) carry a record of what they have eaten and local environmental conditions during growth (Pain *et al.* 2004). For metabolically inert tissues such as feathers, stable isotope ratios can provide a record of the environment at the time of feather growth, which may be in a preceding season or location. In migratory species, variation in stable isotopes ratios have been used to provide an indication of the influence of winter habitat on body condition during migration, timing of migration and breeding success (Marra *et al.* 1998, Norris et al 2004, Bearhop *et al.* 2004, Gunnarsson *et al.* 2005).

Since the 1990s, the population trends of one of Europe's most abundant passerine long-distance migrant species, the willow warbler, *Phylloscopus trochilus,* have varied substantially across Britain. Population trends follow a gradient from sharp declines in the south and east of England to shallow declines and/or slight increases in parts of north and west England and Scotland (Morrison *et al.* 2010). Over a similar time-scale, productivity of willow warblers has declined in the south-east of Britain but not the north-west (chapter 2), and survival rates of adult female willow warblers has been significantly lower in the south-east than the north-west (chapter 6). Although the conditions experienced in different parts of Britain during the breeding season are likely to contribute to these differences in demography and population trends, conditions experienced during the non-breeding season may also contribute, if individuals breeding in different parts of Britain also use different locations or resources in the non-breeding season. For example, as the timing of willow warbler arrival on the breeding grounds is typically earlier in the south of Britain than the north, and males typically arrive earlier than females, the moult and migration schedules of males and females from different parts of Britain may differ. Timing of migration and moult may influence the environmental conditions and resource availability experienced by individuals from different parts of the range, which could influence their subsequent fitness.

Willow warblers start arriving in Africa during late August and September (Cramp 1992). While the wintering range of European breeding willow warblers covers the majority of sub-Saharan Africa (Moreau 1972), willow warblers from north-west Europe are thought to inhabit the Sahel-Sudan zone, just south of the Sahara desert, for 1–2 months before travelling further south in late October or November (Salewski *et al.* 2002), to the Guinea and derived savannahs (Newton 2008) in countries such as Ivory Coast and Ghana (Norman & Norman 2002). These movements are greatly influenced by the seasonal progression of the tropical rain belt, the inter-tropical convergence zone (ITCZ) (Newton 2008), as they track the band of productivity driven by the rains (Salewski *et al.* 2002). Willow warblers are unusual as they complete a full body moult twice a year, on both breeding and wintering grounds (Underhill *et al.* 1992, Weber *et al.* 2010). On their African wintering grounds, willow warblers in active moult have been found from December to March, with the majority moulting in January and February (Underhill *et al.* 1992, Salewski *et al.* 2004).

The annual movements of the ITCZ creates latitudinal habitat bands, running from the northerly grasslands and open savannahs just south of the Sahara, to the woody savannas and forests of the southern coast. Higher δ^{15}N and δ^{13}C isotope ratios in plant and animal tissues are generally associated with drier areas of Africa (Chamberlain *et al.* 2000), with higher δ^{13}C values suggesting a higher abundance of C4 plants (Smith & Epstein 1971, Koch *et al*. 1995, Still *et al.* 2003) and higher δ^{15}N values suggesting lower amounts of rainfall (Heaton 1987, Johnson *et al*. 1997). However, as rainfall within the wintering areas generally declines from December to March, higher δ^{15}N and δ^{13}C values may also reflect drier conditions experienced by later moulting individuals. Finally, δ^{15}N and to a lesser extent δ^{13}C values can also vary between trophic levels (Hobson & Clark 1992), and thus with the trophic composition of the diet (e.g. the relative amounts of fruit or predatory or non-predatory invertebrates) (Gannes *et al.* 1998, Tibbets *et al.* 2008, Diggs *et al.* 2011). Variation in the stable isotope ratios of willow warbler feathers grown during the non-breeding season may therefore reflect variation in the trophic composition of the diet during moult, location during moult and/or timing of moult.

In this study we use stable isotope analysis of δ^{15}N and δ^{13}C values in willow warbler feathers grown in Africa, and collected on breeding grounds within Britain to explore whether the isotope ratios vary between 1. regions of Britain with differing population trends, 2. males and females (which typically arrive in Britain at different times and may thus differ in timing of moult and migration) and 3. individuals captured at different times during the breeding season (which may reflect differences in timing of migration and associated moult schedules).

Methods

Feather sampling

Adult willow warblers undergo a complete body feather moult twice a year; a post-nuptial moult takes place on the breeding grounds and a pre-nuptial moult takes place in spring, prior to arrival on the breeding grounds (Underhill *et al.* 1992). The feathers of breeding willow warblers are therefore grown either on African wintering grounds or during their northward migration. We collected feathers from three regions across Britain (Figure 1); Northern Scotland, where populations are stable and slightly increasing, West Wales, where there are slight population declines, and East England where populations have declined rapidly over the last three decades (Morrison *et al.* 2010). Within each region, willow warbler feather samples were collected (under license) from established ringing sites run by British Trust for Ornithology (BTO) volunteers as part of the Constant Effort Sites (CES) scheme (Table 1), between May and August 2008 and 2009. Approximately two-thirds of the 3rd secondary feather was collected from adult willow warblers that had not yet begun the post-nuptial moult (and hence these feathers had been grown prior to arrival on the breeding grounds). Where possible, willow warbler sex was determined from the presence of a brood patch (female**)** or a cloacal protuberance (male, Svensson 1992). Two individuals were sampled in both years; one from West Wales and one from East England.

Figure 1: The locations of CES ringing sites at which willow warbler feathers were collected from May to August in 2008 (dark grey), 2009 (light grey) and in both 2008 and 2009 (black).

Table 1: Numbers of individual willow warblers from which feathers were collected in each region (see Figure 1) in 2008 and 2009.

Region	**Year**	**# sites**	**# females**	**# males**	***n***
North Scotland	08	5	17	20	37
	09	4	5	13	27
West Wales	08	1	2	1	3
	09	3	3	16	19
East England	08	5	5	16	21
	09	2	5	18	23

Stable isotope analysis

Analysis of feathers was carried out in 2009 at the NERC Life Sciences Mass Spectrometry Facility at SUERC (n = 21 feathers) and in 2010 at the University of East Anglia (n = 98 feathers), an analogous protocol was carried out in both labs. Feather samples were washed with 2:1 chloroform/methanol solvent to remove surface oils and left to dry for 24 hours. Feathers were then clipped into small sections of ~ 2 mm length. This made sure that the sample contained an integrated isotopic signal of diet during the whole period of growth. The carbon and nitrogen isotopic composition of all feather samples was measured.

For nitrogen and carbon isotopic composition of feather material, 0.5 mg of sample was weighed into tin capsules, which were crimped and loaded onto the carousel of a combustion Costech elemental analyser interfaced with a Thermo Scientific Delta XP continuous flow mass spectrometer and Conflo III interface. Both isotope ratios were measured consecutively on each feather sample. All samples were measured in duplicate together with an in-house reference (casein) and standard (gelatine and alanine) materials. At SUERC the precision of the carbon and nitrogen isotopic composition was 0.03 ‰ and 0.15 ‰ respectively, based on replicate analyses of the internal laboratory standard (n=25). At the University of East Anglia the precision of the carbon and nitrogen isotopic composition was 0.13 ‰ and 0.16 ‰ respectively, based on replicate analyses of the internal laboratory standard (n=6).

Stable isotope compositions are reported as deviations from an internationally recognised standard material and are expressed in per mil (‰) units using the δ notation, defined as:

$$\delta_{sample} = [(R_{sample}/R_{standard})-1] \times 1000$$

Where δ_{sample} is the relative isotopic ratio of the sample with respect to a standard, and R_{sample} and $R_{standard}$ are the ratios of the abundance of the heavy to the light isotopes in the sample and standard respectively. The primary international standards to which all isotopic values are reported in this thesis are: V-PDB for carbon and AIR for nitrogen.

Statistical analysis

To examine the variation in $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of feathers of male and female willow warbler breeding in different regions of Britain, we performed an Analysis of Variance (ANOVA) with Tukey HSD post-hoc tests in R (2.12.0, R core development team, 2011). Models with $\delta^{13}C$ and $\delta^{15}N$ as the response variable were constructed separately and, in both cases, included region (N Scotland, W Wales and E England), sex (male or female) and the interaction term as explanatory variables. We also carried out an Analysis of Variance (ANOVA) to test the variation in the $\delta^{13}C$ and $\delta^{15}N$ values of feathers collected in the four months of the breeding season. Separate models were constructed with $\delta^{13}C$ and $\delta^{15}N$ as the response variable and month as the explanatory variable. Pearson correlations were used to explore the association between $\delta^{13}C$ and $\delta^{15}N$ values within individual feathers. This was carried out separately across; all feathers, within each region, within each sex and within each month.

Results

Variation in stable isotope ratios of feathers of breeding willow warblers

Willow warblers breeding in different regions of Britain showed significant variation in both $\delta^{15}N$ and $\delta^{13}C$ feather isotope ratios (Figure 2 & 3, Table 2). Feathers collected in E England had significantly lower $\delta^{15}N$ values than both W Wales (Tukey HSD test $p<0.001$) and N Scotland (Tukey HSD test $p=0.0175$), and significantly lower $\delta^{13}C$ values than N Scotland (Tukey HSD test $p=0.005$). We found no significant difference between the $\delta^{15}N$ and $\delta^{13}C$ values of male and female willow warblers and no significant interaction between region and sex, suggesting that the regional differences in isotope signal were consistent between the sexes (Table 2).

There was considerable overlap in the δ^{13}C and δ^{15}N values of feathers collected in each region (Figure 3). In all three regions, feathers had δ^{15}N values between 6‰ and 12‰, but both N Scotland and E England had two feathers with δ^{15}N values less than 6‰ while in N Scotland had five feathers with δ^{15}N values greater than 12‰. Feathers with δ^{13}C ratios between -18 and -26 were present in all regions but ratios above -18 were only found in N Scotland (Figure 3).

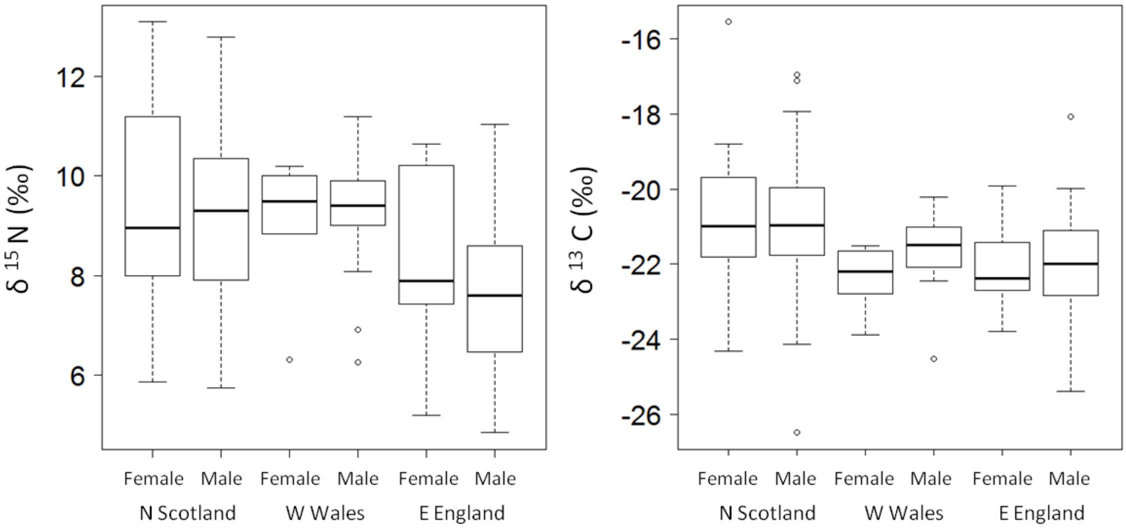

Figure 2: Variation in δ^{15} N and δ^{13} C values of feathers of male and female willow warblers breeding in three regions of Britain in 2008 and 2009 (combined). Horizontal bars indicate medians, boxes indiacte interquartile range, whiskers indicate minimum and maximum values and circles indiate outliers (obervations 1.5 times higher of lower than 1st and 3rd quartile respectively).

Table 2: Analysis of Variance of δ^{13}C and δ^{15}N values of feathers collected from male and female willow warblers breeding within three regions in Britain (see Figure 1).

		df	F value	Pr(>F)
δ^{13}C	region	2	5.65	**0.005**
	sex	1	0.20	0.66
	region*sex	2	0.38	0.69
	Error	115		
δ^{15}N	region	2	8.65	**0.0003**
	sex	1	0.46	0.50
	region*sex	2	0.36	0.70
	Error	115		

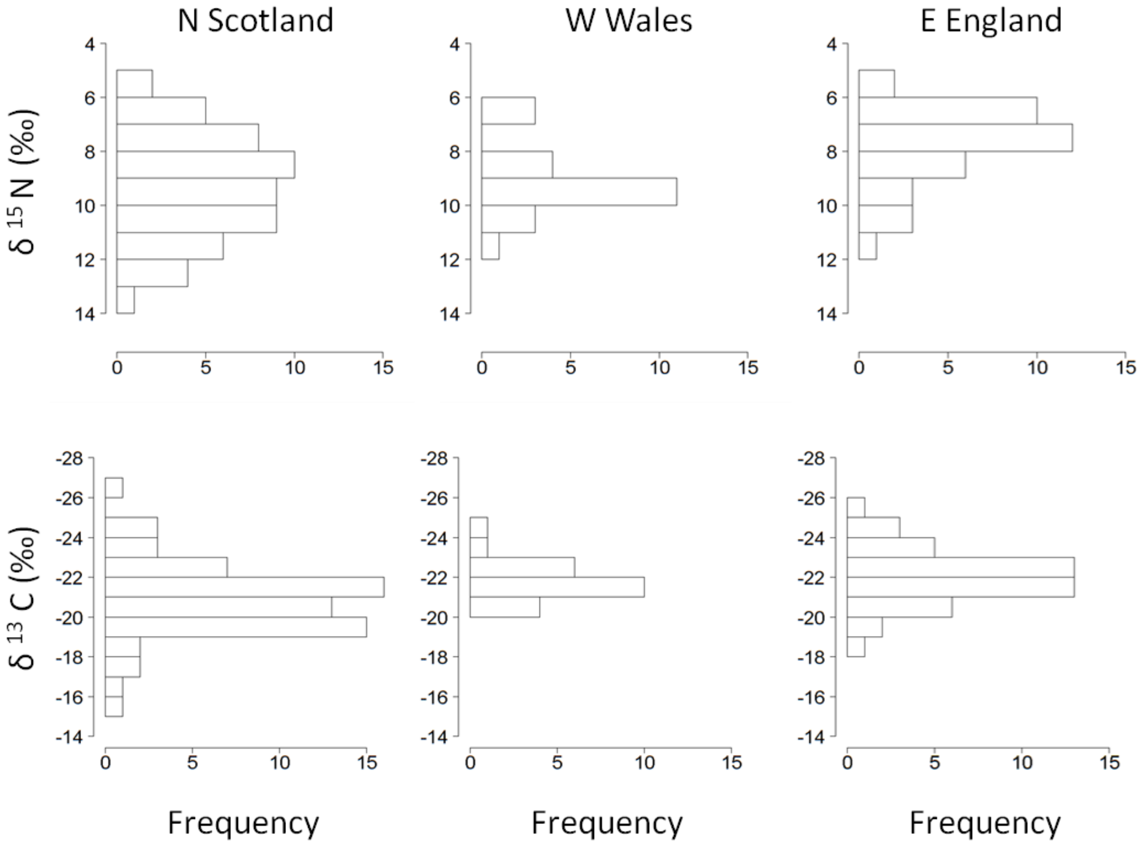

Figure 3: Frequency distributions of δ^{15}N and δ^{13}C values of feathers of willow warblers breeding in three regions of Britain in 2008 and 2009.

Variation in stable isotope ratios of willow warblers captured in different months

The dates on which breeding willow warblers were captured and feathers were sampled ranged from April to July. There was significant variation in the δ^{15}N values of feathers over the four months during which the willow warblers were caught ($F_{1,128}$ = 6.54, p= 0.017, Figure 4), with the feathers of later caught birds containing higher δ^{15}N values. However, δ^{13}C values did not vary significantly between months ($F_{1,128}$ = 3.43, p = 0.06, Figure 4). The seasonal variation in δ^{15}N is primarily a consequence of regional variation in the date of capture, as the proportion of willow warblers caught in E England declined from April to July while the proportion caught in N Scotland increased (Figure 5). The majority of feathers sampled in April and May were from E England, while virtually all of the feathers sampled in July were from N Scotland (Figure 5).

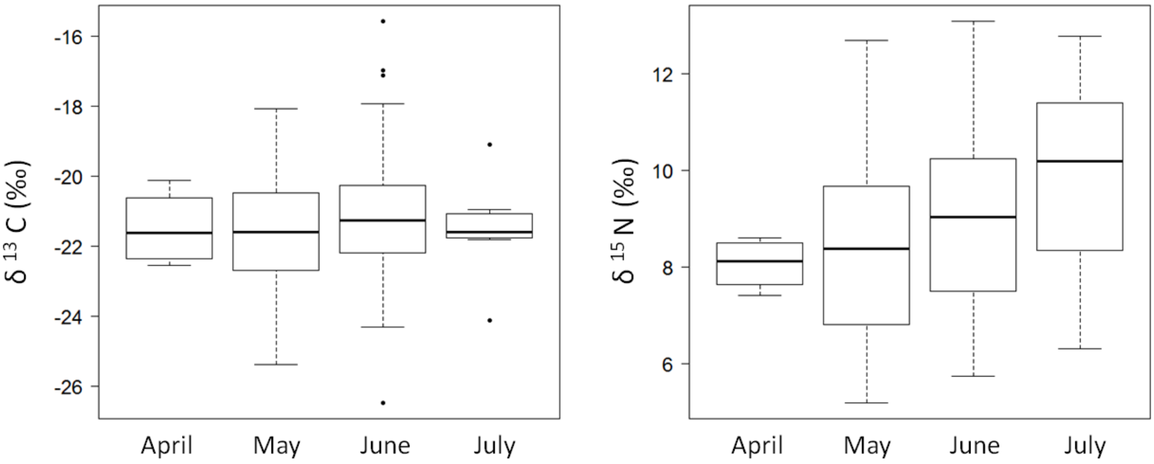

Figure 4: Variation in δ^{13}C and δ^{15}N values of feathers of breeding willow warblers captured in different months across the UK in 2008 and 2009. Horizontal bars indicate medians, boxes indicate interquartile range, whiskers indicate minimum and maximum values and circles indicate outliers (values 1.5 times higher or lower than 1st and 3rd quartile, respectively).

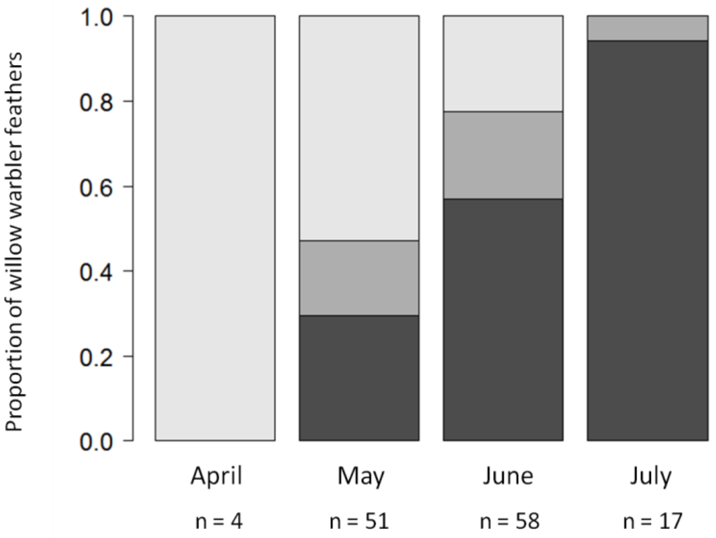

Figure 5 – Monthly variation in the proportion of willow warbler feather samples collected from E England (light grey), W Wales (mid grey) and N Scotland (dark grey).

Association between δ^{13}C and δ^{15}N of individual willow warbler feathers

Within individual feathers, high values of δ^{13}C were weakly associated with high values of δ^{15}N (Figure 6, r = 0.195, p = 0.026). However, within each region, sex and month the only significant correlation between the δ^{13}C and δ^{15}N values of individual feathers was in male willow warblers (Figure 6). Consequently the overall association is likely to be driven by the five feathers which had low values of δ^{13}C and δ^{15}N, collected from male willow warblers, four were caught in E England in May and the remaining one was caught in N Scotland in June (Figure6).

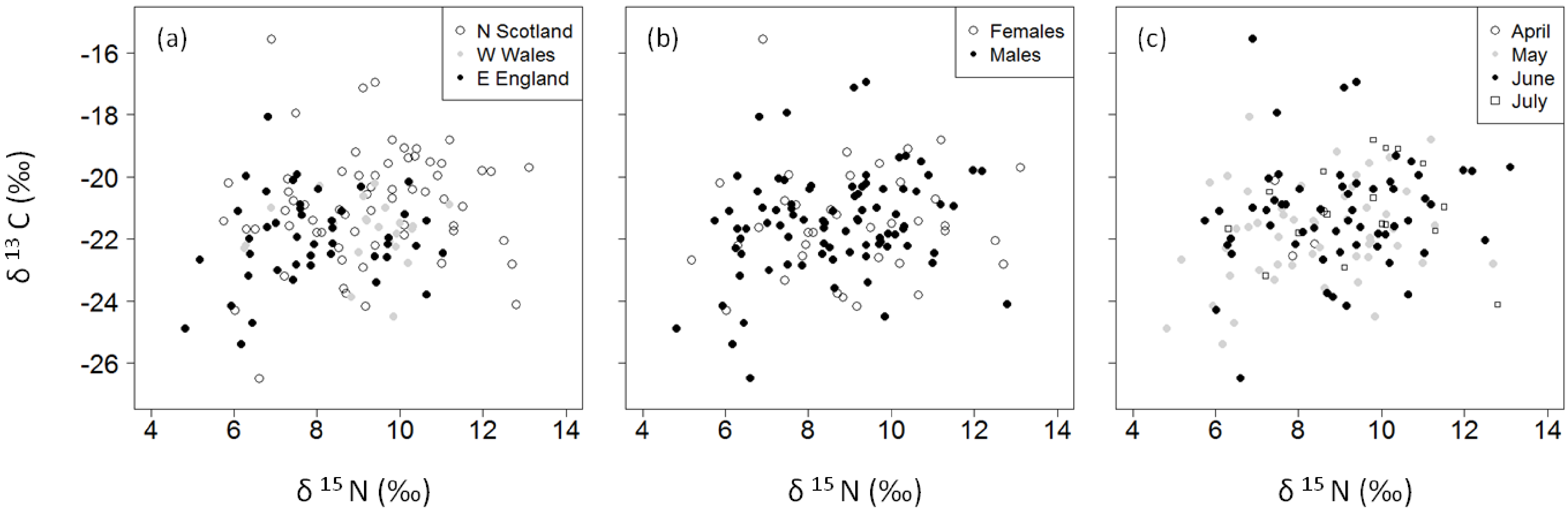

Figure 6 – Associations between δ^{13}C and δ^{15}N values in feathers of individual willow warblers collected across Great Britain (grown in Africa) during 2008 and 2009 in relation to (a) breeding areas (N Scotland: r = 0.12, p = 0.35, W Wales: r = -0.02, p = 0.93, E England: r = 0.15, p = 0.34), (b) sex (Females: r = 0.06, p = 0.72, Males: r = 0.23, p = 0.03) and (c) month of capture (April: r = -0.38, p = 0.62, May: r = 0.24, p = 0.09, June: r = 0.14, p = 0.30, July: r = 0.02, p = 0.94).

Discussion

The $\delta^{15}N$ and $\delta^{13}C$ values of willow warbler feathers collected in different parts of Britain varied significantly (Figure 2), with the highest $\delta^{15}N$ values in feathers collected in N Scotland and W Wales, while $\delta^{13}C$ was higher in N Scotland than both W Wales and E England. However, there was also considerable overlap in the $\delta^{15}N$ and $\delta^{13}C$ values between the regions (Figure 3). The regional differences in $\delta^{15}N$ were both a consequence of a high proportion of willow warblers with low $\delta^{15}N$ values in the E England relative to both W Wales and N Scotland and several willow warblers with particularly high $\delta^{15}N$ in N Scotland. The regional differences in $\delta^{13}C$ are driven by a higher proportion of feathers in N Scotland with high $\delta^{13}C$ values. Although birds caught later in the breeding season had higher $\delta^{15}N$ (but not $\delta^{13}C$) values, this is primarily a consequence of regional variation in date of capture, as E England birds were primarily caught in April and May while N Scotland birds were primarily caught in June and July. Regional variation in $\delta^{15}N$ may therefore potentially reflect differences in timing of moult and/or migration of willow warblers breeding in different areas of Britain.

Despite the relatively fragmented understanding of the geographic distribution of isotope ratios across Africa, previous studies have identified differences in the wintering ranges of willow warblers from different parts of Europe (e.g. Chamberlain *et al.* 2000, Bensch *et al*. 2006). The range of isotope values of feathers collected from two different races of willow warblers breeding in Sweden was similar to that of the feathers collected in Britain in this study, and both $\delta^{15}N$ and $\delta^{13}C$ values in Sweden were higher in the northern breeding *P. t. acredula* than in the more southerly *P. t. trochilus* (Chamberlain *et al.* 2000). The willow warblers breeding in Britain are all of the *P. t. trochilus* subspecies but also show higher $\delta^{15}N$ and $\delta^{13}C$ values in more northerly breeding populations, which also suggest differences in the location and timing of moult and/or migration of willow warblers breeding in different areas of Britain.

Potential causes of variation in feather isotope values

1 – Diet

Regional variation in $\delta^{15}N$ and $\delta^{13}C$ in the feathers of willow warblers may be the result of differences in the trophic composition of the diet. Willow warblers typically eat insects and spiders, but take berries in the autumn when they are widely available on breeding grounds (Cramp 1992). It is therefore possible that willow warblers also take advantage of seasonal variation in fruit availability in during the non-breeding season. Higher proportions of fruit in willow warbler diet would result in lower δ^{15}N and δ^{13}C signals, thus the more southerly breeding birds may potentially consume more resources from lower trophic level. Fruit is a key component in the pre-migratory diets of *Sylvia* warblers (Stoate & Moreby 1995) and it is possible that, in order to gain condition quickly and depart breeding grounds sooner, earlier arriving birds will use it to supplement their diets. In particularly this may be influencing the δ^{15}N and δ^{13}C values of the six birds in which have low values of both δ^{15}N and δ^{13}C, as four are early arriving males (captured in April) in E England. It is also possible that spatial and temporal differences in the abundance of different prey and/or fruiting of trees may result in differences in the diet of willow warblers.

2 - Geographic location during pre-nuptial moult

Differences in the isotopic values of willow warbler feathers may result from broad scale differences their location during the prenuptial moulting period. The lower values of δ^{15}N and δ^{13}C in feathers of willow warblers breeding in E England may mean that they may have moulted in wetter areas with a lower abundance of C4 plants. In West Africa, this suggests that birds in E England may moult at a more southerly latitude than birds from N Scotland. However, during the non-breeding season, willow warblers show considerable itinerancy in their movements (Salewski & Jones 2006, Newton 2008), inhabiting both wooded savannas and dry evergreen forests (Norman & Norman 2002). In the Ivory coast, where the majority of British ringing recoveries have been located (Norman & Norman 2002), willow warblers were found most frequently in scattered patches of isolated forest but also in areas of savanna, open woodland and riparian forest (Salewski *et al.* 2002). It is therefore also possible that the variation in δ^{15}N and δ^{13}C values of feathers is influenced by small scale differences in the proportion of C4/C3 plants in the habitats used during moult.

3 - Timing of moult relative to spring migration

Willow warblers complete a full body moult towards the end of the non-breeding season (Underhill *et al.* 1992). In the Ivory Coast, willow warblers have been found in active moult from December to March, taking an average of 43 (± 5 SE) days to complete secondary moult (Salewski *et al.* 2002). Individual variation in feather isotopes could therefore be the consequence of differences in timing of moult during the non-breeding season, with higher δ^{15}N and δ^{13}C signals potentially reflecting the drier conditions experienced by later moulting individuals. As willow warblers tend to arrive nearly two weeks earlier on breeding grounds in the south of Britain than in the north (BirdTrack, 2011), this could also mean that they complete moult and leave wintering grounds sooner. Therefore the lower mean values of $\delta^{15}N$ and $\delta^{13}C$ in southern breeding birds could be a consequence of a higher proportion of earlier moulting individuals breeding in the south of the Britain. However, as willow warblers have also been found in moult during migration (Bensch *et al.* 2006, see also Gatter 1997), variation in isotope signal could also reflect variation in moult latitude, if northern birds moult at higher latitudes than southerly birds.

Identifying the specific causes of the variation in the isotope ratios of willow warblers breeding in different parts of the UK will require detailed knowledge of both latitudinal and seasonal variation in willow warbler diet and improved ground-truthing of stable isotope signals within West Africa. Sampling of birds during migration through southern Europe and as they enter the breeding locations across Europe could also increase understanding of the influence of timing of migration on the feather isotope signatures.

Implications for population change

Differences in the non-breeding locations of British willow warblers could potentially influence the level of exposure of individuals to changing environmental conditions. If the overlap between breeding and wintering populations is high, then this may result in locally variable demographic rates across breeding grounds. However, if breeding populations winter in geographically distinct areas or migrate at different times, this may result in large-scale variation in population demography across the breeding grounds. In British willow warblers, individuals breeding in the North of Scotland where populations are increasing had slightly different isotope signals than those breeding in the East of England where populations are declining rapidly. If these different signals reflect different non-breeding locations, the conditions experienced during non-breeding season could potentially influence the population trends observed in the breeding season. Environmental conditions on non-breeding grounds can influence rates of mortality and may also influence subsequent breeding success during through carry-over effects. For example, conditions in the non-breeding season can influence body condition, timing of arrival and other factors that influence individual productivity (Marra *et al.* 1998, Bearhop *et al.* 2004, Gunnarsson *et al.* 2005, Norris & Marra *et al.* 2007). In such cases the impact of non-breeding season conditions and carry-over effects on population trends may also be mitigated or exacerbated by conditions in the breeding season their effect. In the south of Britain, willow warbler productivity is lower and timing of breeding has advanced less than in than northerly populations (chapter 3), and it is possible that earlier arrival on breeding grounds is being constrained by their ability to advance their timing of moult on non-breeding grounds. An understanding of the processes influencing the flexibility of species to adjust their timing of moult may therefore be a key step in understanding the factors limiting adaptation to environmental change.

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Chapter six

Sex-biased survival in a declining long-distance migratory bird: implications for population trends.

Abstract

1. Within migratory populations, differences in the impact of environmental change on demographic rates can arise though differences in the quality of breeding and/or wintering season conditions. In recent years, declines in the abundance of many Afro-Palaearctic migratory bird species have been linked to deterioration of conditions in the Sahel region of Africa, which have been related to declines in adult survival. However, despite conditions in the Sahel beginning to improve, declines in migrant populations have continued, highlighting the need for a greater understanding of changes patterns of survival rates in migratory species.

2. Sex-biased mortality may occur in migratory species as males typically arrival on breeding grounds earlier than females and may inhabit different areas during the non-breeding season. Consequently exposure to environmental change during the non-breeding season may vary between the sexes. In addition, differences in behaviour during the breeding season, such as time spent incubating and duration of foraging trips, may influence the relative vulnerability of males and females to changing environmental conditions

3. Since the mid-1990s, one of Britain’s most abundant passerine migrants, the willow warbler, *Phylloscopus trochilus*, has declined in abundance in the south-east of the country but has slightly increased in the north-west. Using mark-recapture data from the British Trust for Ornithology (BTO) Constant Effort Site Scheme (CES), we explore variation in the survival rates of adult male and female willow warblers within these two areas of contrasting population trends from 1986 to 2008.

4. The survival rates of adult willow warblers differ significantly between the sexes and the regions, with higher annual survival in the north-west than the south-east region, and lower annual survival in females than males. However, the extent of the sex bias in survival was similar in both regions, and there was no evidence that survival rates have changed significantly in either sex or region.

5. Annual survival rates may be influenced by processes operating in the non-breeding and/or breeding seasons. We found evidence that female survival was significantly lower in years when Sahel rainfall was low, suggesting that conditions during the non-breeding season may be influencing the sex differences in survival. However, female survival has also been low in years with relatively high Sahel rainfall, suggesting additional factors influencing adult

mortality. The body condition of willow warblers breeding in the south-east region was also significantly lower than those in the north-west, particularly for males. Harsh conditions for willow warblers in the non-breeding season in some years may therefore have been compounded by conditions in the breeding season in the south-east but not the north-west region.

6. While there is no evidence for declines in adult willow warbler survival rates during this time period, the lower overall survival rates in the south-east may be contributing to the population declines, and the lower female survival rates in this region may be limiting breeding opportunities and the potential for population recovery.

Introduction

Individuals of migratory species often travel large distances in order to exploit seasonally available resources. Consequently, they may be exposed to a wider range of environmental pressures than individuals from sedentary populations. Geographic variation in the demography of migratory populations within breeding grounds can therefore result from variation in local breeding and/or non-breeding season processes, particularly if individuals from different parts of the breeding range also differ in their non-breeding season locations or timings of migratory movements.

For Afro-Palaearctic migrants which cross the Sahara, there is strong evidence linking declines in survival to changing rainfall conditions in Africa. During the 1970s, sharp declines in Sahel rainfall were linked to periods of lower annual survival of Afro-Palearctic migratory bird species such as whitethroat *Sylvia communis*, sand martin *Riparia riparia* and sedge warbler *Acrocephalus schoenobaenus* (Møller, 1989, Peach *et al.*, 1991, Szep, 1995). However, more recent population declines in Afro-Palaearctic species have been greatest in those species wintering in the more southerly, humid regions of West Africa, which has raised concern over the impact of ongoing habitat loss due to processes such as localised agricultural intensification and wetland drainage in this region (Hewson & Noble 2009, Thaxter *et al.* 2010). In Britain, population declines in long-distance migrants have been greatest in those species which both winter in the humid zone and breed in England, while populations of the same species breeding in Scotland are typically faring much better (chapter 1). This suggests that the effects of changing conditions in the non-breeding season may not be consistent throughout the population.

Evidence of skewed sex ratios in declining populations was recently highlighted by Donald (2007), suggesting a possible role of sex-biased mortality in population declines. In migratory species, different rates of male and female mortality could arise through a number of mechanisms. Differences in the use of habitats of varying quality of the non-breeding grounds have been shown explain differences in both the rate of mass loss and survival of males and females of migratory species during the winter (Marra *et al.* 2001). Timing of movements may also be an important factor in determining the conditions experienced by individuals during migration, as males are typically on a slightly more advanced migratory schedule than females (Arvidsson & Neergaard 1991, Kokko *et al.* 2006). In addition, as incubation tends to be carried out primarily by females, this may result in higher metabolic demands (Thomson *et al.* 1998) and greater predation risks (Sargenant *et al.* 1984, Post &

Gotmark 2006). Changing environmental conditions may therefore have differing impacts on females and males.

Since the 1990s, one of Europe's most abundant long-distance migrant passerines, the willow warbler, *Phylloscopus trochilus,* has experienced large population declines in parts of its British breeding range, with a decrease of almost 30% in the south-east, while numbers in the north-west have increased by ~20% (Morrison *et al.* 2010, Risely *et al.* 2011). Willow warblers are small insectivorous passerines, breeding in young woodland and scrub habitats throughout most of northern Europe and Asia (Cramp 1992). They arrive in the UK from their African non-breeding grounds in early April, breeding throughout late April, May and early June (chapter 2). From 1965 – 2007, productivity of breeding willow warblers in the south-east of Britain declined from ~3.5 to 2.5 fledglings per breeding attempt, while remaining stable at ~3.6 fledglings per breeding attempt in the north-west (chapter 3). The declines in willow warbler productivity in the south-east were largely a consequence of increases in chick mortality (chapter 4), which could suggest a reduction in the availability of breeding season resources and/or increased nest predation. Such declines in the quality of breeding areas could also influence adult survival rates, the effect of which might vary between males and females.

Departure from breeding grounds takes place in late summer, and willow warblers arrive in Africa in late August and September (Cramp 1992). Within Africa, willow warblers tend to stay in the Sahel-Sudan zone, just south of the Sahara desert, for 1-2 months before travelling further south in late October or November (Salewski *et al.* 2002, Newton 2008). European willow warblers winter over large areas of western and southern Africa, however, the limited evidence available from reports of ringed birds suggests that British-breeding willow warblers winter in the Gulf of Guinea, principally around the Ivory Coast and Ghana (Norman & Norman, 2002). A previous study showed that, in southern Britain, adult willow warbler survival declined from ~45% during 1987 – 1988 to ~24% during 1991 – 1992, while in northern Britain there was no evidence that survival changed during the same period (Peach *et al.* 1995). Since that study, however, abundance has continued to decline in the south-east and the continued role of survival and the implications of possible sex biases in these patterns changes remain unexplored. Here we use mark-recapture data from the British Trust for Ornithology (BTO) Constant Effort Site (CES) scheme to explore variation in survival rates of adult male and female willow warblers breeding in regions of Britain experiencing divergent population trends. We then explore the evidence that these patterns could be driven by non-breeding and breeding season processes using the Sahel rainfall index as a proxy for environmental conditions in Africa. In addition, we use ringing data from 1995 to 2007 across Britain to explore variation in body condition on the breeding grounds.

Methods:

Estimating regional, temporal and sex variation in willow warbler survival

Data collection

Constant effort mist netting

In order to estimate variation in annual (between breeding seasons) survival rates of adult willow warblers, we used mark-recapture data from the British Trust for Ornithology Constant Effort Site scheme (CES, Peach *et al.* 1996 & 1998, Robinson *et al.* 2009). The CES scheme has been running since 1983 and uses standardised mist netting to monitor the abudance, breeding sucess and survival of common passerines in scrub and wetland habitats. At each CE site, licensed ringers erect a series of mist nets in the same postions, for the same length of time, during 12 morning and/or evening visits between May and August.

Estimating survival rates

We used captures (and re-captures) on CES sites to estimate the annual survival of adult willow warblers from breeding season to breeding season. In order to have enough records to accurately estimate survival, we limited our analysis to CES sites that had been running for at least five consecutive years and during that time caught more than 100 individuals in total, providing a dataset which ran from 1986 to 2008. Sites were divided into the two broad geographical regions of Britain with contrasting current willow warbler population trends (Figure 1), thus allowing us to explore the possible role of changes in adult survival on these patterns. This gave a total of 63 sites in the north-west and 284 sites in the south-east (Figure 1). We used only captures of adult willow warblers (ie those in their second calendar year or older) that had been sexed by ringers in the hand using the presence of a brood patch (female) or a cloacal protuberance (male) (Svensson 1992).

Modelling survival rates

In In order to gain robust estimates of survival from this large-scale mark-recapture dataset, robust estimates of recapture probabilities are also required. We used Cormack Jolly Seber (CJS) models to estimate:

1- apparent survival probablilty – the probability that a marked indiviudal alive at a sampling occasion t will survive and remain in the population (i.e. not permanently emigrate) between sampling occasion t and t+1.
2- recapture probability - the probability that a marked individual alive and associated with the population at time t will be recaptured.

The CJS model makes a number of assumptions which, if violated, may bias parameter estimates (see Lebreton *et al.* 1992 for full details). Of particular relevence to the CES dataset is the assumption that every marked individual in the population during a sampling period has the same probability of being recaptured. In the CES dataset this may not be the case, as individuals caught towards the start and end of the season are more likely to be transients (ie individuals that do not breed at that site), which are therefore likely have a lower probability of subsequently being recaught. However, recapture rates for willow warblers caught at CES sites (~20% for males and ~ 10% for females) are similar those found by Siriwardena *et al.* (1998) in an analysis of willow warbler recovery data (ringed birds found dead), which allows estimation of the true survival probability because the finding locations are not constrained to catching sites. Thus, within-season variation in recapture probabilities are unlikely to be sufficient to substantially influence estimates of survival rates from CES data.

Bayesian implementation of CJS survival model

All survival anayses were carried out in Openbugs; a software package that permits Bayesian inference from data using Markov Chain Monte Carlo (MCMC) algorithms (Spiegelhalter *et al.* 2007). To estimate survival and recapture probabilities, we used two MCMC chains, each run for 100,000 iterations in order to ensure that they had reached convergence. In the Bayesian framework, it is possible that the choice of prior distributions can influence the results of the model i.e. the shape of the posterior distribution. To avoid this we specified non-informative beta distributions as priors for both survival and recapature probability. For each parameter, we started the chain at an arbitrary inital value and, because each sucessive draw is dependent on the previous values of each parameter, the actual values chosen for the initals will be noticable for a while (Kery 2010). Therefore in order for the random draws produced from the Markov chains to be a valid sample of the posterior distrbution of our target parameters we discarded the first 20,000 draws (termed burn-in). After this point we verifed that the chains had reached their equilbrium distrbution i.e. that the chains had converged and did not show any trend in direction, by visually inspecting time-series plots of the two MCMC chains for all parameters and monitoring R-hat values, which should be less than 1.5 if convergence has occurred. In order to reduce the autocorrelation between consecutive samples of the chain to create posterior distributions of parameter estimates for survival and recapture propabilities, we sampled every second draw from the MCMC chain. We then took the mean and the standard deviation of the posterior distribution, as a measure of the parameter estimate and the uncertainty around it. We also estimated the Bayesian equivalent of a 95% confidence interval (called a credible interval, 95% CRI), as the smallest region of the posterior distribution containing 95% of the area under the curve (Kery, 2010).

Assessing annual, regional and sex varition in survival rates

Currently model selection for complex models in the Bayesian framework is not well developed (Kery 2010). We therefore used linear models in R (R 2.12.0, R core development team, 2011) to test variation in annual adult survival rates of males and females estimated across Britain and in each region separately. All main effects and their interaction terms were included in each model and then minimum adequate models were constructed by sequential removal of non-significant variables.

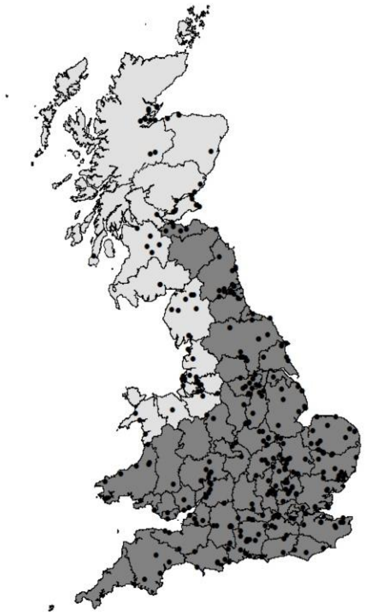

Figure 1: Areas of Britain included within north-west (pale grey) region in which willow warbler populations are stable and south-east (dark grey) region in which willow warbler populations are declining (Morrison *et al.* 2010). Constant Effort Sites from which willow warbler capture data were obtained are shown as filled circles.

Sahel rainfall index

A number of previous studies have shown that the overwinter survival of other Afro-Palaearctic migrants e.g. sedge warbler and white stork *Ciconia ciconia* is strongly correlated with rainfall in the Sahel during the wet season. Rainfall is likely to be important for both food and habitat availability during the non-breeding season (Kanyamibwa *et al.* 1990, Peach *et al.* 1991). We therefore included estimates of Sahel rainfall collected by the Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/data/sahel/#analyses) in survival models. A monthly index of Sahel rainfall was calculated as the monthly deviation from the long-term average (1950 – 1979), for the region bounded by 20°-10°N and 20°W-10°E.The monthly index of Sahel rainfall is calculated as the monthly deviation from the long-term average (1950 – 1979), for the region bounded by 20°-10°N and 20°W-10°E (see Janowiak 1998). This time period contains the period before large scale drought occurred across this region and therefore provides a suitable baseline against which to compare annual rainfall. Following Peach *et al.* (1991), we used the mean of this index from May – October as an annual index of wet season rainfall.

Assessing regional and sex variation in willow warbler body condition

In order to estimate variation in willow warbler body condition, we used records of adult willow warblers ringed as part of the British Ringing Scheme. Only birds that had been sexed by ringers in the hand using the presence of a brood patch (female) or a cloacal protuberance (male) (Svensson 1992) were included in the anaylsis. Ringing records were divided into the same two broad geographical regions based on population trends, as the CES data (Figure 1). Overall, 7,405 records from the north-west and 17,696 from the south-east were included in the analyses.

In order to explore variation in willow warbler body condition, we calculated a condition index by dividing mass by wing-length to give a measure of body mass relative to overall body size. We endeavoured to limit the analysis to breeding willow warblers by restricting the dataset to records collected from May to July. Annual mean body condition from 1995 to 2009 was then calculated for male and female willow warblers ringed in the north-west and south-east of Britain. Body mass can vary with time of day (Macleod *et al.* 2005) but it is unlikely that there is any systematic difference in time of capture of willow warblers from different regions. Thus time of capture was not included in the analyses. We constructed linear models in R 2.12.0 (R Development Core Team, 2011) to assess the significance of variation in body condition, weight and wing length. Years before 1995 were excluded due to low numbers of sexed birds in the north-west, leaving samples of 7237 individuals in the north-west and 16058 individuals in the south-east region for which body condition was estimated. Separate models were created for body condition, weight and wing length, with each of these as the response variable, and sex and region as the explanatory variables. Firstly, all main effects and interactions were included in the model and then a minimum adequate model was constructed by sequential removal of non-significant variables.

Results

Regional and sex differences in survival rates of willow warblers breeding in the UK

From 1986 to 2007, the mean annual of survival of adult willow warblers breeding in the south-east of Britain was significantly lower than that of willow warblers in the north-west (south-east: 0.30 ± 0.01 SE, north-west: 0.35 ± 0.02 SE, Table 1, Figure 2). Mean annual survival of adult male willow warblers was also consistently higher than adult female willow warblers (male: 0.35 ± 0.01 SE, female: 0.29 ± 0.01 SE, Table 1). There were no significant temporal trends in the survival rates of adult willow warblers of either sex in either region (Figure 2), although survival rates of females breeding in the south-east region were above the average for the whole time period in 5 of the 11 of the years before 1996 (the mid-point), but lower than average in 8 of the 11 years after that point, which could suggest an on-going decline in survival rates.

Table 1: Parameter estimates from a linear model of variation in annual survival rates of male and female adult willow warblers breeding in the north-west and south-east regions of Britain. The intercept indicates the mean survival rate for females in the north-west region, while estimate of male indicates the mean difference in annual survival between females and males (sex) and the estimate of south-east indicates the mean difference in annual survival between north-west and south-east.

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	0.35	0.03	12.95	<0.001
male	0.058	0.02	2.80	0.006
south-east	-0.04	0.02	-2.28	0.03

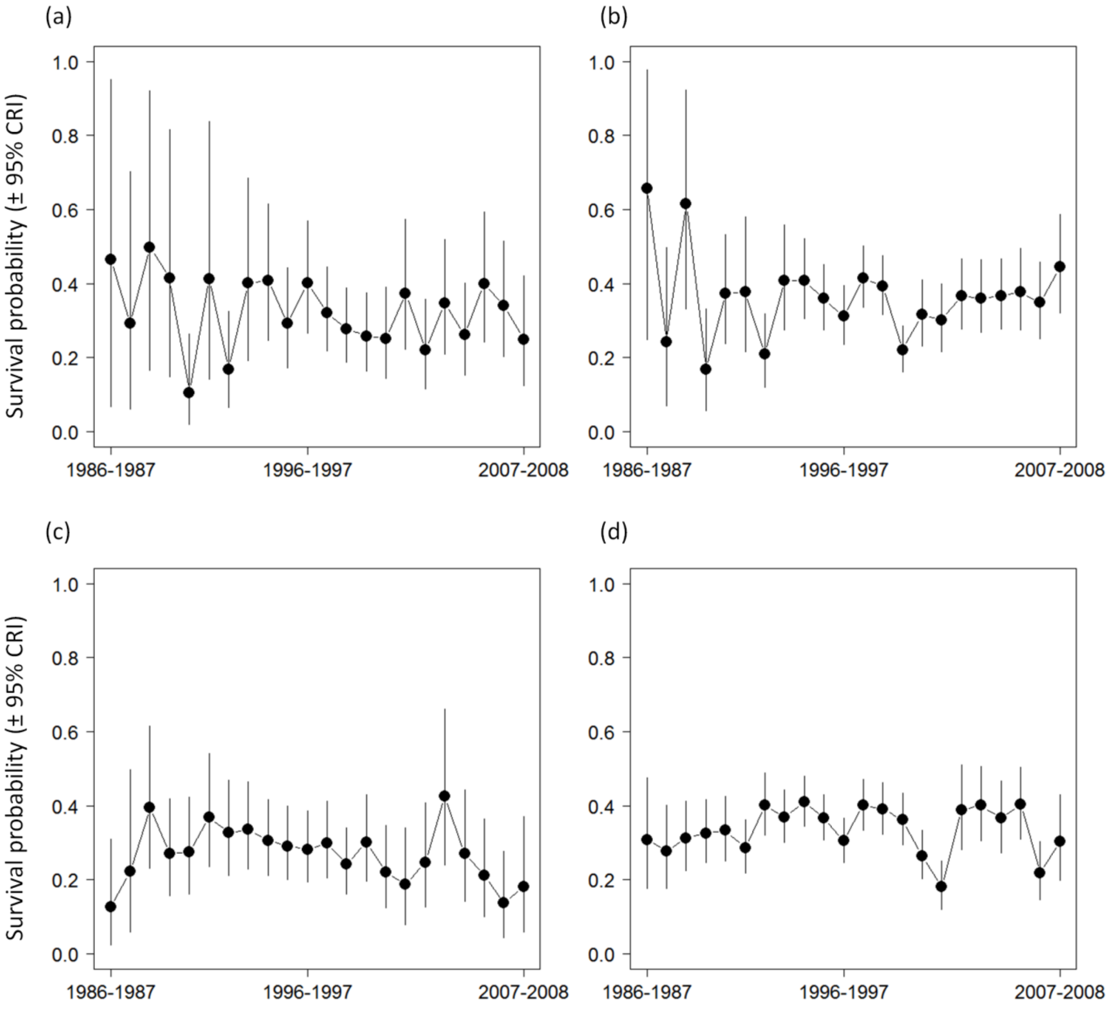

Figure 2: Annual estimates of mean adult annual survival (± 95% CRI) of female (left column: a, c) and male (right column: b, d) willow warblers in north-west (top row: a,b) and south-east (bottom row: c,d) regions of Britain.

The influence of Sahel rainfall on willow warbler survival

Adult female survival increases significantly with increasing Sahel rainfall index (Spearman rank correlation, r = 0.58, p = 0.004, Figure 3a). Female survival was lower in drought years (rainfall < -150), however, female surivival was highly variable in years with higher Sahel rainfall (Figure 3a). In years of moderate drought (index values from -200 to -50), there was a tendency for adult female survival to be lower in years after 2000 (Figure 4a). There was no significant relationship between survival of male willow warblers and Sahel rainfall index (Spearman rank correlation, r = 0.14, p = 0.53, Figure 3b) and, within each region of Britain, Sahel rainfall index was not significantly correlated with survival in either sex (Spearman rank correlations: north-west females: r = 0.41, p = 0.06, north-west males: r = -0.08, p = 0.7, south-east females: r = 0.30, p = 0.17, south-east males: r = 0.18, p = 0.43).

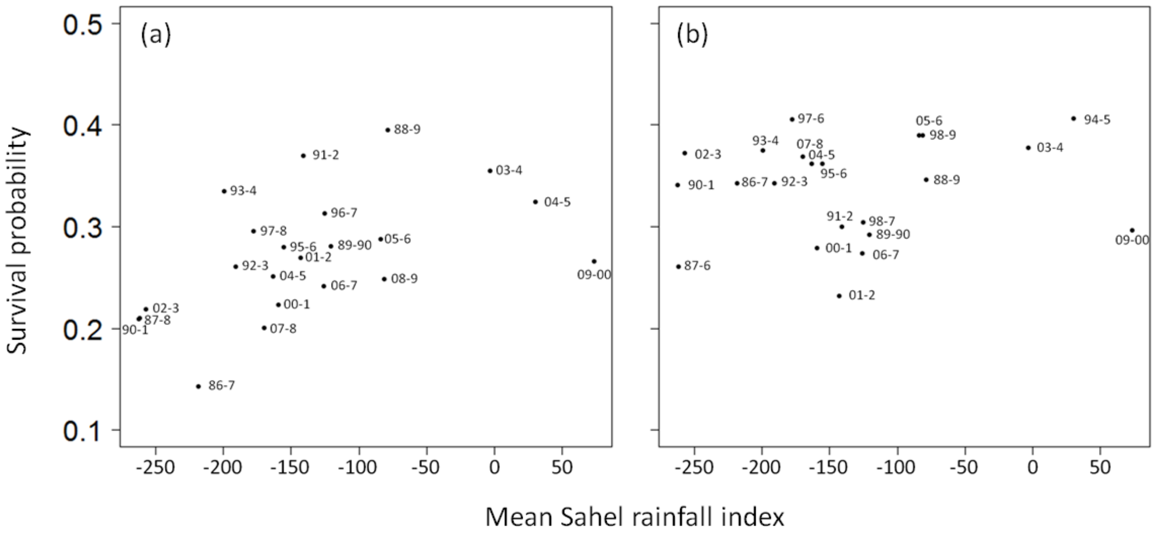

Figure 3: Correlations between the annual index of Sahel rainfall (mean monthly index, May to October) and the estimated annual survival rates in the following year for (a) female and (b) male adult willow warblers breeding in Britain.

Regional and sex differences in willow warbler body condition

From 1995 to 2009, the mean body condition (mass/wing length) of willow warblers during the breeding season was higher in the north-west than the south-east of Britain (south-east: 0.134 ± 0.00009 SE, north-west 0.137 ± 0.0001) (Figure 4a, Table 2a). Mean condition was also significantly lower in male willow warblers than females (male: 0.134 ± 0.00008 SE, female: 0.137 ± 0.0001 SE) (Figure 4a, Table 2a), and the magnitude of this sex difference was significantly greater among willow warblers breeding in the south-east than the north-west of Britain (Figure 4a, Table 2a). The condition of males in the north-west was higher than males in the south-east despite having slightly longer wings (Table 2c), as they were significantly heavier (Figure 4b & Table 2b).

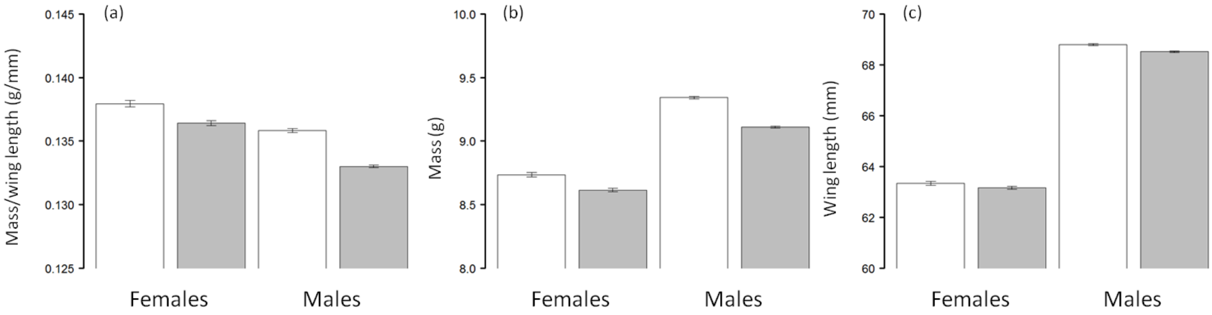

Figure 4: Regional and sex variation in a) body condition (mass/wing), b) mass (g) and c) wing length (mm) of female and male willow wablers in the north-west (white boxes) and south-east (grey boxes) of Britain (n = 2693 females and 4274 males in the north-west, 6809 females and 9249 males in the south east).

Table 2: Results of linear models of (a) condition (mass/wing) (b) mass (g) and (c) wing length (mm) of adult male and female willow warblers caught in the north-west and south-east of Britain from 1995 to 2009.

(a) Condition	Estimate	Std. Error	t-value	Pr (>|t|)
(Intercept)	0.14	0.0002	680.97	< 0.001
Sex	-0.002	0.0002	-6.37	< 0.001
region	-0.002	0.0003	-8.00	< 0.001
sex*region	-0.001	0.0003	-4.06	< 0.001
(b) Mass				
(Intercept)	8.73	0.01	655.27	< 0.001
sex	0.61	0.02	35.02	< 0.001
region	-0.12	0.02	-7.63	< 0.001
sex*region	-0.11	0.02	-5.29	< 0.001
(c) Wing length				
(Intercept)	63.33	0.03	2107.79	< 0.001
sex	5.46	0.04	139.75	< 0.001
region	-0.17	0.04	-4.83	< 0.001
sex*region	-0.10	0.05	-2.14	0.0323

Discussion

Variation in adult mortality can greatly influence species abundance and consequently may be a major driver of changes in population abundance (Peach *et al.* 1991, Peach *et al.* 1995, Siriwardena *et al.* 1998, Nevoux *et al.* 2008, Pearce-Higgins *et al.* 2010). In British willow warblers, the annual survival rates of adult birds breeding in the north-west of Britain, where abundance has recently slightly increased, are significantly higher than those in the south-east, where populations have declined severely. In addition, adult female willow warblers in both regions have lower annual survival rates than adult males and, while the extent of the difference in survival rates between the sexes does not vary regionally, the lowest survival rates consequently occur in adult female willow warblers breeding in the south-east and the highest in adult males in the north-west. We found evidence that lower female survival was significantly associated with years when Sahel rainfall was low, suggesting that conditions during the non-breeding season may be influencing the sex differences in survival. However, we also found that willow warblers breeding in the south-east had poorer body condition than those in the north-west, particularly among males. While this could be the result of a carry-over effect from the non-breeding season, lower body condition in the south-east may also indicate lower quality conditions during the breeding season.

Non-breeding season drivers of variation in survival rates

At the national-scale, we found years of low Sahel rainfall were associated with years of low survival in females but not males. Sahel rainfall has been found to be correlated with overwinter survival and abundance of a number of Afro-Palaearctic species. Typically, however, these are wetland species (Kanyamibwa *et al.* 1990, Peach *et al.* 1991) for which habitat availability may be greatly limited by severe drought in sub-Saharan Africa (Peach *et al.* 1991). Ringing recoveries place British-breeding willow warblers south of the Sahel in the Guinean humid forest (Norman & Norman 1992), where they are thought to be highly mobile during the non-breeding season, occupying a variety of habitats including woodland and forest edges, areas of tall grass, swamps and mangroves (Cramp 1992). This means that they may be less likely to be constrained to exploiting resources in one area (Salewski *et al.* 2002) and also suggests that their reliance on resources in the Sahel may be mainly when on passage.

Differences in the timing of migration through the Sahel may be influencing the impact of droughts on the survival of males and females. In particular, conditions in the Sahel are important for refuelling before and after the trans-Saharan migration (Newton 2008, Jenni-

Eiermann *et al.* 2011). In years of poor rainfall, the availability of resources for migrants may become depleted faster, leading to greater competition and a greater cost of later migration. As willow warblers in Europe show strong protandry (Sanio *et al.* 2010), with female willow warblers arriving up to three weeks later on breeding grounds than males (Arvidsson & Neergaard 1991), it is likely that female willow warblers also cross the Sahel later in the season, which may make them more susceptible to declines in resources in this region. However, in Britain, willow warblers breeding in the south of the country tend to arrive nearly two weeks earlier on breeding grounds than northern birds (BirdTrack, 2011). Therefore, if later arrival on breeding grounds means crossing the Sahel later, we might expect survival of southern males to be highest and northern females to be lowest, which is the opposite of the observed pattern (lowest survival in southern females and highest survival in northern males). Thus, while timing of migration may be contributing to the differences in survival between the sexes, additional processes occurring during the breeding season may be driving the regional differences.

A further indication that willow warbler survival is influenced by factors other than Sahel rainfall is that there are several years of higher Sahel rainfall when female survival rates remain low (e.g. 1999-2000) and, since 2000, female survival rates have been low in years with higher levels of rainfall. This could be due to additional non-breeding season pressures, e.g. increased habitat degradation could mean that the resources available in years of low rainfall become even more depleted, or the effects of higher costs of breeding for females could be exacerbated. The fact that we only found a correlation with female survival and Sahel rainfall at the national but not regional scale may be a consequence of the lack of precision in our estimates of survival limiting the power to find a within region relationship.

Breeding season drivers of variation in survival rates

The lower survival rates of adult females could also be the consequence of local environmental conditions on the breeding grounds. One of the greatest costs for females during the breeding season is the additional resources needed to produce and incubate eggs, which is not only energetically expensive but can also make females more vulnerable to predation on the nest (Robinson *et al.* 2010). Differences in the foraging areas of males and females may also lead to differences in their exposure to predators. Willow warblers are also unusual in that they carry out a biannual moult (Underhill *et al.* 1992), which may be energetically demanding as, during the peak of moult, the daily energy demand for passerines may increase by 20% (Jenni & Winkler 1994). On the breeding grounds, females start their post-nuptial moult an average of

10 days later than males (Underhill *et al.* 1992), suggesting that females are leaving breeding areas later than males. This may mean that they experience less favourable conditions during migration.

Regional variation in survival rates may also be the influenced by local environmental conditions on breeding grounds and poorer body condition during the breeding season of southern birds may be an indication of this. In recent years, changes in the quality of breeding grounds have been linked to reductions in habitat quality (Browne & Aebischer 2001, Pearce-Higgins *et al.* 2010), increased predation rates (Evans *et al.* 2004) and/or shifts in the phenology of food peaks relative to the breeding period (Both *et al.* 2001 & 2006) for migratory bird populations. Such processes may greatly increase the costs of breeding, if adults have to work harder to feed themselves and provision young (Peach *et al.* 2004). The poorer body condition of willow warblers in the south-east could therefore be a consequence of reduced food availability in this region, which may also be influencing the declines in fledgling success in this region (chapter 4). A decrease in the ability of adults to obtain food could also make them more vulnerable to predation, if they have to make more or longer foraging trips, while leaving chicks unattended for longer could also increase their vulnerability to predation (Dunn *et al.* 2011).

Consequences for population change

While there were no clear temporal trends in adult willow warbler survival rates, we found lower survival of adults in the south-east, where severe declines in abundance have occurred, and higher survival in the north-west where populations are slightly increasing. In both regions, the differences in survival of adult male and female willow warblers suggest differential impacts of drivers on survival, with low female survival being associated with Sahel droughts and low male survival with low body condition during the breeding season. As CES data only start in the late 1980s, the current low survival rates in adult females in the south-east are potentially part of a longer-term declining trend in survival from before the period of population decline in the mid 1980s. The lower adult survival coupled with the declining success of breeding attempts is therefore likely to be contributing to the population declines in the south-east. Additionally, sex differences in survival may be causing a sex ratio bias, reducing the number of breeding attempts that can occur and further limiting the potential for population recovery.

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Chapter seven

Exploring the population level consequences of sex-biased mortality in a long-distance migratory passerine.

Abstract

1. Current evidence suggests that, in many bird species, higher rates of mortality among females than males may be leading to sex ratio biases. However, the causes and population-level consequences of such sex ratio biases remain widely unexplored. In particular, the potential role of changes in female mortality rates in driving population changes is unclear.

2. In recent decades, declines in abundance have been apparent among several Afro-Palaearctic migratory bird species. Environmental changes in the breeding and non-breeding seasons may have contributed to these losses, but the extent to which these changes may have disproportionately affected males and females is not known. Sex ratio biases and trends in sex-specific mortality may also be difficult to detect, as many surveys primarily monitor populations by records of singing males.

2. Willow warblers, *Phylloscopus trochilus*, are long-distance migrants that have declined across Europe in recent decades. In Britain, these declines have been apparent in the south-east but not the north-west of the country, and there is evidence for declines in nesting success and higher mortality rates of adult females than males. We use national-scale bird ringing data from the British Trust for Ornithology (BTO) Constant Effort Site scheme (CES) to explore the impact of higher female mortality rates on adult sex ratios within these two regions, and the consequences for trends in productivity.

3. Sex ratios of willow warblers on CES sites were male-biased in both regions of Britain, and there were significantly fewer females per male in the south-east than the north-west. Sex ratios also declined significantly between 1990 and 2008 in both regions, from ~0.87 to 0.52 females per male in the north-west and ~0.64 to 0.37 in the south-east.

4. Numbers of juveniles per male caught on CES sites were similar in both north-west and south-east Britain but were significantly lower than the number of juveniles per female in each region, suggesting that some adult males failed to gain breeding opportunities. Between 1990 and 2008, the number of juveniles per male declined at a similar rate in both regions, but significantly faster than the declines in numbers of juveniles per female in each region, also suggesting an ongoing decline in breeding opportunities for male willow warblers.

5. Higher female mortality in willow warblers in Britain appears to have led to an increase in the number of unpaired males in the population, and consequently a faster decline in the number of juveniles per adult male than per adult female. As singing males are the primary records used in estimations of population abundance, this sex ratio bias may mean that the extent of recent population declines has been under-estimated, and that declines in the number of breeding attempts may be occurring in addition to declines in numbers of fledglings per breeding attempt. Willow warbler population declines therefore appear to have been influenced by changes in both productivity and sex-biased mortality.

Introduction

Skewed adult sex ratios as a consequence of higher female mortality have recently been shown to be more common in populations of globally threatened than non-threatened bird species (Donald *et al.* 2007). Lower survival rates of females can have important consequences for population abundance and recruitment, as the number of breeding females typically limits the number of breeding attempts that can occur. Quantifying the impact of female-biased mortality on population sex ratios and productivity may therefore be an important step in understanding the processes driving changes in population abundance.

Biases in adult sex ratios can arise from sex biases at egg production (Komdeur *et al.* 1997) or sex-biased mortality at the nestling, juvenile or adult stages (Donald 2007). Higher female mortality may occur as a result of breeding and/or non-breeding season processes which, for migratory species, may operate over huge geographic areas. For example, differences in the location and timing of movements may greatly influence the conditions experience by male and female birds and their survival rates (Gill *et al.* 2001, Newton 2006). Additionally during the breeding season, the majority of incubation tends to be carried out by females, requiring higher metabolic demands (Thomson *et al.* 1998) and carrying greater predation risks (Post & Gotmark 2006, Sargeant *et al.* 1984), which may also result in higher mortality rates.

One group of species which have recently undergone rapid and severe declines in abundance are European breeding long-distance migrants (Sanderson *et al.* 2006, Hewson & Noble 2009). For some of these species, declines in abundance have been linked to lowered survival associated with deterioration in the quality of wintering grounds (Møller 1989, Peach *et al.* 1991, Szep 1995). However, recent evidence suggests that the effect of such changes on the survival of migrants may differ between the sexes (chapter 6). Lower female survival could lead to a higher number of unpaired males in the population and lower recruitment, both of which may contribute to population declines and limit the rate of population recovery.

In willow warblers, *Phylloscopus trochilus*, recent analyses have shown that the survival rates of adult females are significantly lower than of adult males, with the lowest rates of female survival occurring in the south-east where populations have recently declined (chapter 6). Higher mortality rates of adult females may result in sex ratio biases and differences in the relative productivity of males and females, with consequences for population abundance. In order to explore the effect of sex-biased mortality on willow warbler sex ratios and productivity, we use national-scale data from the British Trust for Ornithology (BTO) Constant Effort Sites (CES) scheme, to explore changes in the sex ratio of willow warblers breeding in two regions of Britain with differing current population trends. We then explore variation in the number of juveniles caught per male and per female at CES sites in order to explore the influence of biased adult sex ratios on productivity.

Methods

Data collection

Constant effort mist netting

The British Trust for Ornithology (BTO) Constant Effort Site (CES) scheme has been running since 1983, and uses standardised mist-netting to monitor the abundance, breeding sucess and survival of common passerines in scrub and wetland habitats across the UK. At each CES, licensed ringers use a series of mist-nets in the same postions, for the same amount of time, during 12 morning and/or evening visits between May and August. For full details of the CES scheme methodology, see Peach *et al.* (1996 & 1998).

Constant effort sites were divided into the two broad geographical regions of the UK (Figure 1) with contrasting willow warbler population trends; since the 1990s, willow warbler populations have declined rapidly in the south-east but have been stable or slightly increasing in the north-west (Morrison *et al.* 2010). We limited our analysis to sites that had been operated for at least five consecutive years and, during that time, caught at least 100 individual willow warblers. Adult willow warblers (second calendar year or older) were included in the study only if they had been sexed using brood patches = female or cloacal protuberance = male (Svensson 1992).

Figure 1: Areas of Great Britain included within the north-west (pale grey) region in which willow warbler populations are stable and south-east (dark grey) region in which willow warbler populations are declining (Morrison *et al.* 2010).

Estimating sex ratios and productivity

We used generalised linear mixed models in the lmer function of R (2.13.0, R core development team, 2011) to produce annual estimates of both adult willow warbler sex ratio (females per males) and productivity (ratio of juveniles to adults) on Constant Effort sites. Sites were divided into the two broad geographical regions of Britain with contrasting current willow warbler population trends (Figure 1). Years before 1990 were excluded from the model due to low sample sizes in the north-west (Figure 2). Thus we were able to explore the role of changes in sex ratio in the regional variation in population trends. We constructed separate models to explore annual variation in the number of females per males, juveniles per male and juveniles per female in the south-east and north-west of Britain (Figure 1). All models were constructed with binomial error distributions and a logit link function, with females coded as 1 and males as 0 in the sex ratio models and juveniles as 1 and adults (males or females) as 0 in the productivity models. In all models region, year and region*year were fitted as categorical fixed effects and only significant variables were kept in the final model. Site was included as a random effect in order to account for the fact that not all sites were included in all years. We present the results as the number of females per male or juveniles per adult, which are calculated by taking the exponential of the parameter estimates.

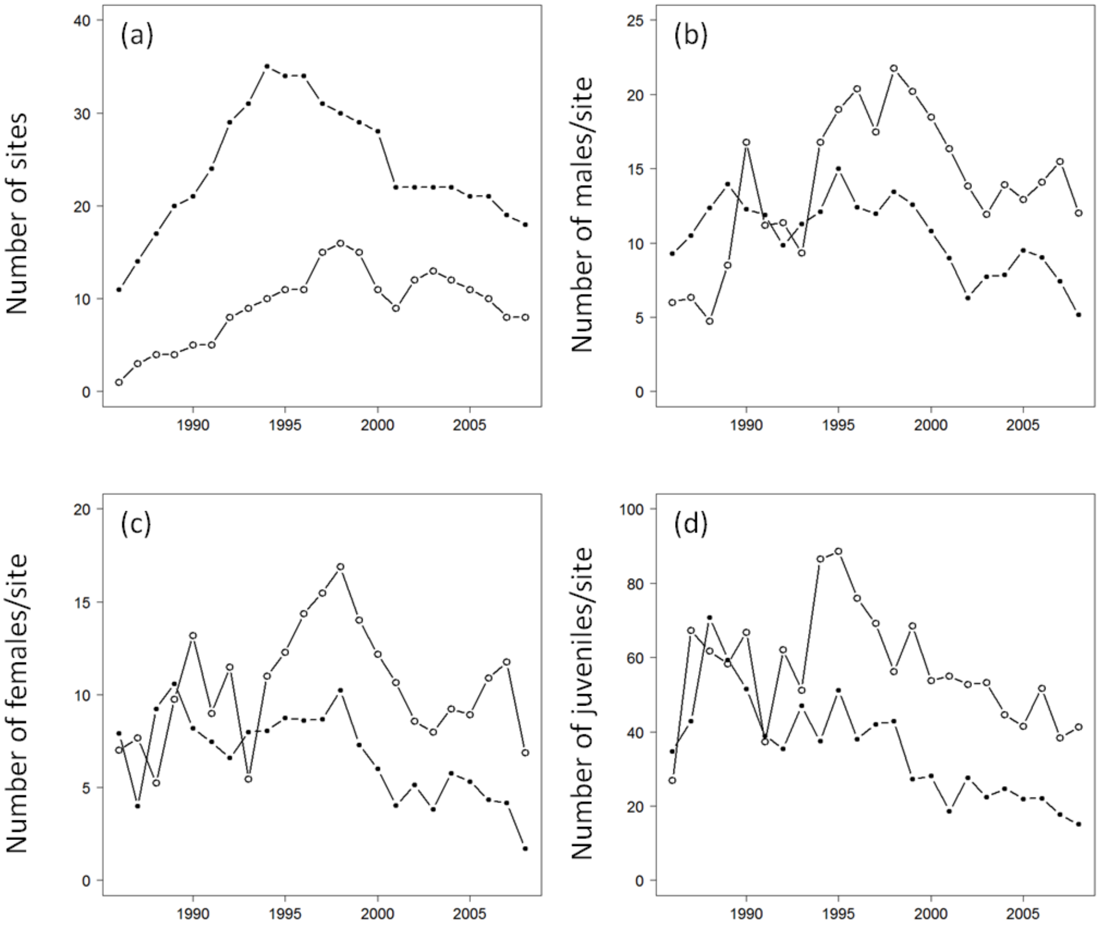

Figure 2: Annual variation in the number of (a) Constant Effort Sites on which sufficient willow warblers were caught for inclusion in the study, and in the number of individual (b) males, (c) females and (d) juveniles caught per site from 1986 – 2008, in the north-west (open circles) and south-east (black circles) regions of Britain.

Results

Between 1986 and 2008, willow warblers were caught in an average of 9 (± 4.1 SD) and 24 (± 6.7 SD) CES sites per year in north-west and south-east Britain, respectively (Figure 2a). The number of CES sites where willow warblers were caught increased steadily from the start of the scheme in 1986 until the 1990s, but declines in the number of sites on which willow warblers were caught have occurred since then, particularly in the south-east (Figure 2a). During this time the number of individual willow warblers caught also varried greatly, with the number of males, females and juveniles caught increasing steadly until the late 1990s in both regions, and declining rapidly thereafter (Figure 2b-d). From 1998 onwards, despite a higher number of CES sites in the south-east than the north-west (Figure 2) similar total numbers of males, females and juveniles were caught in each region (Figure 2b-d).

Between 1990 and 2008, the mean number of female willow warblers caught per male on CES sites was significantly male-biased in both regions of Britain (north-west: mean = 0.70, 95% CIs = 0.65 - 0.76; south-east: mean = 0.63, 95% CIs = 0.58 – 0.68) and significantly lower in the south-east than the north-west region (Figure 3, Table 1). The number of female willow warblers caught per male also declined significantly in both regions over this time period, from ~0.87 to 0.52 females per male in the north-west and ~0.64 to 0.37 in the south-east (Figure 3, Table 1).

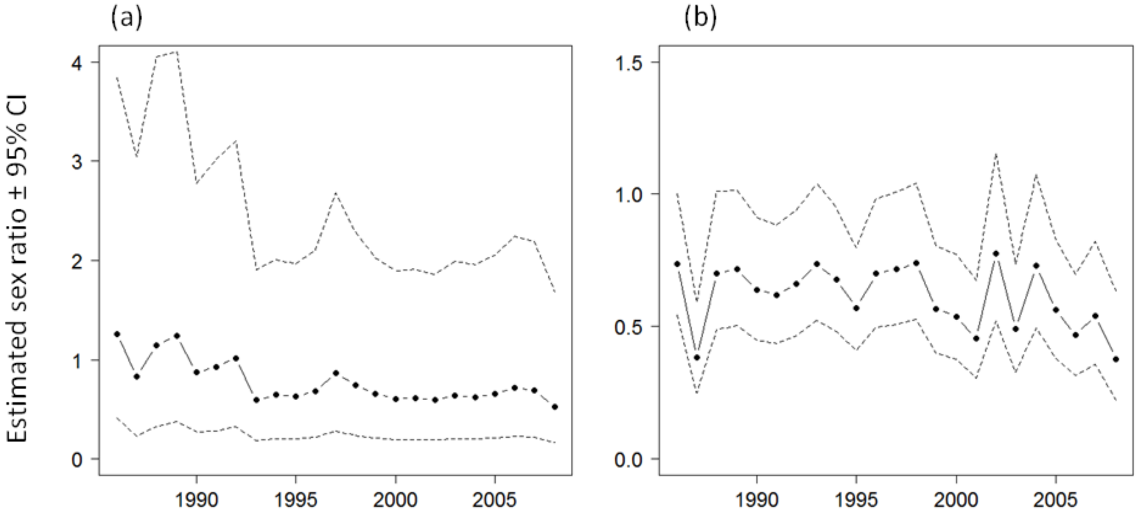

Figure 3: Changes in estimated sex ratio (mean number of females per male) of willow warblers on constant effort sites (±95% CI) from 1986 – 2008 in (a) north-west (b) south-east of Britain.

Table 1: Results of binomial GLMs of the regional and annual variation in the number of female willow warblers per male recorded on constant effort sites from 1990 to 2008. Years before 1990 were excluded from the model due to low sample sizes in the north-west. There was no significant effect of the interaction between region and year on sex ratios.

	Estimate	Std. Error	z-value	Pr (>|z|)
(Intercept)	-0.14	0.08	-1.79	0.07
Region	-0.13	0.07	-1.99	**0.04**
Year	-0.016	0.004	-3.66	**< 0.001**

The mean number of juvenile willow warblers caught per male on CES sites over the last two decades was similar in north-west and south-east Britain (Figure 4, Table 2) but significant declines in numbers of juveniles per male have occurred in both regions, and at similar rates (Figure 5, Table 2). The mean number of juveniles caught per female was also similar in both regions but was significantly higher than numbers of juveniles per males (Figure 4, Table 2). Between 1990 and 2008, the number of juvenile willow warblers caught per female declined significantly in both regions, with the rate of decline being slightly but not significantly faster in the south-east than the north-west (Figure 4a, Table 2).

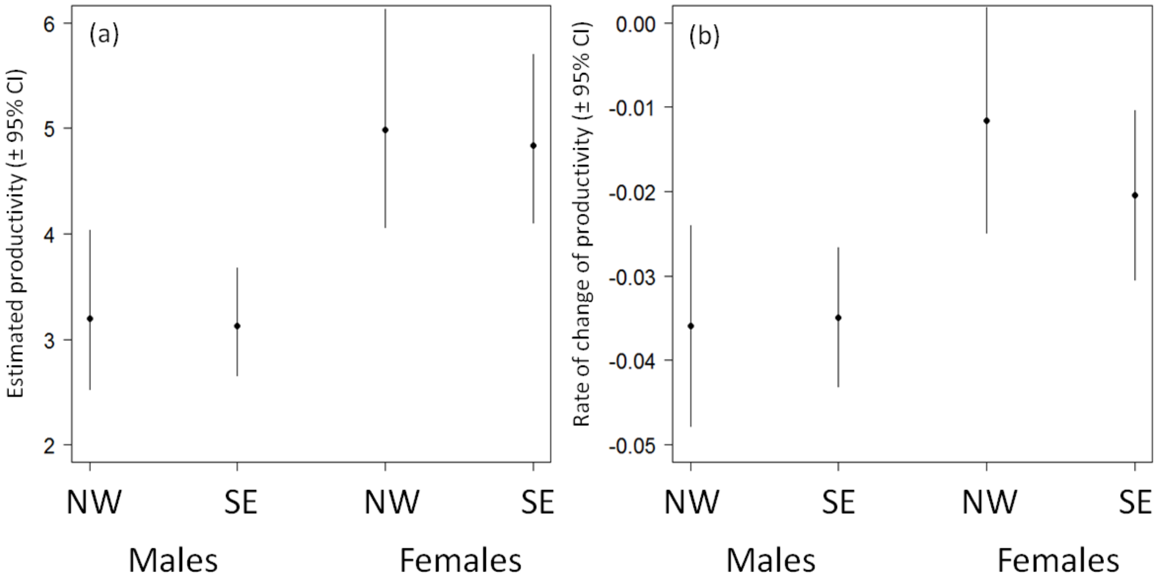

Figure 4: Variation in estimated (a) mean productivity (mean number of juveniles per adult) and (b) annual rate of change in productivity (juveniles per adult) of male and female willow warblers caught on Constant Effort sites in the north-west (NW) and south-east (SE) of Britain, between 1990 and 2008.

Table 2: Results of binomial GLMs of regional and annual variation in the number of juvenile willow warblers per (a) male and (b) female caught on constant effort sites from 1990 to 2008. There was no significant effect of the interaction between region and year on the number of juveniles per male or per female.

(a)	Estimate	Std. Error	z-value	Pr (>|z|)
(Intercept)	1.66	0.13	12.42	< 0.001
Region	-0.12	0.15	-0.78	0.44
Year	-0.047	0.003	-10.64	< 0.001
(b)				
(Intercept)	1.77	0.13	13.53	< 0.001
Region	0.02	0.14	0.11	0.916
Year	-0.02	0.004	-4.21	< 0.001

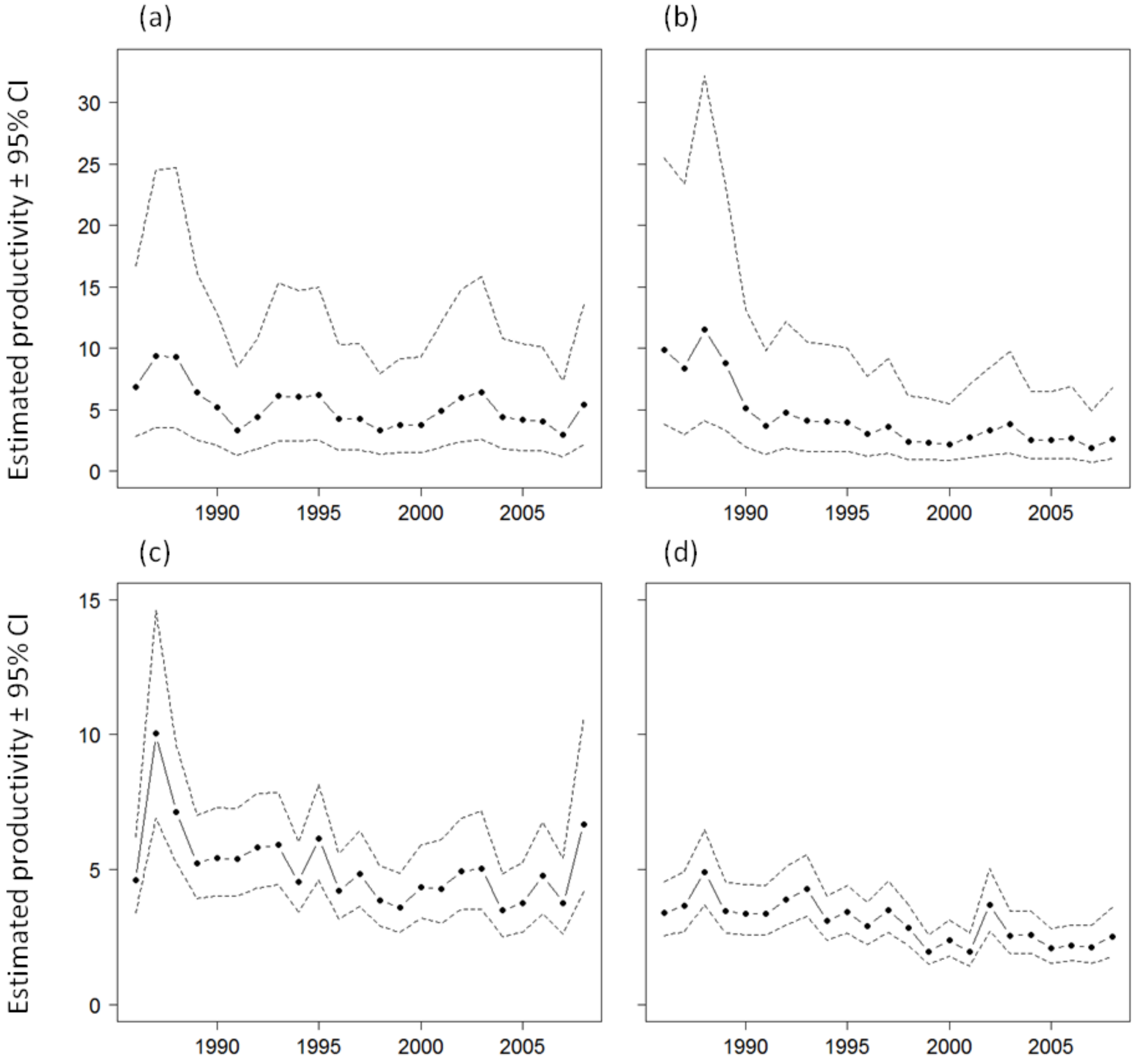

Figure 5: Estimated annual productivity (mean number of juveniles per female (a, c) and male (b, d)) of willow warblers caught on Constant Effort sites in north-west (a, b) and south-east (c, d) Britain.

Discussion

Since 1990, the sex ratios of willow warblers caught on CES sites in Britain have been significantly male-biased and significantly more male-biased in the north-west than the south-east. Previous studies have shown that survival of adult female willow warblers in both regions of Britain has been lower than that of adult males over the last two decades (chapter 6). However the difference between male and female adult survival was similar in both regions (chapter 6). It is therefore unlikely that that the regional differences in sex ratio are due to sex-biased adult survival and may be a consequence of higher mortality before this stage (e.g. in the nest, post fledging or first year) in the south-east. In both regions sex ratios have become increasing male-biased at a similar rate and the greater rate of declines in the number of juveniles per male than per female suggests that fewer males may be able to find a mate and breed.

Males and females can differ greatly in their ecology and behaviour and therefore unbiased sampling of individuals is difficult (Donald 2007). For example, during the breeding season, males more likely to be actively singing and defending territories while females are laying and incubating eggs. These different levels of activity may mean that the probability of capture differs between male and females. Recapture probabilities of willow warblers on Constant Effort sites have been shown to be lower for females than males (chapter 6 & Peach *et al.* 1995) and thus male-biased sex ratios in CES catches may be expected. However, the regional differences and temporal trends in willow warbler sex ratios are unlikely to be influenced by catching biases, particularly as the catching effort as CES sites is designed to remain constant through time.

The regional and temporal differences in the sex ratio of the CES catch may be influenced by changes in the survival of adult willow warblers. However while we found declines in the number of females per male in both regions, there were no clear trends in the survival of adult male and female willow warblers (chapter 6). The number of females caught per male was also lower in the south-east than the north-west but, while adult survival was lower in the south-east, the difference between the survival of adult male and female willow warblers is similar between the regions (chapter 6). It is therefore unlikely that the greater male-bias in the sex ratio of southern CES sites is driven by the higher survival of adult males than females.

Annual variation in the total CES catch is not just a record of the number of adult birds present in the breeding season but also the number of first year birds in the population. Differences in the patterns of adult survival and sex ratio trends are therefore likely to be driven by variation survival prior to adulthood and subsequent recruitment into the breeding population. This may be a consequence of a lower number of females surviving their first year and recruiting into sites in the south-east than the north-west or a higher number of males surviving their first year and recruiting into sites in the north-west than the south-east. This suggests that juvenile birds may be vulnerable to changes in different environmental conditions than adults, which may be due to differences in their timing and location of non-breeding areas or vulnerability to conditions on breeding areas post-fledging. As first years are also likely to be the smallest birds in the population they may also be the most vulnerable to periods of extreme weather or low food availability.

In both regions, the greater rates of decline in numbers of juveniles per male than per female suggest an increase numbers of unpaired males in the population. Since the mid 1980s, willow warbler productivity in the south-east has declined from ~4.5 to ~3.5 fledglings per breeding attempt, while remaining stable at ~ 4.5 in the north-west (chapter 3). Despite this, the mean number of juveniles per male and female in the CES catch are similar and declining at the same rate in both regions. Differences in the trends in fledglings per breeding attempt and productivity will be a consequence of post-fledgling mortality and/or dispersal. This could suggest that post-fledgling mortality is higher or that natal dispersal occurs earlier in the north-west than the south-east.

Implications for population monitoring

During the breeding season, monitoring of the abundance of many bird species, epsecially passerines, is based on records of male song (Newson *et al.* 2005). As sex ratio bias is likely to lead to a high number of males in the population remaining unpaired, the number of males encoutered singing is likely to be greater than the number of breeding pairs (Amrhein *et al.* 2007, Broughton *et al.* 2011). Evidence also suggests that that once mated the singing frequency of males is considerably reduced (Amrhein *et al.* 2002). Consequently as the number of unpaired males increases the number of males encountered singing may actually increase. Therefore when surveys are conducted mainly on male song, increasing numbers of unpaired males can result in a negative relationship between estimated population size and true functional population size (Donald 2007). Male-biased sex ratios in the British willow warbler population may be causing over-estimation of abudance and masking the true extent of declines in the breeding population.

Conclusions

Within the British willow warbler population, females are increasingly becoming the rarer sex. Declines in the number of females per male are reflected in the greater rate of decline in the number of juveniles per male than per female, suggesting that the number of unpaired males in the population is increasing. Consequently the number of males recorded singing is likely to be an over-estimate of true breeding population size, masking the true extent of population losses. Recovery of the population is therefore likely to be limited by both declines in productivity (number of juveniles per female) and decline in the number of breeding attempts (number of juveniles per male).

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Conclusions

Conclusions

The willow warbler population of the British Isles is among the most well-monitored of breeding populations in the world, yet we are only just beginning to understand the complexity of the processes regulating its size. This thesis uses national-scale datasets to intensively explore willow warbler demography during periods and regions of contrasting population trends within Britain (Table 1, Figure 1), and presents one of the first integrated demographic studies of an Afro-Palaearctic migrant within Europe. From 1966 to 2008, despite regional variation in willow warbler demography, no measure of productivity or survival was estimated to be higher in populations breeding in the south-east than the north-west of Britain (Table 1). In particular, the success of individual breeding attempts and female survival was significantly lower in the south-east than the north-west (Table 1). While this might implicate harsher breeding season conditions in south-east Britain, e.g. higher predation rates or lower food availability, the regional consistency in the rate and direction of change in sex ratios and declines in numbers of juveniles per adult (Table 1), may also suggest that individuals are exposed to additional and similar pressures outside of the breeding season, regardless of their breeding areas. If willow warblers from throughout Britain are exposed to similar pressures during the non-breeding season, then the higher productivity and adult survival in the north-west region may be buffering the impact of these pressures, while the declines in productivity and lower adult survival may be exacerbating these impacts in the south-east. Given the consistency of the geographical variation in population trends between Scotland and England across Afro-Palaearctic migrants (chapter 1), similar processes may also be occurring in other species.

Table 1: Regional difference and trends in the population demography of willow warblers breeding in north-west and south-east Britain. Significance of regional differences is indicated by: > = <0.05, >> = <0.01, >>> = <0.001, significance of trends is indicated by: ↓ = <0.05, ↓↓ = <0.01, ↓↓↓ = <0.001 and the direction of the arrow gives the direction of the trend. (Statistical tests reported in chapters 3 – 7). NRS: Nest Record Survey and CES: Constant Effort Scheme.

Demographic rate	**Dataset**	**North-west : South-east**	**North-west**	**South-east**
Fledglings per breeding attempt	NRS: 1965 – 2007	NW > SE	-	↓↓
Clutch size	NRS: 1965 – 2007	NW = SE	-	-
Daily nest failure rate at egg stage	NRS: 1965 – 2007	NW = SE	-	-
Daily nest failure rate at chick stage	NRS: 1965 – 2007	NW >>> SE	-	↓↓
Adult male survival	CES: 1986 – 2008	NW = SE	-	-
Adult female survival	CES: 1986 – 2008	NW > SE	-	-
Sex ratio (females per male)	CES: 1990 – 2008	NW > SE	↓↓↓	↓↓↓
Juveniles per male	CES: 1990 – 2008	NW = SE	↓↓↓	↓↓↓
Juveniles per female	CES: 1990 – 2008	NW = SE	↓↓↓	↓↓↓

Figure 1: Schematic diagram of different demographic factors and rates that can influence population changes. In bold are the stages for which estimates for willow warblers have been calculated in this thesis, and survival rates are in italics.

Changes in willow warbler abundance from 1966 to 1993

From 1966 to 1993, the abundance of willow warblers in the UK was monitored by the Common Bird Census (CBC). During this time, the number of willow warblers on CBC plots declined by 48% in Scotland and by 51% in England. Periods of rapid population decline occurred first in Scotland (26% decline between 1983 and 1987) and then in England (43% decline between 1988 and 1992). CBC plots are mainly on woodland or farmland, between which there have also been slight differences in the timing of population declines, with willow warbler abundance on woodland plots declining from 1983 onwards while declines on farmland plots did not start until 1987 (Peach *et al.* 1995). It is therefore possible that the temporal differences in the declines in Scotland and England may be a result of a higher proportion of woodland plots in Scotland. Overall, however, the similarity of the decline in both countries and habitats suggests that a broad-scale factor has influenced the willow warbler population decline during this time period.

Possible demographic drivers of willow warbler abundance from 1966 to 1993

The analysis of BBS data reported in chapter 2 identified the differing population trends of willow warblers in north-west and south-east Britain. As the trends estimated from the CBC/BBS data (Introduction, Figure 2) are for Scotland and England, which do not directly match the north-west and south-east regions identified in chapter 2, the regional patterns from the two datasets are similar but not identical. Differences in demographic rates may be more likely to be apparent within the north-west and south-east regions, as the consistency of the population trends within these regions is higher than within Scotland and England.

Using data from the Nest Record Scheme (NRS), we were able estimate annual changes in productivity from 1965 onwards. This analysis revealed that a higher number of fledglings per breeding attempt were produced in the north-west than the south-east (Table 1). There were also declines in the number of fledglings per breeding attempt which began as early as the 1970s in the south-east, while there was no clear temporal trend in the number of fledglings per breeding attempt in the north-west (Table 1). Therefore, while declines in abundance are evident in both regions during this period, declines in productivity may only have contributed to this trend in the south-east. Given the similarity of the population declines in Scotland and England at this time, it seems likely that an additional demographic driver was involved in these declines.

Peach *et al.* (1995) explored the variation in abundance and survival of willow warblers in northern (north of latitude 53°30’ N) and southern (south of latitude 53°30’ N) Britain from 1987 to 1993, the period after population decline in Scotland and during the population decline in England. During this time, adult survival rates on Constant Effort Scheme (CES) sites in the south declined from ~45% to ~25% between 1991 and 1992, while there was no change in adult survival rates in northern CES sites. This study concluded that the differences in population trends from 1987 to 1993 in the northern and southern regions were the consequence of differences in survival rates. However, as this study did not cover the period of population change in Scotland, it is possible that earlier declines in survival had also occurred in northern populations. In chapter 6, we calculated annual adult survival rates across all CES sites that had been running for more than five years, and during which time they had caught more than 100 individuals. These constraints meant that survival rates could only be estimated from 1986 onwards, again missing the period of rapid population decline in the north. Peach *et al.* (1995) suggest that the decline in willow warbler abundance from 1987 to 1993 was particularly influenced by one year of exceptionally low adult survival (1991-1992). In that case, the lack of a temporal trend in adult survival does not mean that years of particularly low survival rates have not been influential in population declines (Green 1999). However, as population declines were evident in both regions before 1991, it is unlikely that occasional low survival rates are the sole driver of population declines. Analyses of the survival rates of adult willow warblers with respect to periods of population change has also been carried out from recovery data (Siriwardena *et al.* 1998). This study showed no relationship between the magnitude of adult survival or first-year survival and the direction of population trends. However, this analysis was carried out at the national scale and consequently regionally variable trends may have been masked.

Changes in willow warbler abundance from 1994 to 2008

Between 1994 and 2006, the abundance of willow warblers breeding in the north-west of the UK recovered, while in the south-east populations continued to decline. During this time the abundance of willow warblers in the north-west fluctuated at ~4.5 per BBS square, while abundance in the south-east declined from ~ 2.0 to ~ 1.0 willow warblers per BBS square (chapter 2). The majority of BBS coverage is in the south and east of the UK and the coverage is particularly low in the north (chapter 2, Figure 1). Consequently most of the data on the abundance trends of willow warblers come from areas with relatively low breeding densities. Therefore, while the relative rate of population decline is highest in the south-east, these losses have only occurred over a relatively small proportion of the population.

Possible demographic drivers of willow warbler abundance from 1994 to 2008

Within the north-west and south-east regions, there were no significant trends in either clutch size or the daily nest failure rate at egg stage (Table 1). At the national level, the BTO has reported a significant increase in the daily nest failure rate at egg stage during this time period (Bailie *et al.* 2010). The 5-year trends presented in chapter 4 indicate that, between 1965 and 1970, only 1% more nesting attempts failed at egg stage in the south-east than the north-west. However, by 2000 to 2007 this difference increased to 11%, as a consequence of increasing daily nest failure rates at egg stage in the south-east. Despite this pattern, the overall increase in daily nest failure rates at egg stage in the south-east was not statistically significant (Table 1). Differences in the trends reported in this thesis and in the BTO national trends could be due to reductions in statistical power resulting from the lower sample sizes available within the regions. However, in chapter 4, temporal changes in daily nest failure rates at egg stage were modelled as a function of both year and first egg dates. As daily nest failure rates at egg stage are significantly higher at the start of the breeding season, it is possible that advances in laying dates or earlier nest recording could have lead to an increase in the estimates of daily nest failure rates at egg stage. Separating a true increase in daily nest failure rates at egg stage from such sampling biases may therefore require further analysis.

Regional differences in the number of fledglings per breeding attempt, and the significant declines in fledglings per breeding attempt in the south-east, are mostly due to differences in the success of nesting attempts at the chick stage. Between 1965 and 1970, 7% more nests failed at chick stage in the south-east than the north-west. However, by 2000 – 2007, this difference had increased to 13% (chapter 4). Therefore, while the proportion of nests failing at the chick stage has historically been higher in the south-east, the regional difference has also increased (Table 1). In previous studies, the impact of variation in nest failure rates on the population trends of Afro-Palaearctic migrant species has been shown to be low (Freeman & Crick *et al.* 2003, Browne *et al.* 2004 & 2005), and declines in the number of breeding attempts within the breeding season are thought to be a larger component of population loss (Browne *et al.* 2004 & 2005). Additionally, in a study of 12 species of farmland granivorous species, population declines were only associated with breeding performance in one species (Siriwardena *et al.* 2000). However, as willow warblers are ground-nesting insectivorous birds, their breeding success may be particularly sensitive to changes in environmental conditions, especially as losses of nestlings have been shown to be higher in open-nesting warblers than other Afro-Palaearctic migrant species (Baillie & Peach 1992).

Although fledglings per breeding attempt measures the success of individual breeding attempts, it does not provide an indication of the proportion of the population breeding (Figure 1). Using ringing data collected on CES sites, we found evidence to suggest that declines in the number of breeding attempts have occurred across the whole of Britain, as a result of a declines in the number of breeding females (chapter 7). While the analyses of survival rates indicated no statistically significant trends in adult survival in either region (chapter 6), there was an indication of lower than average survival of adult females in recent years. However, the CES ringing data indicate that the willow warbler sex ratios have become more male-biased in both regions, suggesting possible declines in the survival of females prior to adulthood in both regions. Thus, while numbers of unpaired males may be increasing in both regions, the impact on population size may be greater in the south-east because of the additional declines in the success of nesting attempts and lower adult survival rates. As the survival rates of adult females in the south-east are particularly low (Table 1), the proportion of females completing more than one breeding season may be lower in the south-east than the north-west, which may exacerbate declines in recruitment in the south-east.

Further quantifying the impact of demographic change on population abundance

Previous demographic studies of population dynamics in birds have highlighted the importance of juvenile survival in population declines (Freeman & Crick *et al.* 2003, Robinson *et al.* 2004, Freeman *et al.* 2007). In this study, there is also an indication that declines in post-fledgling and/or first-year survival may be occurring in both the north-west and south-east regions (chapter 7). In Afro-Palaearctic migrant species, key-factor analysis has shown that variation in the losses between fledging and the following breeding season can account for most of the variation in population size (Baillie & Peach 1992). Accurate estimation of survival during the first year of life may therefore be critical to our understanding of population declines, and may be important in the population declines of many Afro-Palaearctic migrants. However, as natal dispersal in migrants has been shown to be typically higher than in resident species (Paradis *et al.* 1998), obtaining accurate measures of juvenile survival may be hampered by low sample sizes.

Using the CES data, we attempted to estimate survival rates of juvenile willow warblers using the same methodology as for adult survival (chapter 6). Although these estimates were unlikely to be accurate measures of actual survival rates, they did indicate significantly higher juvenile survival in the north-west than the south-east of Britain (north-west: mean annual survival rate = 0.06, 95% CRIs = 0.02 – 0.4, south-east: mean = 0.04, 95% CRIs = 0.003 – 0.07), but there was no evidence of temporal trends (1986 – 2008) in juvenile survival rates in either region (north-west: r = -0.24, p = 0.30, south-east: r = -0.18, p = 0.42). However, as the mean number of juvenile willow warblers re-trapped as adults on CES sites is extremely low (north-west: mean = 5.5, SD = 7.1, south-east: mean = 12.0, SD = 7.8), of these analyses may lack sufficient statistical power to detect trends in juvenile survival rates. However, while our estimates of annual survival rates of juvenile willow warblers are much lower than ~0.24 which was estimated by Siriwardena *et al.* (1998) using recovery data collected between 1962 and 1991, the regional differences in juvenile survival may be accurate and may be an important component of the higher population densities of the north-west.

Future directions

The findings reported in this thesis suggest that changes in first-year survival may be playing a key role in the declines in British willow warblers, but that the impacts of these changes may be exacerbated by declining productivity and low adult survival in south-east

Britain and buffered by higher productivity and adult survival in north-west Britain. In chapter 1, we highlighted the importance of seasonal interactions on the population trends of Afro-Palaearctic migrant species breeding in the UK, and it is possible that similar demographic processes are occurring in other migrant species. In willow warblers, quantification of the relative roles of changes in productivity and adult survival in buffering against declines in juvenile survival requires further population modelling, however, this may be key in determining where best to focus conservation efforts. In a previous study in which changes in different demographic measures were integrated to explore population change, only when estimates of adult survival from national ringing recoveries were combined with data collected by an intensive study of breeding performance, did the non-significant declines in first-year and adult survival become sufficient together to explain the population declines (Bradbury *et al.* 2000). It is therefore possible that, through large-scale population modelling, similar processes may become evident in British willow warblers.

In the UK, conservation and protection of the habitats used by migrant bird populations may help to increase productivity and adult survival, however these actions will only be effective if they can outweigh costs incurred during the non-breeding season. Consequently, there is a pressing need to increase our understanding of the winter ecology of these species. Identification of fine-scale, species-specific habitat requirements and how their availability varies across non-breeding ranges can greatly improve our comprehension of the pressures faced by migrants outside of the breeding season. Such studies could be carried out by a combination of fieldwork, large-scale GIS based studies and deployment of satellite tags and/or geolocators to track individual birds from different areas of the breeding ranges throughout their annual cycle, and can help to link demographic processes to changes in environmental conditions. Used in conjunction with tagging studies, stable isotope studies maybe able to become more targeted and also provide evidence of the consistency non-breeding season movements across populations. Understanding the challenges faced by migrants on their non-breeding grounds may greatly help us to focus efforts to reduce future population declines within the UK and at wider European scales.

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Appendix 1: Ecological and demographic characteristics of species used in analysis. n = mean number of BBS squares surveyed per year.

Species	England BBS trend (n)	Scotland BBS trend (n)	Migratory status	Bioclimatic zone	Breeding habitat
Chiffchaff *(Phylloscopus collybita)*	44 (1001)	217 (30)	Long-distance	Arid	wood
Cuckoo *(Cuculus canorus)*	-56 (578)	39 (67)	Long-distance	Humid	wood
Garden warbler *(Sylvia borin)*	-11 (328)	229 (19)	Long-distance	Humid	Scrub
House martin *(Delichon urbica)*	-3 (671)	152 (52)	Long-distance	Humid	farm
Redstart *(Phoenicurus phoenicurus)*	43 (76)	276 (11)	Long-distance	Arid	wood
Sand martin *(Riparia riparia)*	15 (74)	50 (22)	Long-distance	Arid	wetland
Sedge warbler *(Acrocephalus schoenobaenus)*	-11 (170)	28 (49)	Long-distance	Arid	wetland
Spotted flycatcher *(Muscicapa striata)*	-53 (142)	-61 (22)	Long-distance	Humid	wood
Swallow *(Hirundo rustica)*	25 (1290)	5 (148)	Long-distance	Southern	farm
Swift *(Apus apus)*	-41 (820)	-53 (45)	Long-distance	Southern	farm
Tree pipit *(Anthus trivialis)*	-38 (66)	31 (25)	Long-distance	Humid	scrub
Wheatear *(Oenanthe oenanthe)*	0 (136)	24 (75)	Long-distance	Arid	moor
Whinchat *(Saxicola rubetra)*	-25 (30)	-28 (24)	Long-distance	Humid	farm
Whitethroat *(Sylvia communis)*	28 (997)	85 (66)	Long-distance	Arid	farm
Willow warbler *(Phylloscopus trochilus)*	-27 (864)	31 (182)	Long-distance	Humid	scrub
Curlew (*Numenius arquata)*	-20 (269)	-48 (120)	Short-distance		

Kestral *(Falco tinnunculus)*	-15 (509)	-56 (41)	Short-distance
Linnet *(Carduelis cannabina)*	-27 (894)	26 (83)	Short-distance
Lapwing *(Vanellus vanellus)*	5 (505)	-38 (86)	Short-distance
Oystercatcher *(Haematopus ostralegus)*	47 (139)	-27 (122)	Short-distance
Meadow pipit *(Anthus pratensis)*	-17 (360)	-23 (197)	Short-distance
Mistle Thrush *(Turdus viscivorus)*	-23 (863)	39 (66)	Short-distance
Redshank *(Tringa tetanus)*	-29 (51)	-8 (21)	Short-distance
Mute swan *(Cygnus olor)*	-17 (182)	23 (15)	Short-distance
Cormorant *(Phalacrocorax carbo)*	8 (164)	-53 (10)	Short-distance
Lesser redpoll *(Carduelis cabaret)*	12 (53)	54 (36)	Short-distance
Pied wagtail *(Motacilla alba)*	17 (861)	16 (122)	Short-distance
Song Thrush *(Turdus philomelos)*	20 (1317)	12 (148)	Short-distance
Blackbird *(Turdus merula)*	21 (1696)	25 (166)	Short-distance
Grey wagtail *(Motacilla cinerea)*	48 (126)	34 (28)	Short-distance
Siskin *(Carduelis spinus)*	155 (38)	0 (55)	Short-distance
Snipe *(Gallinago gallinago)*	2 (63)	58 (54)	Short-distance
Goldfinch *(Carduelis carduelis)*	23 (1050)	91 (72)	Short-distance
Tufted duck *(Aythya fuligula)*	49 (117)	-7 (12)	Short-distance
Stonechat *(Saxicola torquata)*	216 (52)	254 (32)	Short-distance

Blackcap *(Sylvia atricapilla)*	51 (1117)	146 (38)	Short-distance
Grey partridge *(Perdix perdix)*	-36 (200)	-45 (22)	Resident
Corn bunting *(Emberiza calandra)*	-34 (133)	-63 (6)	Resident
Starling *(Sturnus vulgaris)*	-35 (1332)	1 (134)	Resident
Yellow hammer *(Emberiza citrinella)*	-27 (945)	15 (92)	Resident
Skylark *(Alauda arvensis)*	-21 (1214)	2 (193)	Resident
Sparrowhawk *(Accipiter nisus)*	-23 (260)	-10 (18)	Resident
House sparrow *(Passer domesticus)*	-18 (1168)	30 (80)	Resident
Jay *(Garrulus glandarius)*	-13 (550)	253 (13)	Resident
Rook *(Corvus frugilegus)*	3 (898)	-12 (101)	Resident
Red Grouse *(Lagopus lagopus)*	-17 (48)	6 (52)	Resident
Stock dove *(Columba oenas)*	-4 (627)	75 (22)	Resident
Magpie *(Pica pica)*	-2 (1374)	14 (39)	Resident
Long-tailed tit *(Aegithalos caudatus)*	2 (686)	3 (23)	Resident
Blue Tit *(Cyanistes caeruleus)*	10 (1619)	16 (138)	Resident
Chaffinch *(Fringilla coelebs)*	18 (1655)	10 (206)	Resident
Treecreeper *(Certhia familiaris)*	-12 (226)	60 (30)	Resident
Tree sparrow *(Passer montanus)*	1 (121)	57 (17)	Resident
Moorhen *(Gallinula chloropus)*	9 (538)	25 (14)	Resident

Carrion crow *(Corvus corone)*	27 (1656)	6 (165)	Resident
Coal Tit *(Periparus ater)*	14 (437)	14 (104)	Resident
Robin *(Erithacus rubecula)*	26 (1607)	7 (166)	Resident
Woodpigeon *(Columba palumbus)*	27 (1714)	-11 (174)	Resident
Dunnock *(Prunella modularis)*	19 (1445)	40 (115)	Resident
Wren *(Troglodytes troglodytes)*	12 (1641)	88 (196)	Resident
Collared dove *(Streptopelia decaocto)*	32 (1040)	-25 (42)	Resident
Greenfinch *(Carduelis chloris)*	27 (1339)	10 (93)	Resident
Mallard *(Anas platyrhynchos)*	36 (932)	6.96 (92)	Resident
Green woodpecker (*Picus viridis)*	38 (634)	-55.85 (7)	Resident
Reed bunting *(Emberiza schoeniclus)*	19 (309)	56 (49)	Resident
Jackdaw *(Corvus monedula)*	49 (1130)	23 (100)	Resident
Pheasant *(Phasianus colchicus)*	47 (1284)	-5.6 (115)	Resident
Goldcrest *(Regulus regulus)*	55 (476)	86 (78)	Resident
Great Tit *(Parus major)*	43 (1511)	87 (123)	Resident
Buzzard *(Buteo buteo)*	106 (412)	36 (115)	Resident
Raven *(Corvus corax)*	267 (77)	155 (40)	Resident
Great spotted woodpecker *(Dendrocopos major)*	133 (729)	327 (29)	Resident
Greylag goose *(Anser anser)*	141 (106)	422 (18)	Resident

Bullfinch *(Pyrrhula pyrrhula)*	-18 (398)	13 (32)	Resident